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Pair bond characteristics and maintenance in free-flying jackdaws *Corvus monedula*: effects of social context and season

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Abstract

Most birds rely on cooperation between pair partners for breeding. In long-term monogamous species, pair bonds are considered the basic units of social organization, albeit these birds often form foraging, roosting or breeding groups in which they repeatedly interact with numerous conspecifics. Focusing on jackdaws *Corvus monedula*, we here investigated 1) the interplay between pair bond and group dynamics in several social contexts and 2) how pair partners differ in individual effort of pair bond maintenance. Based on long-term data on free-flying birds, we quantified social interactions between group members within three positive contexts (spatial proximity, feeding and sociopositive interactions) for different periods of the year (non-breeding, pre-breeding, parental care). On the group level, we found that the number of interaction partners was highest in the spatial proximity context while in the feeding and sociopositive contexts the number of interaction partners was low and moderately low, respectively. Interactions were reciprocated within almost all contexts and periods. Investigating subgrouping within the flock, results showed that interactions were preferentially directed towards the respective pair partner compared to unmated adults. When determining pair partner effort, both sexes similarly invested most into mutual proximity during late winter, thereby refreshing their bond before the onset of breeding. Paired males fed their mates over the entire year at similar rates while paired females hardly fed their mates at all but engaged in sociopositive behaviors instead. We conclude that jackdaws actively seek out positive social ties to flock members (close proximity, sociopositive behavior), at certain times of the year. Thus, the group functions as a dynamic social unit, nested within are highly cooperative pair bonds. Both sexes invested into the bond with different social behaviors and different levels of effort, yet these are likely male and female proximate mechanisms aimed at maintaining and perpetuating the pair bond.

Birds are widely considered as model species for studies of monogamy, since it is the most common avian mating system (Lack 1968, Mock and Fujioka 1990). Both partners benefit from social monogamy through biparental provision and offspring care (Lack 1968, Clutton-Brock 1991, Black 1996), while it also entails paternity assurance for males (Voland 2000). On the other hand, monogamous pair bonds may confer certain fitness disadvantages due to reduced polygamous mating opportunities (Voland 2000). Jackdaws *Corvus monedula* show patterns of explicit social and genetic monogamy: birds form long-term monogamous pairs, often staying together for life (Goodwin 1976, Henderson et al. 2000). Pair partners are known to cooperate with each other throughout the year in several contexts, e.g. embarking together on foraging bouts or assisting each other during conflicts (Röell 1978, Haffer 1993). Birds seek mutual spatial proximity, which is important for maintaining cooperation between partners (Nowak et al. 1994). Mates also share food and exchange services such as allo-preening (Röell 1978, Wechsler 1989), behaviors that characterize relationships with high immediate value (Reichard 2007, Fraser and Bugnyar 2010). During breeding, pair partner cooperation includes the joint acquisition and defense of a nesting site (Röell 1978, Haffer 1993), mate and offspring provisioning and offering ongoing parental care once the young have fledged and joined the group (Lorenz 1931, Henderson and Hart 1993). However, which behaviors contribute to the pair bond at certain times and how pair partners contribute to its maintenance throughout the year is still debatable. For example, Wechsler (1989) analyzed twelve quantitative measures of jackdaw pair-relationships but found no correlation between allo-feeding and allo-preening, deeming them independently motivated of each other. In contrast, Emery et al. (2007) did find such correlations within preferred partnerships in juvenile rooks, a closely related and sympatrically occurring species, raising the possibility that the expression of certain behaviors may be affected by season and/or developmental stage. Further, while both sexes invest into provisioning and parental care, paternal and maternal roles essentially differ: males are predominantly the ones providing hatchlings (Henderson and Hart 1993) and their female mates with food (Wechsler 1989), while females incubate and rarely leave the nest before hatchlings are 20 d old (Henderson and Hart 1993). It may be expected that both sexes not only differ in their contribution to parental care but also to the maintenance of their bond.

Although jackdaws' pair bonds are regarded as the basic unit of jackdaw society (Goodwin 1976, Röell 1978, Wechsler 1989, Emery et al. 2007), they are exceptionally gregarious passerine birds (Haffer 1993) that live and breed in social colonies. Large winter roosts may incorporate up to several thousand individuals (Goodwin 1976, Haffer 1993, Clayton and Emery 2007). Roosts and foraging aggregations constitute open groups with constantly changing group size and composition due to frequent immigration and emigration events (Krause and Ruxton 2002). Jackdaws benefit from joining these large aggregations mainly through the collaborative solicitation of foraging patches but may also defend better against competitors such as the carrion crow *Corvus corone* (Haffer 1993). A prominent factor of intra-group cohesion in jackdaw colonies is the establishment of a dominance hierarchy. Socially dominant birds receive priority access to resources such as nesting sites and food (Röell 1978), and dominance also seems to play a role in jackdaws' breeding success (Henderson and Hart 1995, Verhulst and Salomons 2004). In corvids, dominance rank is dependent on pair status: pair bonded individuals are in general more dominant than

unpaired birds (Röell 1978, Haffer 1993, Braun and Bugnyar 2012; in females only: Wechsler 1988). In addition, jackdaws maintain within-male and within-female social hierarchies. Mated females acquire a rank similar to the one of their mate (Lorenz 1931, Wechsler 1988); in dyadic interactions, however, males are generally dominant over females (Tamm 1977, Röell 1978, Wechsler 1988). Nevertheless, shifts and turnovers in social rank are common both in the winter months and during the breeding season (Tamm 1977, Röell 1978). This combination of long-term monogamous bonds embedded in the framework of a (semi-) colonially breeding species (Henderson et al. 2000) may result in high levels of structural complexity: dynamic social interactions between animals define group structure, which in turn determines how individuals interact and exchange information (Hinde 1976). This may lead to intricate feedback-loops between individual interactions and population dynamics (Krause and Ruxton 2002). Therefore, questions of how animals are integrated into existing social structures or how higher levels of social structure arise from relationships between conspecifics (Hinde 1976, Krause et al. 2007) remain interesting areas of research. For the reasons detailed above, jackdaws pose an intriguing study system.

The aim of this study was to determine contextual and temporal patterns of monogamous pair bonds imbedded within the larger social group in a free-flying jackdaw population. Here, we used an outdoor population that was established in 2007 by releasing a group of aviary birds simultaneously into free flight in order to facilitate behavioral studies in jackdaws under natural conditions (for details of the procedure see Wagner et al. 2011). Data collection in natural populations, in contrast to laboratory studies, incorporates the environmental conditions that animals have adapted to in nature and allow proper conclusions about the ecology of the species to be drawn (Kendal et al. 2010, Lonsdorf and Bonnie 2010). To this end, we quantified 1) patterns of interplay between pair bonds and group dynamics within several social contexts and between discrete periods of the birds' annual breeding cycle, and 2) differences in pair partner effort in the maintenance of the pair bond. We observed social interactions between group members in a flock of free-flying jackdaws over a 10-month period. We focused on social contexts known to be of high relevance to pair partners, all of which represent positive interactions of increasing intensity in terms of resource investment, i.e. time and energy: mutual spatial proximity (including approaching and following; for a full definition of behavioral parameters see Table 1), sociopositive/affiliative behavior (including contact sitting and contact standing, touching, allo-preening and female copulatory display), and allo-feeding (including active food sharing and sharing after receiving food calls or begging calls).

Albeit the pair bond is being regarded as the most relevant social unit in jackdaws, previous research has shown that differentiated social interactions with non-mated conspecifics in the group occur as well (Scheid et al. 2007, von Bayern et al. 2007, Schwab et al. 2008). Allo-preening, for example, may be used by subordinate birds to appease dominants and, more generally, to confirm one's relationship status with conspecifics (Katzir 1983). Therefore, we predict that pair partners actively seek interactions with conspecifics outside the pair bond but that the frequency of these interactions will be highly context-specific and vary seasonally: behavior associated with high investment of time and energy, such as allo-feeding, should be shared the least frequently with non-mated birds, whereas less costly sociopositive behavior should be shared more frequently. In contrast, spatial proximity

interactions, which are both non-costly and highly beneficial to individuals in terms of group benefits (Galef and Giraldeau 2001, Krause and Ruxton 2002), should be exchanged frequently among group members. Further, we predict that interactions with the pair partner will become more exclusive before the onset of the breeding season. Lastly, we expect male and female mates to exhibit differential roles in the maintenance of the pair bond: male jackdaws, for example, are known to perform the majority of food sharing (Röell 1978).

Material and methods

Subjects and living conditions

Between November 2008 and September 2009, we observed the social behavior of 27 jackdaws in total: 12 females (9 adults, 3 juveniles) and 15 males (11 adults, 4 juveniles). However, group size varied between observational periods from $n = 10$ to $n = 21$ due to natural fluctuations such as predation, emigration, immigration and offspring fledging (see below and Table 2) and thus, not all individuals were present in each observational period. Some individuals ($n = 10$) were handreared in 2005 and 2006 and subsequently released into free-flight in 2007 (Wagner et al. 2011). In the following years, wild dispersing individuals ($n = 8$) as well as bird-raised offspring ($n = 9$) joined the flock. The majority of mated pairs, six out of nine, were of mixed origin (wild and released birds, Table 2) which we consider a reliable indication of a functional social and mating system, resulting in a socially intact population representative of conditions in the wild.

The study was conducted at the Konrad Lorenz Research Station (KLF) and the Herzog von Cumberland game park Grünau, situated in an alpine valley in Austria. Birds were free to roam the valley and had access to water (river Alm) and naturally occurring food resources. Additionally, once a day in the morning birds were provided with supplementary food (cereals, fruits, corn, beans and added vitamin pellets for insectivorous song birds (Nutribird: BEO complete) to prevent dispersal in autumn and allow the nearby presence of a human observer). However, as the birds were readily foraging in the meadows for the rest of the day, the provided food did not account for the birds' full diet.

The majority of birds were color-banded for individual identification. In few cases ($n = 4$), when a bird could not be trapped for individual marking, specific phenotypic characteristics (e.g. stiff leg) allowed identification with a high degree of certainty. Blood samples were taken for sex determination. Age of birds was either known (for handreared birds and fledged juveniles) or, in the case of wild birds, individuals were classified being either juvenile or adult based on assessment of morphological traits such as plumage maturation and coloration of the oral cavity. Birds were deemed adults when they were older than 1 yr.

Behavioral observations and observational periods

Behavioral data were collected on a daily basis and consisted of 1-min focal observations. The order of focal observations was semi-randomized depending on the presence of individuals, and counter-balanced for frequency of observations per individual. Focal observations were conducted while birds were ranging freely in the wild, either in the meadows surrounding the KLF or in the grounds of the Herzog von Cumberland game park

Grünau. We recorded mutually exclusive interactions that expressed sociopositive behavior, that were observed in a food context and that served to establish or maintain spatial proximity between individuals (Table 1).

Longitudinal data were partitioned into distinct periods following the birds' annual breeding cycle, i.e. the non-breeding period, the pre-breeding period and the post-fledging parental care period. The non-breeding period was further split into periods I and II, representing early and late winter, respectively, since first indications of pairing become evident already in late winter (Lorenz 1931). This resulted in four observational periods in total: the non-breeding period I (NB I; 24 November–22 December; $n = 14$; 41.79 ± 8.51 observations/focal individual), the non-breeding period II (NB II; 5 January–4 March; $n = 10$; 53.50 ± 3.38 observations/focal individual), the pre-breeding period (PB; 5 March–19 April; $n = 12$; 80.25 ± 37.97 observations/focal individual) and the post-fledging parental care period (PC; 10 July–10 September; $n = 21$; 31.71 ± 9.88 observations/focal individual). The breeding season lasted approximately from mid-April until mid-June and no data were collected between 20 April and 9 July. The breeding season was omitted from data collection because the social group becomes extensively fragmented during this period such that essentially all forms of non-aggressive interaction are restricted to pair partners (Röell 1978). While antagonistic interactions with conspecifics, such as the defense of nest sites and maintenance of the social hierarchy, are both frequent and vital to reproductive success (Tamm 1977, Henderson and Hart 1995, Verhulst and Salomons 2004), the focus of the present study was not on the aggressive context. During the post-fledging parental care period, fledged juveniles of the preceding breeding season joined the group but were not yet independent of their parents. Here, observational data were collected by two field researchers during the second half of the period for 32 d. Inter-observer reliability was excellent (Cohen's Kappa $\kappa = 0.7246$) and therefore, the two separate data sets were pooled for analysis.

Generating distinct social networks

First, behavioral parameters were tentatively classified as belonging to either one of three social contexts, depending on their function: a) interactions aiming at the establishment and perpetuation of close spatial proximity, b) interactions involving the sharing of food items and c) affiliative (sociopositive) interactions. It is noteworthy to point out that all three contexts represent active social interactions exchanged between group members and are thus comparable with each other. Also, spatial proximity, allo-feeding and sociopositive behavior all constitute positive contexts expected to be of high relevance to paired mates. Second, separately within each social context, matrix correlations (Mantel tests; 10 000 permutations; MatMan 1.1 by Noldus Technologies; de Vries et al. 1993) were computed to test whether behavioral parameters that were assigned to each context (Table 1) were correlative. Following Bonferroni–Holm corrections for multiple testing (Holm 1979), only those parameters that significantly correlated with each other in any given context were retained and pooled for further analysis. This resulted in three distinct social networks (parameters listed in brackets): a) the spatial proximity (approaching, following), b) the feeding (food sharing, food sharing after a food call or a begging call) and c) the sociopositive network (contact sitting, contact standing, touching, allo-preening, female copulatory display). Here, we use the term 'social network' defined as a sociomatrix (see

below) computed within each social context and for each observational period. Behavioral parameters were then corrected for individual sampling effort, i.e. variation in the number of focal observations per individual, to minimize any skew in the data. These corrections were calculated twice: first, when the focal individual was the initiator of an interaction and second, when the focal individual was the receiver of an interaction. Both corrections were then summed for further steps in the procedure. Corrections were made to one focal sample (1 min observation time). For analyses on the individual level, the dataset was filtered to include solely interactions between pair partners (mean interaction frequencies).

Data analysis: patterns of interplay between pair bonds and group dynamics

In order to investigate structural patterns of pair bonds embedded within a social group, we employed Social Network Analysis (SNA). SNA is based on connections between individuals which may constitute essentially any kind of interaction or association, such as cooperative male display at a lek (McDonald 2007) or preferential associations in fission-fusion societies (Sundaresan et al. 2007). Social networks generally consist of nodes (here: individuals) connected by ties (here: social interactions in different contexts; Wasserman and Faust 1994, Croft et al. 2008, Wey et al. 2008). SNA allows analyses on multiple hierarchical levels, from the population to the individual, thereby addressing the interrelatedness of social structure (Hinde 1976, Wasserman and Faust 1994, Croft et al. 2008). Here, we used SNA to investigate two organizational levels: the level of the group, comprising the population as a whole, and the level of subgroups, comprising clusters or groupings of animals (Wasserman and Faust 1994, Wey et al. 2008). Subgroups, in our case, constituted mated pairs as separate units from each other and from unmated adult individuals. If not indicated otherwise, observational data on social interactions were weighted, i.e. representing quantified frequencies of behaviors, and directed, i.e. being addressed from an initiator towards a receiving individual.

On the group level, we implemented the connectivity measure mean degree as well as relative reciprocity. Mean degree represents the average number of ties that connect to a node in a network (Croft et al. 2008), or, simply put, the average number of partners that any given individual interacts with. Mean degree requires binary (presence/absence) data. We here implement a normalized version, describing the percentage of available interaction partners (Borgatti et al. 2002). Mean degree metrics were derived using the Ucinet 6 for Windows software package (Borgatti et al. 2002) and statistical analyses were performed using SPSS Statistics 20.0 by IBM. All tests are two-tailed; post-hoc tests were carried out as planned comparisons with repeated contrasts. Secondly, relative reciprocity investigates whether individuals exchange interactions of the same kind (here: belonging to the same social context) in a quantitative manner, i.e. whether individuals initiate relatively more interactions towards those conspecifics from whom they themselves receive interactions frequently (Hemelrijk 1990). Relative reciprocity also takes individual variation into account. We compared each network with its respective transposed form within each context and period (row-wise matrix correlations: K_r -tests; 10 000 permutations; MatMan 1.1 by Noldus Technologies; de Vries et al. 1993; for details of the procedure see Hemelrijk 1990). A significant correlation indicates the reciprocation of behavior in a given social network.

On the subgroup level, we tested for preferential interactions within pair bond units by using constant homophily models. These models assume that individuals that are similar by some characteristic (here: being engaged in the same pair bond) preferentially interact with each other, and assess whether ties within such groups occur more frequently than ties between groups (Hanneman and Riddle 2005). In other words, constant homophily models determined whether interactions occur preferentially between pair mates. We used a number of groups equal to the number of existing pair bonds within each period, while unmated adult individuals always formed separate one-member sets (singletons were not grouped together but ties between a mated individual and a singleton were assessed). A pair was defined as two birds defending a nest site together and attempting to breed, irrespective of the eventual breeding success (see also the definition by McGraw et al. 2010). We applied constant homophily models for each context and period (10 000 permutations; Ucinet 6 for Windows; Borgatti et al. 2002). Significant values indicate a strong preference for within-group ties in a given network.

Data analysis: differences in pair partner effort

To determine patterns of differential investment of pair mates into the perpetuation of their pair bond, we quantified frequencies of initiated social interactions between partners. We asked 1) whether either sex changes frequencies of initiated interactions over the course of the annual breeding cycle, and 2) whether pair mates differ in their patterns of doing so. All tests (Kruskal–Wallis tests, Mann–Whitney U tests) are two-tailed; post-hoc tests were carried out as planned comparisons with repeated contrasts. Statistical analyses were performed using SPSS Statistics 20.0 by IBM.

Results

Patterns of interplay between pair bonds and group dynamics

Overall, differences between contexts in the number of interaction partners were more pronounced than differences between periods within contexts. Comparisons between the three social networks yielded significant differences in the number of average interaction partners within all four periods (Friedman test: NB I: $\chi^2 = 26.24$, $p < 0.001$, $n = 14$; NB II: $\chi^2 = 18.59$, $p < 0.001$, $n = 10$; PB: $\chi^2 = 22.95$, $p < 0.001$, $n = 12$; PC: $\chi^2 = 38.00$, $p < 0.001$, $n = 21$): in the spatial proximity network individuals were connected to most of their conspecifics in the group (Fig. 1a, Table 3a), whereas feeding and sociopositive networks were generally fragmented (Fig. 1b–c) and mean degrees were considerably smaller (Table 3a). In all four periods the number of interaction partners in the spatial proximity network (mean across periods: 77.8%) was significantly higher than in the feeding network (6.9%) as well as in the sociopositive network (9.5%, Fig. 1a–c, Table 3a, Table 4a). Comparisons between the sociopositive and the feeding networks showed, however, that in both non-breeding periods subjects had significantly more interaction partners in the former than in the latter (12.2% on average in the sociopositive network vs 6.6% in the feeding network), a pattern that was not significant in the pre-breeding period (9.1 vs 7.6%) and reversed in the post-fledging parental care period (4.8 vs 6.7%; Fig. 1b–c, Table 3a, and Table 4a). Here, the number of interaction partners was significantly higher in the feeding than in the sociopositive network due to the dependent offspring present in this period.

The pattern of high connectivity in the spatial proximity network and greater exclusiveness in the feeding and sociopositive networks was similar throughout the year. However, some networks showed pronounced differences in mean degree between observational periods (Kruskal–Wallis test: spatial proximity network: $\chi^2 = 20.12$, $p < 0.001$, $n = 57$; sociopositive network: $\chi^2 = 26.01$, $p < 0.001$, $n = 57$), whereas the feeding network did not ($\chi^2 = 3.89$, $p = 0.274$, $n = 57$). While the number of interaction partners in the spatial proximity network showed a highly significant peak in late winter (increase from NB I to NB II and subsequent decrease from NB II to PB; Fig. 1a, Table 4b), the mean degree in the feeding network did not significantly differ over the course of the year (Fig. 1b). However, mean degree did significantly and consistently decrease from the non-breeding period II to the post-fledging parental care period in the sociopositive network (Fig. 1c, Table 4b).

Relative reciprocity was significant ($p < 0.05$) within all social networks and within all observational periods (Table 3b), with a single non-significant exception of the feeding network in the non-breeding period II. Here, only paired males initiated feeding interactions whereas females did not feed at all, resulting in a unidirectional and thus non-reciprocal network. In all other networks and periods individuals initiated most interactions towards those conspecifics from which they themselves received interactions most frequently.

On the subgroup level, results for the constant homophily models showed that spatial proximity, feeding and sociopositive interactions were significantly directed towards one's pair mate, as opposed to individuals outside the pair bond, within all four observational periods (Table 3c). In addition, effect sizes were considerably large, explaining as much as 90.1% of the variance in dyadic ties in the spatial proximity network (Table 3c) and supporting the robustness of our results.

Differences in pair partner effort

This section focuses specifically on interactions within the pair bond, i.e. between male and female pair partners. Both sexes significantly altered their frequencies of spatial proximity interactions over the course of the year (Kruskal–Wallis test: males: $\chi^2 = 14.35$, $p = 0.002$, $n = 19$; females: $\chi^2 = 12.65$, $p = 0.005$, $n = 19$) by showing an increase of interactions from early to late winter (NB I to NB II; Mann–Whitney U test: males: $U = 0$, $Z = -2.24$, $p = 0.025$, $n = 8$; females: $U = 0$, $Z = -2.24$, $p = 0.025$, $n = 8$) and a following decrease towards the post-fledging parental care period (Mann–Whitney U test: decrease from NB II to PB: males: $U = 0$, $Z = -2.25$, $p = 0.024$, $n = 8$; females: $U = 1$, $Z = -1.94$, $p = 0.053$, $n = 8$; decrease from PB to PC: males: $U = 0$, $Z = -2.75$, $p = 0.006$, $n = 11$; females: $U = 0$, $Z = -2.74$, $p = 0.006$, $n = 11$; Fig. 2a, d). This pattern was shown by both sexes and female and male pair partners did not differ in any observational period (Mann–Whitney U test: NB I: $U = 9$, $Z = -0.73$, $p = 0.465$, $n = 5$ females/5 males; NB II: $U = 3$, $Z = -0.66$, $p = 0.513$, $n = 3$ females/3 males; PB: $U = 10$, $Z = -0.52$, $p = 0.600$, $n = 5$ females/5 males; PC: $U = 15$, $Z = -0.48$, $p = 0.631$, $n = 6$ females/6 males).

However, sexes showed significant differences with regard to feeding interactions: in several periods (Mann–Whitney U test: NB I: $U = 0$, $Z = -2.62$, $p = 0.009$, $n = 5$ females/5 males; NB II: $U = 0$, $Z = -2.09$, $p = 0.037$, $n = 3$ females/3 males; PB: $U = 0$, $Z = -2.69$, $p = 0.007$, $n = 5$ females/5 males) paired males initiated significantly more feeding interactions

than their female mates that hardly fed their partners at all. Males fed their mates over the entire year at similar rates without a significant peak in any of the periods (Kruskal–Wallis test: $\chi^2 = 6.49$, $p = 0.090$, $n = 19$; Fig. 2b). Also, males distributed their sociopositive interactions at similar rates throughout the year (Kruskal–Wallis test: $\chi^2 = 6.95$, $p = 0.073$, $n = 19$; Fig. 2c). On the contrary, females significantly adjusted their sociopositive interactions over the course of the breeding cycle (Kruskal–Wallis test: $\chi^2 = 12.37$, $p = 0.006$, $n = 19$). They showed a significant peak in the pre-breeding period (Mann–Whitney U test: increase from NB II to PB: $U = 1$, $Z = -1.94$, $p = 0.053$, $n = 8$; decrease from PB to PC: $U = 0$, $Z = -2.75$, $p = 0.006$, $n = 11$; Fig. 2f), although there were no significant differences between sexes in sociopositive interactions (Mann–Whitney U test: NB I: $U = 9$, $Z = -0.73$, $p = 0.465$, $n = 5$ females/5 males; NB II: $U = 4$, $Z = -0.23$, $p = 0.822$, $n = 3$ females/3 males; PB: $U = 6$, $Z = -1.36$, $p = 0.175$, $n = 5$ females/5 males; PC: $U = 17.5$, $Z = -0.08$, $p = 0.936$, $n = 6$ females/6 males).

Discussion

Patterns of interplay between pair bonds and group dynamics

Our results indicate a complex, nested relationship between pair bond and group dynamics in jackdaws. On the level of the group, mean degree (the number of interaction partners) showed great disparity between distinct networks, indicating a diverse functional relevance of the social context. Birds in the spatial proximity context were connected to most others (between 64.6 and 95.6% of group members, depending on the observational period). In direct comparison, the sociopositive context was far more exclusive, reflected by a low number of interaction partners (9.5% on average), and this trend was even more pronounced in the feeding context (6.9% on average). Importantly, the spatial proximity context in this study encompassed solely ‘active’ interactions of birds approaching and following each other rather than ‘passive’ associations (e.g. nearest neighbor or the ‘gambit of the group’; Croft et al. 2008). Thus, the establishment and especially maintenance of spatial proximity between subjects is based on birds’ behavioral decisions that were directly observed, not on spatial aggregation patterns. Birds sought each other’s proximity especially in late winter, as the number of interaction partners showed a significant peak. These results seem to reflect the establishment of a large, cohesive winter flock (Röell 1978). As a result, individuals were in close physical proximity to each other and probably, this well connected spatial proximity network serves as an interaction ‘platform’ on which members of a colonially breeding species engage with each other and where they can utilize social group benefits. Such benefits include the propagation of information (Galef and Giraldeau 2001) by, for example, following conspecifics to rich foraging spots (Röell 1978) or retaining public information on the followed subject’s own associations.

In line with expectations, in winter birds were interacting within the sociopositive context also with a few other group members (1.7 interaction partners on average in non-breeding period I and 1 interaction partner on average in non-breeding period II, respectively; however, in late winter also non-pair mates were sharing affiliative interactions). Thus, sociopositive behavior was relatively exclusive – but not as exclusive, by means of focusing entirely on the pair mate, as is often inferred in the literature from the prominence of the pair

bond (Goodwin 1976, Röell 1978, Wechsler 1989, Emery et al. 2007). We propose that sociopositive behavior may function in a similar way as spatial proximity, albeit to a much more limited degree in terms of the numbers of interaction partners involved, and it is likely that the two contexts, both representing positive interactions, work in unison to increase the social cohesion of winter flocks. Numbers of interaction partners within the sociopositive context were on average significantly greater than those within the feeding context but affiliative behavior became more and more exclusive towards the pre-breeding and post-fledging parental care periods, as indicated by a significant decrease in interaction partners. Lastly, a high degree of exclusiveness was evident in the feeding context throughout the year without notable variation, reflecting indeed a select long-term focus on the pair mate in line with expectations (Goodwin 1976, Röell 1978, Wechsler 1989, Emery et al. 2007).

Interactions within each social network, not just feeding interactions alone, were significantly reciprocated between interaction partners (in fact, feeding behavior in late winter was non-reciprocal and posed the single exception to this pattern). Thus, while jackdaws interacted most frequently with their respective mate within each social context, and while this strong preference was present throughout the course of the year, degrees of exclusiveness of interactions showed strong variation both within contexts and between periods of the birds' annual cycle: exclusiveness decreased from the feeding context towards the spatial proximity context but increased from the non-breeding period towards the breeding period. Here, we are able to add further support to the existing body of literature regarding the monogamous pair bond as the predominant, basic unit of jackdaw society (Goodwin 1976, Röell 1978, Wechsler 1989, Emery et al. 2007) but at the same time show that social ties to conspecifics within the flock associated with low costs to the individual (proximity) are sought out as well, at certain times of the year. In jackdaw society, the group functions as a dynamic social unit, nested within are closely knit pair bonds, whose pair partners cooperate extensively.

Differences in pair partner effort

Patterns of pair partner interaction patterns corroborate results on the group level. Both sexes exhibited a similar pattern of seeking close mutual proximity during the course of the year but especially doing so in late winter. Interestingly, this corresponded with the establishment of cohesive winter flocks (Röell 1978), within which mutual investments between pair mates may serve to refresh the pair bond before the onset of the upcoming breeding season.

However, we found that pair partners showed differential investment into sociopositive and feeding interactions, indicating that males and females contribute differently to pair bond maintenance. Paired males provided their mates with food while females hardly fed their partners at all. Interestingly, males did so not only right before the onset of the actual breeding season (Wechsler 1989, Henderson 1991, Henderson and Hart 1993) but throughout the year at similar rates. Allo-feeding delivers immediate fitness benefits (Wilson 1975, Clutton-Brock 1991, Reichard 2007) and contributes directly to the quality of the pair bond (Henderson and Hart 1993, Clayton and Emery 2007, von Bayern et al. 2007). However, allo-feeding has also been proposed to function as a social signal, ritually

displaying active food sharing either 1) to alert potentially competing male group members to an ongoing, successful pair bond (displaying the ‘unavailability’ of a mate; Simpson 1991), 2) to reaffirm social rank (Rijksen 1978) or 3) as a costly signal to the pair mate (Zahavi 1990, Scheid et al. 2008). In jackdaws, we hypothesize that enhancement of social prestige by means of costly signaling may be the most likely explanation: by sharing food repeatedly, males communicate their ability to exploit food sources successfully to female partners, signaling high mate quality in order to maintain attachment to a female. Honest signals of male provider qualities appear to be under strong selection in this species: the most dominant factor influencing annual reproductive output in jackdaws is nestling mortality, which is highest during the first ten days after hatching (Henderson and Hart 1993). Nestling mortality significantly correlates with provisioning rates of male parents, which also feed female mates during the time of egg incubation (Henderson and Hart 1993). Furthermore, efficiency in provisioning offspring may improve with age and experience (Greig et al. 1983, Black 1996) and a pair’s reproductive success can increase with the duration of the bond (Oring 1982, Scott 1988). Further evidence demonstrating the importance of male food provisioning can be found in another corvid species: in Eurasian jays *Garrulus glandarius*, males are proficient in attributing a correct desire-state to their mates, i.e. providing food items in accordance with females’ current preferences (Ostojic et al. 2013), and this ability may consequently improve reproductive success in established pairs. In line with this, von Bayern et al. (2007) proposed that food sharing facilitates the formation of social bonds already in juvenile jackdaws by communicating the ‘collaborative intent’ of the food donor.

Interestingly, the females’ contribution to pair bond maintenance worked differently than that of males and was restricted to a certain period: females initiated most sociopositive interactions towards their mates before the onset of the breeding season. It is thus likely that affiliative behavior serves females to strengthen the bond to their mate right before breeding commences. The differences of the pair partners’ investment into the pair bond are ultimately rooted in the reproductive strategies themselves but the kinds of investment, i.e. type of social interactions, are the proximate mechanisms to perpetuate the cooperation between pair partners: allo-feeding being the mechanism employed predominantly by males, whereas allo-preening is the one selectively used by females during certain periods. In jackdaws, the presence and care of both male and female parent is necessary for the survival of offspring (Henderson and Hart 1993). Therefore, the maintenance of the pair bond seems to be in the best interest of both sexes (McGraw et al. 2010), linking both partners by a common motivation: to secure reproductive output (Lack 1968, Clutton-Brock 1991, Henderson and Hart 1993, Black 1996).

Wechsler (1989), in a study of pair relationships in captive jackdaws, also found allo-feeding and allo-preening to be highly exclusive between pair partners, although the two behaviors did not correlate in his analysis and were hypothesized to be motivated independently from each other. Our study, however, shows that sociopositive behavior is not as exclusive over the course of the year as previously assumed but may also be directed towards other conspecifics, especially in early and late winter. Furthermore, while Wechsler (1989) argues that allo-feeding and allo-preening might function particularly during the

establishment of close social relationships (see also von Bayern et al. 2007), becoming less and less relevant over time, our study highlights that these behaviors remain important for already mated pairs and do so possibly throughout the birds' entire social life. We note, however, that Wechsler (1989) analyzed allo-preening as a solitary parameter, whereby in our case allo-preening makes up the sociopositive context alongside other parameters, such as contact-sitting. However, while allo-feeding and sociopositive behavior continue to be functionally relevant social tools for paired jackdaws as seen from the point of view of pair partners' life-history, there seems to be also seasonal variation in the employment of allo-preening to keep some level of social attachment to other conspecifics during the non-breeding period.

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Figure 1.

Mean percentage of interaction partners (normalized mean degree). (a) The spatial proximity, (b) the feeding and (c) the sociopositive network, across observational periods. Mann–Whitney U tests; p-values are two-tailed. Note the different scales on the y-axes. NB I: non-breeding period I ($n = 14$); NB II: non-breeding period II ($n = 10$); PB: pre-breeding period ($n = 12$); PC: post-fledging parental care period ($n = 21$).

Figure 2.

Mean frequencies of initiated spatial proximity, feeding and sociopositive interactions across observational periods. (a–c) Paired males and (d–f) paired females. Mann–Whitney U tests; p-values are two-tailed. Note the different scales on the y-axes. NB I: non-breeding period I ($n = 5$ females/5 males); NB II: non-breeding period II ($n = 3$ females/3 males); PB: pre-breeding period ($n = 5$ females/5 males); PC: post-fledging parental care period ($n = 6$ females/6 males).

Table 1

Definitions of behavioral parameters.

Context	Parameter	Definition
Spatial proximity	approach	an individual approaches a conspecific within 1 m with no subsequent interaction
	follow	an individual immediately follows a conspecific that is leaving, thereby maintaining close proximity
Feeding behavior	food sharing	an individual actively shares food with a conspecific by placing a food item into the conspecific's throat
	food sharing after food call or begging	an individual actively shares food in response to a conspecific's food calls or distinct begging behavior
Sociopositive behavior	contact sit	an individual sits within pecking distance to a conspecific [< 10 cm], mostly on branches, no interactions occur
	contact stand	an individual stands within pecking distance to a conspecific [< 10 cm], mostly on ground, no interactions occur
	touch	an individual touches or nudges a conspecific gently with its beak
	allo-preening	an individual preens a conspecific by streaking through the plumage with its beak
	female copulatory display	an individual fans its tail followed by rapid horizontal vibrations; predominantly shown by females

Shown are only parameters that significantly correlated within each of the social contexts and which were then used to generate the respective social networks.

Table 2

Study subjects observed throughout the study period, ordered by age (year of hatching) and pairing.

Subject	Sex	Pair	Origin	Parents	Year of hatching	Present in period
I	m	a	h		2005	NB I
F	f	a	h		2005	NB I
E	m	b	h		2005	NB I, NB II
WJ	f	b	w		2007	NB I
D	m	c	h		2005	NB I, NB II, PB, PC
AY	f	c	w		2008	PB, PC
S	m	d	h		2006	NB I, NB II, PB, PC
Q	f	d	h		2006	NB I, NB II, PB, PC
TC	m	e	w		2006	NB I, NB II, PB, PC
HR	f	e	h		2006	NB I, NB II, PB, PC
PP	m	f	h		2006	NB I, NB II, PB, PC
VL	f	f	w		2007	NB I, NB II
G	m	g	h		2006	NB I, NB II, PB, PC
RO	f	g	b		2008	PB, PC
ER	m	h	w		2007	NB I, NB II, PB, PC
BO	f	h	w		2007	PB, PC
LM	m	i	b		2008	PB, PC
AM	f	i	w		2008	PC
PT	m		h		2006	NB I
NB	m		w		2008	PC
JU (j)	m		b	Q, S	2009	PC
BS (j)	m		b	Q, S	2009	PC
FN (j)	m		b	HR, TC	2009	PC
SA (j)	f		b	HR, TC	2009	PC
YI (j)	f		b	BO, ER	2009	PC
MY (j)	m		b	NB	2009	PC
HT (j)	f		b	NB	2009	PC

Note that not all subjects were present in each observational period. Specifically, if one partner of a given mated pair was absent during a period, its respective mate was considered single. Identical small letters in the Pair column indicate mated pairs; the Parents column designates juveniles' biological parents. NB I: non-breeding period I (n = 14); NB II: non-breeding period II (n = 10); PB: pre-breeding period (n = 12); PC: post-fledging parental care period (n = 21). f: female; m: male; b: birdraised (biological offspring from the study population; h: handraised (reared under controlled laboratory conditions); w: wild immigrant; j: juvenile.

Table 3

Group and subgroup level measures.

	Non-breeding I	Non-breeding II	Pre-breeding	Parental care				
Network	%	%	%	%				
(a) Mean degree $\pm$ SD								
Spatial proximity	78.02 $\pm$ 13.59	95.56 $\pm$ 7.37	72.73 $\pm$ 21.00	64.76 $\pm$ 17.89				
Feeding behavior	6.59 $\pm$ 2.69	6.67 $\pm$ 5.44	7.58 $\pm$ 3.39	6.67 $\pm$ 4.96				
Sociopositive behavior	13.19 $\pm$ 6.12	11.11 $\pm$ 0.00	9.09 $\pm$ 5.25	4.76 $\pm$ 3.61				
Network	τ_{rw}	p	τ_{rw}	p	τ_{rw}	p	τ_{rw}	p
(b) Relative reciprocity (network and its transposed form)								
Spatial proximity	0.361	< 0.001***	0.567	< 0.001***	0.494	< 0.001***	0.295	< 0.001***
Feeding behavior	0.667	< 0.001***	0	n.s.	0.333	0.004**	0.120	0.018*
Sociopositive behavior	0.735	< 0.001***	0.889	< 0.001***	0.895	< 0.001***	0.560	< 0.001***
Network	R^2	p	R^2	p	R^2	p	R^2	p
(C) Homophily								
Spatial proximity	0.636	< 0.001***	0.889	< 0.001***	0.901	< 0.001***	0.573	< 0.001*** [†]
Feeding behavior	0.297	< 0.001***	0.252	< 0.001***	0.362	< 0.001***	0.162	0.005*** [†]
Sociopositive behavior	0.428	< 0.001***	0.588	0.001***	0.740	< 0.001***	0.375	< 0.001*** [†]

(a) Mean degree (average number of ties connected to a node) given in its normalized version, (b) relative reciprocity between a network and its transposed form (row-wise matrix correlations; 10 000 permutations) and (c) constant homophily models according to membership in discrete pair bonds (10 000 permutations); see text for definitions. Periods are: non-breeding I (n = 14); non-breeding II (n = 10); pre-breeding (n = 12); post-fledging parental care (n = 21).

[†] juveniles omitted from the model; n = 14.

Significant results are given in bold:

* p 0.05;

** p 0.01;

*** p 0.001.

Table 4

Test statistics for comparisons of mean degree.

Periods	<u>Spatial proximity – feeding behavior</u>			<u>Spatial proximity – sociopositive behavior</u>			<u>Feeding behavior – sociopositive behavior</u>		
	n	Z	p	n	Z	p	n	Z	p
(a) Contextual comparisons									
Non-breeding I	28	3.32	0.001***	28	3.32	0.001***	28	2.70	0.007**
Non-breeding II	20	2.97	0.003**	20	2.91	0.004**	20	2.00	0.046*
Pre-breeding	24	3.07	0.002**	24	3.07	0.002**	24	1.41	0.157
Parental care	42	4.03	< 0.001***	42	4.03	< 0.001***	42	2.53	0.011*
(b) Longitudinal comparisons [†]									
Networks	<u>Non-breeding I – non-breeding II</u>			<u>Non-breeding II – pre-breeding</u>			<u>Pre-breeding – parental care</u>		
	n	U	p	n	U	p	n	U	p
Spatial proximity	24	16	0.001***	22	19	0.005**	33	89	0.164
Sociopositive behavior	24	70	1	22	20	0.004**	33	61	0.011*

(a) Comparisons across social networks (contextual comparisons; Wilcoxon signed rank tests) and (b) comparisons across observational periods (longitudinal comparisons; Mann–Whitney U tests). Mean degree given in its normalized version; p-values are two-tailed. Periods are: non-breeding I (n = 14); non-breeding II (n = 10); pre-breeding (n = 12); post-fledging parental care (n = 21).

[†] feeding network excluded since no significant differences in mean degree were found between observational periods (Kruskal–Wallis tests). Significant results are given in bold:

* p 0.05;

** p 0.01;

*** p 0.001.