DISSERTATION

Titel der Dissertation

Social relations affect social learning in ravens, *Corvus corax*, and jackdaws, *Corvus monedula*

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Synopsis

Over a decade ago Coussi-Korbel and Fragaszy (1995) proposed in a trend-setting paper on social learning to take the influence of social systems and social relations into account when investigating social learning in animals. So far, most work on social learning, i.e. learning that is influenced by observation of, or interaction with, other individuals or their products (Galef, 1988; Heyes, 1994), has concentrated on the mechanisms involved (stimulus or local enhancement, observational learning, imitation, emulation, etc.). Coussi-Korbel and Fragaszy (1995) now suggested that the social organisation of animal groups might influence the likelihood of social learning, the pattern how information is transmitted between individuals, and also the speed of information transfer. Highly despotic societies are "characterized by a high degree of asymmetry in the direction of initiated aggression and the frequency of affiliative interactions among dyads" (Coussi-Korbel & Fragaszy, 1995). Strong, linear rank hierarchies, for example, make it likely that animal societies split into subgroups of individuals that tolerate each other in close proximity. This kind of distribution of social dynamics within a group clears the way for directed social learning to occur when the identity of particular individuals make them more influential models for certain conspecifics than are others. The social setting of tolerating each other in close proximity most of the time allows most detailed information to be transferred and increases the efficiency with which specific information is transmitted (Coussi-Korbel & Fragaszy, 1995). On the other end of the continuum there are highly egalitarian societies with even distributions of aggression and affiliation across and within dyads. Similar tolerance levels and spatial proximity among all members of the group favour non-specific social learning and rapid transfer of information between individuals (Coussi-Korbel & Fragaszy, 1995).

Although also other influential authors discuss the circumstances under which social learning occurs and the identity of individuals involved (Galef & Giraldeau, 2001; Laland, 2004) there is surprisingly little empirical evidence testing these ideas. There are studies on social learning focusing on dominance (Nicol & Pope, 1999; Nicol & Pope, 1994; Pongrácz et al., 2008), sex (Benskin et al., 2002; Katz & Lachlan, 2003; Mason & Reidinger, 1981), age (Choleris et al., 1997; Galef & Whiskin, 2004), kinship (Hatch & Lefebvre, 1997; Valsecchi et al., 1996) or familiarity (Benskin et al., 2002; Lachlan et al., 1998; Swaney et al., 2001; Ward & Hart, 2005) but only few work has concentrated on affiliation between individuals (Bonnie & de Waal, 2006; Russon & Galdikas, 1995). In my PhD, I therefore investigated the effect of this factor on social learning performance.

For my studies I chose a comparative approach working with common ravens, *Corvus corax*, and european jackdaws, *Corvus monedula*. Being phylogenetically closely related these two species show similarities but also differences with regard to their social systems. The social structure of raven and jackdaw groups is more despotic than egalitarian, structured by within-male and within-female rank hierarchies (Heinrich, 1989; Röell, 1978; Tamm, 1977) which increases the likelihood of directed social learning to occur in both species. Furthermore, as in most avian species, social groups are open for outsiders to join and the social organization of both species differs between reproductive and non-reproductive state. Jackdaws live in groups throughout their lifes. They mainly breed in colonies and forage together in flocks which vary seasonally (Haffer & Bauer, 1993). In autumn and winter flocks are larger than during and after breeding, when the birds move around in family groups or often consist only of a mated pair (Röell, 1978). Relatively high variations in spatial cohesion, party composition and party size (Aureli et al., in press) arise over the course of a year. Ravens, on the other hand, become territorial when pairing at 3-4 years of age (Haffer & Bauer, 1993). Adults outside the breeding season tend to join others for activities such as foraging or roosting, but juveniles usually flock year-round (Marzluff & Angell, 2005), assembling at overnight roosts and splitting into variable groups during daytime foraging (Heinrich et al., 1994). Variations in spatial cohesion, party composition and party size (Aureli et al., in press) are generally higher than in jackdaws and occur on a daily basis. Nevertheless, these non-breeder flocks, just like the life-long jackdaw groups, provide the opportunity, especially for juvenile ravens, to develop different social relations with conspecifics by consistently interacting with certain other individuals. Testing ravens for directed social learning should be most promising during this non-breeder period when different sources of information, provided by other individuals, are available. For reasons of comparability, study subjects were therefore juvenile individuals of both species.

I called the working hypothesis "social dynamics hypothesis". According to this hypothesis, directed social learning should occur more in intermediate to despotic than in egalitarian structured groups and should be most efficient for the transfer of specific information between individuals that are highly tolerant and affiliated to each other, i.e. that spend most time together in the same place (Coussi-Korbel & Fragaszy, 1995). Hence, as a first step for my studies, I investigated the social relations within our groups of handraised individuals of both species based on behavioural observations.

Pair bonds between adult jackdaws develop early in life, usually in their first year. They are generally monogamous and last for life (Henderson et al., 2000). Pair partners stay

together year-long, they spend most of their time in close proximity, allofeed and allopreen each other and support each other in agonistic interactions (Wechsler, 1988; Wechsler, 1989) which led to the assumption that these long-term partnerships resemble long-term alliances of many primates and other mammals (Clayton & Emery, 2007). Jackdaw pairs can be considered as the basis and starting point when investigating jackdaw social structure. We characterized relations between adult pair partners in jackdaws, using the concept of valuable relationships (van Schaik & Aureli, 2000), which is defined by spending more time in physical proximity, exchanging more friendly behaviours, having less agonistic conflict and supporting each other more in agonistic interactions than average dyads in the group. We widened this approach by also analyzing object-related and food-related interactions to meet concerns that also play and food-sharing may be important in establishing and/or maintaining strong bonds (Colvin & Tissier, 1985; Emery, 2004). We then characterized relations between juvenile nestmates in the same way and compared relations between pair partners and between nestmates qualitatively and quantitatively. Results showed that both, relations between adult pair partners and between juvenile nestmates, meet most of the criteria, apart from less agonistic conflicts, of valuable relations, i.e. that they are qualitatively similar, but that the expression of behaviours used for characterization differs in intensity, i.e. that relations are quantitatively different. This may be due to different functions of behaviours with regard to maintaining and/or establishing social relations between nestmates or pair partners and strengthens the assumption that social dynamics are not evenly distributed between individuals in jackdaw groups. Behavioural observations in our group of juvenile ravens were less detailed as in jackdaws but yielded similar results with raven nestmates/siblings showing closer affiliated relations than do non-nestmates/non-siblings.

To test for the social dynamics hypothesis that relations between individuals that are highly tolerant towards each other and spend most of the time in close proximity, i.e. that maintain affiliated relations, should increase the efficiency of information transfer and social learning, subjects were tested in nestmate or sibling and non-nestmate or non-sibling dyads in a comparative stimulus enhancement experiment. In this task the model bird was allowed to manipulate a small plastic object while watched by an observer bird. After demonstration the model bird was removed and the observer bird got a set of 5 objects presented, including the object that has been manipulated by the model bird beforehand. Raven observers manipulated this specific object significantly longer than the other objects and also matched their decision to cache or not to cache with the model`s caching behaviour, but only if the model was a sibling and not, if the model was a non-sibling. These results supported the social dynamics

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hypothesis given above. Jackdaw observers, on the other hand, did not show any behaviour that would allow to state that they have been socially learning from any other conspecific, affiliated or not. Because tested subjects maintained comparable social relations, possible explanations for these divergent results, and especially the negative results in jackdaws, may be sought in the species-specific feeding ecology. Ravens intensely cache food (Bugnyar & Kotrschal, 2002; Heinrich & Pepper, 1998) and intra-specific competition at monopolizable food sources is high (Heinrich & Marzluff, 1991). For getting access to food and developing adequate cache protection strategies ravens need experiences with conspecifics and potential pilferers about their own caches. Most experiences they probably gain from those individuals with which they spend most time in close proximity, i.e. their nestmates/siblings. This increases the value of nestmates as a source of relevant information and may result in directed social learning from them. Furthermore, a recent study has shown that caching of objects may be important for ravens to develop cache protection strategies for food caches (Bugnyar et al., 2007). Both considerations may account for the result that ravens learned more readily from siblings than from non-siblings in this non-food context. Jackdaws, on the other hand, do not cache food. They do not have to develop cache protection strategies. Probably, conspecifics that are manipulating objects are of no specific relevance for them which would not lead to social learning in this non-food experiment. We therefore conducted another experiment with our jackdaws, now in a food context.

The experimental set-up was similar to the former one, but now a model bird was allowed to feed mealworms while watched by an observer bird. In this context, observers did learn socially to discriminate two differently coloured boxes, but only if the model bird was a non-affiliated individual (non-nestmate in juvenile, non-pair partner in adult birds), but not if it was an affiliated individual (nestmate in juvenile, pair partner in adult birds). These results did not support the social dynamics hypothesis but may be based on certain characteristics of affiliated relations and on specific benefits of social spacing in jackdaws. One remarkable characteristic of affiliation in jackdaws is that birds show high levels of active food-sharing (de Kort et al., 2006; von Bayern et al., 2007). This allows valuable partners to profit from each other`s food findings and may result in relying on the knowledgeable affiliated partner to secure food because food could be more likely shared with affiliated than with non-affiliated individuals. Furthermore, jackdaws forage mainly on distributed food sources and mainly need spatial information about where feeding is profitable. Spending most time in close proximity with affiliated individuals increases the likelihood that both partners gather similar information about their environment. On the contrary, non-affiliated individuals may face

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different foraging situations and therefore provide different and/or more relevant information. Hence, physical distance, as an outcome of social relations, may increase the value of non-affiliated individuals and may result in directed social learning from them.

This allows the conclusion that even similar qualities of social relations between birds in ravens and jackdaws may not lead to similar outcomes in social learning experiments. While in our ravens spending most time together in the same place indeed increased the efficiency of information transfer, this does not seem to account for jackdaws. Social relations obviously do not solely account for learning patterns but also the value and use made of social spacing and social relations, as well as different feeding ecologies between species have to be taken into account when investigating the phenomenon of directed social learning in corvids.

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Zusammenfassung

Vor über einem Jahrzehnt wiesen Coussi-Korbel und Fragaszy (1995) in einem richtungsweisenden Artikel zu sozialem Lernen darauf hin, dass bei der Untersuchung dieses Phänomens Sozialsysteme und soziale Beziehungen verstärkt berücksichtig werden müssten. Bis dahin war das Hauptaugenmerk auf die Mechanismen, wie „stimulus" oder „local enhancement", „observational learning", Imitation, Emulation, etc., gerichtet, die soziales Lernen, also lernen, das durch Beobachtung von, oder Interaktion mit anderen Individuen oder ihren Produkten beeinflusst wird (Galef, 1988; Heyes, 1994), regulieren. Coussi-Korbel und Fragaszy schlugen nun vor, dass die soziale Organisation tierischer Gruppen die Wahrscheinlichkeit des Auftretens von sozialem Lernen, das Muster, wie Information zwischen Individuen übertragen wird und auch die Geschwindigkeit des Informationstransfers beeinflussen könnte. Hochgradig despotische Gesellschaften seien durch einen hohen Grad an Asymmetrie hinsichtlich der Richtung initiierter Aggression und der Häufigkeit von soziopositiven Interaktionen innerhalb von Dyaden charakterisiert (Coussi-Korbel & Fragaszy, 1995). Starke, lineare Ranghierarchien, erhöhten beispielsweise die Wahrscheinlichkeit, dass tierische Gesellschaften sich in Subgruppen unterteilten, deren Mitglieder einander in enger räumlicher Nähe tolerierten. Eine derartige Verteilung sozialer Dynamiken innerhalb einer Gruppe bereite den Weg für gerichtetes soziales Lernen, in dem die Identität bestimmter Individuen diese zu einflussreicheren Modellen für bestimmte Artgenossen werden lasse als andere. Dieses soziale Szenario, einander in enger räumlicher Nähe zu tolerieren, erlaube die Übertragung detailliertester Information und erhöhe die Effizienz, mit der spezifische Information weitergegeben werde (Coussi-Korbel & Fragaszy, 1995). Am anderen Ende des sozialen Kontinuums stehen hochgradig egalitäre Gesellschaften mit einer ausgeglichenen Verteilung von Aggression und Affiliation innerhalb und zwischen Dyaden. Ähnliche Grade an Toleranz und räumlicher Nähe zwischen allen Mitgliedern einer Gruppe begünstigten nicht-gerichtetes soziales Lernen und eine schnelle Übertragung von Information innerhalb der gesamten Gruppe (Coussi-Korbel & Fragaszy, 1995).

Obwohl auch andere einflussreiche Autoren, die Umstände, unter welchen soziales Lernen auftritt, und die Identität der beteiligten Individuen, diskutieren (Galef & Giraldeau, 2001; Laland, 2004), gibt es erstaunlich wenige empirische Untersuchungen dazu. Studien zum sozialen Lernen konzentrieren sich auf Dominanzverhältnisse (Nicol & Pope, 1999; Nicol & Pope, 1994; Pongrácz et al., 2008), Geschlecht (Benskin et al., 2002; Katz & Lachlan, 2003; Mason & Reidinger, 1981), Alter (Choleris et al., 1997; Galef & Whiskin, 2004), Verwandtschaft (Hatch & Lefebvre, 1997; Valsecchi et al., 1996) oder Bekanntheitsgrad

(Benskin et al., 2002; Lachlan et al., 1998; Swaney et al., 2001; Ward & Hart, 2005), aber nur wenige beschäftigen sich mit soziopositiven Beziehungen zwischen Dyaden (Bonnie & de Waal, 2006; Russon & Galdikas, 1995). Daher untersuchte ich in meiner Dissertation den Einfluss derselben auf soziales Lernen.

Für meine Studien wählte ich einen vergleichenden Ansatz und arbeitete mit Kolkraben, *Corvus corax*, und Turmdohlen, *Corvus monedula*. Diese beiden phylogenetisch nahe verwandten Arten weisen sowohl Ähnlichkeiten als auch Unterschiede hinsichtlich ihres Sozialsystems auf. Die soziale Struktur von Raben- und Dohlengruppen ist stärker despotisch als egalitär strukturiert, auf Ranghierarchien innerhalb von Männchen und Weibchen basierend (Heinrich, 1989; Röell, 1978; Tamm, 1977), was die Wahrscheinlichkeit des Auftretens von gerichtetem sozialen Lernen in beiden Arten erhöht. Darüber hinaus sind ihre sozialen Gruppen, wie bei vielen Vogelarten, offen für Außenstehende sich der Gruppe anzuschließen und die soziale Organisation beider Arten zeigt Unterschiede zwischen reproduktiver und nicht-reproduktiver Phase. Dohlen leben ihr gesamtes Leben in Gruppen. Sie sind vorzugsweise Koloniebrüter und gehen gemeinsam auf Nahrungssuche, wobei die Größe dieser Gruppen saisonal variiert (Haffer & Bauer, 1993). Im Herbst und Winter sind die Gruppen größer als im Frühling und Sommer, also während und nach der Brutsaison, wenn die Vögel vor allem im Familienverband oder häufig nur im Paar anzutreffen sind (Röell, 1978). Räumlicher Zusammenhalt, Gruppenkomposition und Gruppengröße (Aureli et al., in press) variieren somit über das Jahr hinweg relativ stark. Im Gegensatz zu Dohlen werden Raben in einem Alter von 3-4 Jahren, wenn sie sich verpaaren, territorial (Haffer & Bauer, 1993). Außerhalb der Brutsaison tendieren Adulttiere dazu sich anderen bei der Nahrungssuche oder an den gemeinsamen Schlafplätzen anzuschließen, aber Jungtiere verbringen üblicherweise das gesamte Jahr in der Schar (Marzluff & Angell, 2005). Sie versammeln sich an den nächtlichen Schlafplätzen und teilen sich untertags in variable Gruppen zur Nahrungssuche auf (Heinrich et al., 1994). Schwankungen hinsichtlich des räumlichen Zusammenhalts, der Gruppenkomposition und –größe (Aureli et al., in press) sind generell höher als bei Dohlen und treten im Tageszyklus auf. Nichtsdestoweniger bieten diese Nicht-Brüter-Verbände, ebenso wie Dohlengruppen, vor allem für Jungraben die Möglichkeit, unterschiedliche soziale Beziehungen mit Artgenossen zu entwickeln. Will man Raben im Hinblick auf gerichtetes soziales Lernen testen, so sollte dies innerhalb dieser Nicht-Brüter-Periode am vielversprechendsten sein, wenn unterschiedliche Informationsquellen in Form verschiedenster Artgenossen zur Verfügung stehen. Aus Gründen der Vergleichbarkeit wurden daher Jungtiere beider Arten getestet.

Die Arbeitshypothese nannte ich „soziale Dynamik"-Hypothese, gemäß derer gerichtetes soziales Lernen eher in despotisch als in egalitär strukturierten Gruppen auftreten und für den Austausch spezifischer Information zwischen jenen Individuen am effizientesten sein sollte, die zueinander höchst tolerant sind und eine enge Beziehung pflegen, also jene, die die meiste Zeit in enger räumlicher Nähe zueinander verbringen (Coussi-Korbel & Fragaszy, 1995). Als ersten Schritt meiner Studien untersuchte ich daher, auf Verhaltensbeobachtungen basierend, bei beiden Arten die sozialen Beziehungen unserer handaufgezogenen Individuen in der Gruppe.

Paarbindungen adulter Dohlen entwickeln sich üblicherweise bereits im ersten Jahr. Sie sind generell monogam und von lebenslanger Dauer (Henderson et al., 2000). Paarpartner bleiben das Jahr über beisammen, sie verbringen die meiste Zeit in unmittelbarer Nähe zueinander, füttern und putzen sich gegenseitig und unterstützen einander in agonistischen Interaktionen (Wechsler, 1988; Wechsler, 1989). Diese soziale Nähe führte zu der Auffassung, dass diese langjährigen Partnerschaften die langdauernden Allianzen von Primaten und anderen Säugetieren widerspiegeln (Clayton & Emery, 2007). Dohlenpaare können als Basis und Ausgangspunkt zur Untersuchung der Sozialstruktur von Dohlen herangezogen werden. Mit der Verwendung des Konzepts wertvoller Beziehungen (van Schaik & Aureli, 2000), charakterisierten wir die Beziehungen zwischen adulten Paarpartnern in Dohlen. Dieses Konzept definiert wertvolle Beziehungen zwischen zwei Individuen, im Vergleich zu durchschnittlichen Dyaden in der Gruppe, dadurch, als erstere mehr Zeit in räumlicher Nähe zueinander verbringen, mehr freundliche Verhaltensweisen austauschen, weniger agonistische Konflikte austragen und einander mehr in agonistischen Interaktionen unterstützen als letztere. Wir erweiterten diesen Ansatz insofern, als wir ebenso objekt- und nahrungsbezogene Interaktionen analysierten, um jenen Überlegungen Rechnung zu tragen, die Spiel und das Teilen von Nahrung als wesentliche Faktoren für die Etablierung und/oder Aufrechterhaltung enger Beziehungen betrachten (Colvin & Tissier, 1985; Emery, 2004). In ebendieser Weise analysierten wir die Beziehungen zwischen juvenilen Nestgeschwistern und verglichen letztlich die Beziehungen zwischen Paarpartnern und zwischen Nestgeschwistern in qualitativer und quantitativer Hinsicht. Die Ergebnisse zeigten, dass sowohl die Beziehungen zwischen adulten Paarpartnern als auch jene zwischen juvenilen Nestgeschwistern die meisten Kriterien, mit Ausnahme einer geringeren Zahl agonistischer Interaktionen, wertvoller Beziehungen erfüllen, dass sie also qualitativ ähnlich sind. Da die Intensität jener Verhaltensweisen, die zur Charakterisierung herangezogen werden, jedoch unterschiedlich stark ausgeprägt ist, sind sie quantitativ unterschiedlich. Die Ursache dafür

könnte in den unterschiedlichen Funktionen der Verhaltensweisen, in Bezug auf die Beziehung zu Nestgeschwistern oder Paarpartnern, zu suchen sein, die sie in Hinblick auf Etablierung und/oder Erhaltung sozialer Beziehungen einnehmen. Diese Ergebnisse stärken die Auffassung, dass die sozialen Dynamiken zwischen den Individuen von Dohlengruppen nicht gleichmäßig verteilt sind. Die Verhaltensbeobachtungen an unseren juvenilen Raben waren weniger detailliert, brachten jedoch ähnliche Ergebnisse. Auch Raben zeigten engere soziale Beziehungen zu ihren Geschwistern oder Nestgeschwister als zu ihren Nicht-Geschwistern oder Nicht-Nestgeschwistern.

Um die soziale Dynamik-Hypothese zu testen, dass hohe gegenseitige Toleranz und räumliche Nähe zueinander, also enge soziale Beziehungen, das Auftreten von sozialem Lernen und die Effizienz des Informationstransfers zwischen Individuen steigert, wurden die Vögel in einem vergleichenden „stimulus enhancement" Experiment, in Dyaden, bestehend aus Geschwistern oder Nestgeschwistern und Nicht-Geschwistern oder Nicht-Nestgeschwistern getestet. In diesem Versuch durfte der Modell-Vogel ein kleines Plastikobjekt manipulieren, während ihm ein Beobachter-Vogel zusah. Nach der Demonstration wurde das Modell aus den Experimenträumen entlassen und dem Beobachter 5 Objekte präsentiert, unter denen sich jenes befand, welches das Model zuvor manipuliert hatte. Raben-Beobachter manipulierten jenes spezifische Objekt signifikant länger als die übrigen verfügbaren Objekte und glichen ihr Verhalten zu verstecken oder nicht zu verstecken dem jeweiligen Versteckverhalten des Modells an, jedoch nur dann, wenn das Modell ein Geschwister, aber nicht, wenn das Modell ein Nicht-Geschwister war. Diese Ergebnisse unterstützen die soziale Dynamik-Hypothese. Dohlen-Beobachter hingegen zeigten keinerlei Verhalten, welches den Schluss zuließe, sie hätten sozial von Artgenossen gelernt. Da die getesteten Individuen vergleichbare soziale Beziehungen pflegten, könnten mögliche Erklärungen für diese unterschiedlichen Ergebnisse an der jeweiligen artspezifischen Nahrungsökologie liegen. Raben verstecken ihre Nahrung zu einem großen Teil (Bugnyar & Kotrschal, 2002; Heinrich & Pepper, 1998) und die innerartliche Konkurrenz an monopolisierbaren Nahrungsressourcen ist hoch (Heinrich & Marzluff, 1991). Um Zugang zu Nahrung zu bekommen und um entsprechende Schutzstrategien für ihre Nahrungsverstecke zu entwickeln benötigen Raben Erfahrungen mit Artgenossen und potentiellen Versteckplünderern rund um ihre eigenen Verstecke. Die meisten Erfahrungen machen sie vermutlich mit jenen Individuen, mit denen sie die meiste Zeit in unmittelbarer Nähe verbringen, also ihren Geschwistern/Nestgeschwistern. Dies würde den Wert von Nestgeschwistern als Quelle relevanter Information erhöhen und in sozialem Lernen, welches

auf sie gerichtet ist, münden. Darüber hinaus zeigte eine Studie, dass das Verstecken von Objekten für Raben wichtig sein könnte, um später Schutzstrategien für ihre Nahrungsverstecke zu entwickeln (Bugnyar et al., 2007). Beide Erwägungen könnten die Ergebnisse begründen, dass Raben eher von Geschwistern als von Nicht-Geschwistern im Objektkontext lernen. Dohlen hingegen verstecken ihre Nahrung nicht. Sie müssen daher keine Schutzstrategien für ihre Verstecke entwickeln. Möglicherweise stellen für sie Artgenossen, die Objekte manipulieren, keinen besonderen relevanten Wert dar, weshalb sie in diesem Kontext auch nicht sozial lernen würden. Wir haben unsere Dohlen daher in einem weiteren Experiment, nun im Nahrungskontext, getestet.

Der experimentelle Aufbau war ähnlich zum vorhergehenden, nun aber durfte das Modell Mehlwürmer fressen, während der Beobachter zusah. In diesem Kontext nun lernten die Beobachter auf soziale Weise zwei unterschiedlich gefärbte Dosen voneinander zu unterscheiden, allerdings nur, wenn das Modell ein Individuum war, mit dem der Beobachter keine enge soziale Beziehung pflegte (Nicht-Nestgeschwister bei juvenilen, Nicht-Paarpartner bei adulten Vögeln). Sie lernten nicht von Modellen zu denen sie in enger sozialer Beziehung standen. Diese Ergebnisse unterstützen die soziale Dynamik-Hypothese nicht, ihr Ursprung könnte aber in bestimmten Charakteristika enger Beziehungen und in spezifischen Vorteilen der räumlichen Verteilung von Individuen in Dohlengruppen liegen. Ein herausragendes Charakteristikum enger sozialer Beziehungen bei Dohlen ist der hohe Anteil des aktiven Futterteilens (de Kort et al., 2006; von Bayern et al., 2007). Dies ermöglicht engen Partnern von den Nahrungsfunden des jeweils anderen zu profitieren und könnte darin resultieren, dass sie sich auf den kundigen Partner verlassen Nahrung zu sichern, da diese wahrscheinlicher mit sozial enger stehenden Individuen als mit weiter entfernten geteilt wird. Darüber hinaus ernähren sich Dohlen vor allem von verstreuten Nahrungsressourcen weshalb sie vor allem räumliche Information darüber benötigen, wo sich die Nahrungssuche lohnt. Viel Zeit in enger räumlicher Nähe zu verbringen erhöht die Wahrscheinlichkeit, dass beide Partner einer solcherart engen Beziehung ähnliche Informationen aus ihrer Umwelt beziehen. Im Gegensatz dazu könnten Individuen, die in keinem engen Kontakt stehen, mit unterschiedlichen Situationen hinsichtlich der Nahrungssuche konfrontiert sein, weshalb sie andersartige und/oder relevantere Information bereit stellen könnten. Physische Distanz, als Ergebnis sozialer Beziehungen, könnte daher den Wert von Individuen steigern, die nicht in enger Beziehung zueinander stehen und in sozialem Lernen, welches auf sie gerichtet ist, resultieren.

Daraus ist zu schließen, dass selbst ähnliche Qualitäten sozialer Beziehungen bei Raben und Dohlen nicht zwangsläufig zu denselben Ergebnissen in sozialen Lernexperimenten führen. Während bei unseren Raben enge soziale Beziehungen tatsächlich zu größerer Effizienz beim Informationstransfer führte, scheint dies für Dohlen nicht zu gelten. Soziale Beziehungen sind offensichtlich nicht alleine für Lernmuster verantwortlich. Ebenso müssen Wert und Gebrauch sozialer Beziehungen und ihre räumliche Verteilung, genauso wie unterschiedliche Nahrungsökologien verschiedener Arten in Betracht gezogen werden, wenn man das Phänomen des gerichteten sozialen Lernens in Korviden untersucht.

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Similarities and differences of relationships between adult pair partners and between juvenile nestmates in jackdaws (*Corvus monedula*)

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Abstract

As in most avian species jackdaw, *Corvus monedula*, groups are open for individuals to join or leave the flock. Within a year flocks show relatively high variations regarding spatial cohesion, party composition and party size but monogamous long-term pair bonds have been considered as the basis of jackdaw social structure. They can be regarded as representing valuable relationships in this species, relationships from which individuals can draw functionally diverse benefits. In this study we asked if also other relationships, those between juvenile nestmates, could play an integral role in jackdaw social structure. We therefore characterised relationships between pair partners and between nestmates, in comparison to non-pair partners and non-nestmates, and compared them qualitatively and quantitatively. Via focal and *ad libitum* behavioural observations of a handraised aviary group of 36 jackdaws over a two-year period we considered social interactions characteristic for valuable relationships which were assigned to six interaction categories: a-physical proximity, b-sociopositive physical contact, c-object related interactions, d-food related interactions, e-agonistic interactions, and f-agonistic support. We found significantly higher frequencies or longer durations of these interactions, except for agonistic interactions, between pair partners in adult birds and between nestmates in juvenile birds compared to non-pair partners and non-nestmates. However, intensities of adult interaction patterns with pair partners were significantly higher than those between nestmates. We therefore conclude that valuable relationships between pair partners and between nestmates are qualitatively similar but interactions differ quantitatively, reflecting the different functional contexts in establishing and/or maintaining relationships between nestmates or between pair partners.

Living in a social environment has been proposed to select for cognitive abilities by challenging individuals with intentionally behaving conspecifics whose behaviour is difficult to predict and to manipulate (Humphrey, 1976; Jolly, 1966). At least in primates, social group interactions are based on individual recognition and have been considered as the crucial driving force for cognitive evolution (Byrne and Whiten, 1988; Whiten and Byrne, 1997). Such individualized social groups are characterized by variable dyadic social relationships influenced by the value certain individuals can represent for certain conspecifis. These values might be expressed as sex, age or skills, as tendencies towards conspecifics such as fighting or caring, and as availability for conspecifics, influenced by physical distance and presence of third parties (Kummer, 1978). The benefits individuals may draw from ´valuable relationships´, are divided into two major kinds, alliance formation and protective services (van Schaik and Aureli, 2000). Functional aspects of these benefits range from aspects, such as hygiene (Hutchins and Barash, 1976), tension reduction (Schino et al., 1988) and endorphin release (Keverne et al., 1989), to physical intactness and reducing social threats (Smuts and Smuts, 1993), to defense of or access to resources, to restoring disrupted valuable relationships after conflicts (Aureli et al., 2002).

The mechanistic basis of such valuable relationships are strong bonds between individuals which spend more time in close proximity and show more friendly behaviours such as grooming towards each other, lower rates of agonistic conflict, and more mutual agonistic support than average dyads in the group (van Schaik and Aureli, 2000). Behavioural complexes, such as reconciliation (for reviews, see (Aureli et al., 2002; de Waal, 1993; Kappeler and van Schaik, 1992), consolation (Das, 2000), grooming (Cords, 1997), or play (Colvin and Tissier, 1985) are considered to express bonds between individuals and to serve developing and maintaining these bonds and, in part, simultaneously express benefits of these bonds. Alliances and long-term dyadic social bonds are now increasingly shown in non-primate mammals such as elephants, *Loxodonta africana* (Moss and Poole, 1983), hyenas, *Crocuta crocuta* (Holekamp and Engh, 2002; Holekamp et al., 2007) and dolphins, *Tursiops truncatus* (Connor et al., 1999; Connor et al., 1992) as well as in birds such as greylag geese, *Anser anser* (Scheiber et al., 2005). Corvids in particular, seem to meet many of the criteria for the use of social knowledge in their interactions with conspecifics (Emery, 2004). Common ravens, *Corvus corax*, and western scrub-jays, *Aphelocoma californica*, alter their pilfering and caching behaviour with regard to social context (Bugnyar and Heinrich, 2006; Dally et al., 2006). Consolation was described in rooks, *Corvus frugilegus* (Seed et al., 2007) and alliance formation in common ravens, *Corvus corax* (Loretto et al., 2005).

In this study, we investigated the manifestation of valuable relationships in jackdaws, *Corvus monedula*. Applying a concept in birds which has been developed for primates needs to take into account that most primate groups are "closed" with regard to resistance against joining strangers (Cords, 1997; Smuts et al., 1987) whereas most avian social groups are "open" for outsiders to join. Jackdaw flocks/colonies are no exception.

Jackdaws live in groups lifelong. They mainly breed in colonies and forage together in flocks (Haffer and Bauer, 1993). Resident colony members usually form the core of a flock. Still individuals or small parties leave or join the flocks (Röell, 1978). Spatial cohesion, party composition and party size (Aureli et al., in press) of jackdaw groups vary over the course of a year, in parallel with reproductive and non-reproductive states and depending on food availability and quality (Emery et al., 2007). In autumn and winter flocks are larger than during and after breeding, when the birds move around in family groups and often consist only of a mated pair (Röell, 1978). Jackdaws typically pair up in their first autumn (Lorenz, 1931) and form life-long monogamous bonds (Henderson et al., 2000). Pair partners remain together year-long, spending most of their time in close proximity, allofeeding and allopreening each other (Wechsler, 1989) and supporting each other in agonistic interactions (Wechsler, 1988). Such, these long-term partnerships are regarded as the core of social structure (Emery et al., 2007) and to resemble the long-term alliances of many primates and other mammals, such as dolphins (Clayton and Emery, 2007). Still, the question remains whether other relations than the pair bond, such as relations between juvenile nestmates may play an important role for structuring jackdaw groups.

Social relationships, apart from rank relations, between juvenile or immature animals still receive limited attention (van Schaik and Aureli, 2000). In rhesus monkeys mothers pass on their social network to their infants (Berman, 1982; Loy and Loy, 1974) and strong affiliative relations are maintained between relatives (Berman, 1982; Colvin and Tissier, 1985; Loy and Loy, 1974). However, in corvids also relationships between juvenile birds only play an important role for social structure (Emery et al., 2007; von Bayern et al., 2007). They found characteristics of valuable relations between juvenile birds, but no differences between siblings and non-siblings in jackdaws (de Kort et al., 2006; von Bayern et al., 2007), except for agonistic support which was rather found between nestmates than non-nestmates in rooks (Emery et al., 2007). However, there are significant differences between nestmates and non-nestmates in corvids in how they relate to each other in a functional way: Relationships between siblings and non-siblings affected exploratory behaviour in ravens (Stöwe et al., 2006), paying attention in ravens and jackdaws (Scheid et al., 2007) as well as social learning

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in ravens (Schwab et al., 2008) and jackdaws (Schwab et al., in press). These findings suggest underlying valuable dyadic relationships also prior to adult pair bonds, between juvenile nestmates before they reach sexual maturity.

In this study we therefore asked whether relationships between juvenile nestmates in comparison to non-nestmates resemble the characteristics of valuable relationships between adult pair partners. First, we characterized interactions between adult pair partners in comparison with non-pair partners in jackdaws following van Schaik & Aureli (2000), by employing behavioural parameters that indicate physical proximity, friendly behaviours expressed through affiliative contact behaviour (Connor et al., 2006), agonistic conflict and agonistic support. Furthermore, we analyzed object-related and food-related interactions to meet concerns that play and food-sharing may be important in establishing and/or maintaining strong bonds (Colvin and Tissier, 1985; Emery, 2004). In the same way we characterized interactions between juvenile nestmates in comparison to non-nestmates. Finally, we examined whether relationships between pair partners are qualitatively and quantitatively similar to relationships between nestmates.

Methods

Subjects, handraising, nest composition, and housing

Subjects were 36 jackdaws (*Corvus monedula*) handraised in two different years, 2005 and 2006. All birds were taken out of nests in the wild and have been handraised under standardized conditions from 13-20 days after hatching to fledging at the Konrad Lorenz Research Station in Gruenau, Austria. For handraising birds were kept in artificial nests indoors. A nest consisted of a cardboard box (length 70cm, width 40cm, height 30cm) filled with hay and napkins for easy cleaning. Feeding rate at the beginning of the handraising period was 9 times a day and was reduced to 5 times a day at fledging. Diet consisted of a mixture of dry insects, minced beefheart, cooked egg yolk, cottage cheese, water, calcium and a vitamin preparation. During this period all birds were individually marked with coloured metal rings for identification.

Biological siblings (i.e. those from the same original nests) were always raised together in one nest but other nests were composed of nestmates, i.e. unrelated individuals. In May/June 2005 20 jackdaws (14 males, 6 females) were handraised in 6 separate nests. Nest one and two consisted of four biological siblings each, nest three consisted of two unrelated nestmates, nest four was composed of three unrelated nestmates, nest five consisted of two sibling pairs and nest six was composed of one sibling pair plus one unrelated bird (see Table 1). In

May/June 2006 another 16 jackdaws (9 males, 7 females) were handraised in 7 separate nests. Nest one and two consisted of three biological siblings each, nest three consisted of a sibling pair, nest four was composed of three unrelated nestmates, nest five was composed of one sibling pair plus one unrelated bird and two more birds were singly raised in nests six and seven (see Table 1).

After fledging, the birds were transferred to an outdoor aviary and from then on housed together in one social group. Birds had *ad libitum* access to water and were now fed three to four times a day. Their diet included various kinds of fruits, grain, vegetables, bread and milk products. The aviary in 2005 consisted of one outdoor compartment (60m², maximum height of 4 m) which was equipped with wooden perches, breeding boxes, rocks and natural vegetation and outdoor experimental compartments (30m2, 2.5 m high) which were roofed and equipped with wooden perches. In June 2006, the aviary was rebuilt and, from then on consisted of two outdoor compartments (each 30m2, maximum height of 3 m) with wooden perches, breeding boxes, sheltered sleeping areas, rocks and natural vegetation plus the outdoor experimental compartments. When not being tested in behavioural experiments, birds could move around freely in all areas.

Behavioural observations and inter-observer reliability

Behavioural observations were recorded from June 2005 to April 2007 with the exception of May and June 2006 (breeding season). They were carried out daily to every second day, alternating during morning and afternoon feedings. One observational session lasted 30 minutes and consisted of 5-minutes focal observations from six birds. In total 2576 five-minutes focal observations were recorded. Focal observations were counterbalanced for frequency and order of observations for each individual. We recorded all social interactions between the focal individual and any other conspecific. Also, from June 2005 to April 2007 we recorded agonistic support occurrences (138 observations) and, additionally, from July 2006 to April 2007 we recorded food-sharing occurrences (265 observations) via *ad libitum* sampling.

To determine affiliate relationships, we analysed 12 parameters, assigned to six categories of social interactions:

A) physical distance. 1: nearest neighbour - frequency with which each conspecific was the focal individual`s nearest neighbour at the beginning of each 5 minute focal observation, 2:

sitting close - the total duration [s] that the focal individual sat within 10 cm to any other conspecific.

B) sociopositive physical contact. 3: touching – frequency with which the focal individual gently touched any body part (apart from legs) of any other conspecific with its beak, 4: allopreening – the total duration [s] that the focal individual was preening any other conspecific with its beak.

C) object-related interactions. 5: approach object - frequency with which the focal individual approached any other conspecific that was manipulating an object with its beak and/or feet and frequency with which the focal individual was approached by any other conspecific when itself was manipulating an object with its beak and/or feet, 6: joint manipulation – frequency with which the focal individual was manipulating an object with its beak and/or feet together with any other conspecific.

D) food-related interactions. 7: approach food – frequency with which the focal individual approached any other conspecific that was manipulating a food item with its beak and/or feet and frequency with which the focal individual was approached by any other conspecific when itself was manipulating a food item with its beak and/or feet, 8: food-sharing – frequency with which a donor bird transferred food to a recipient, regardless if the recipient has been begging at the donor beforehand or not.

E) agonistic interactions. 9: landing on back – frequency with which the focal individual was landing on the back of any other conspecific, 10: fighting – frequency with which the focal individual was fighting with any other conspecific by trying to rise higher than the opponent and turning the opponent on its back through wingflapping, grabbing with feet and/or beak and pecking. Due to the low number of occurrences of parameters 9 and 10 they were jointly analyzed as severe aggression. 11: pecking – frequency with which the focal individual was pecking or trying to peck any other conspecific not followed by a displacement of the conspecific.

F) 12: agonistic support: frequency with which an individual was intervening in an agonistic interaction between two conspecifics, either actively (by physically attacking or chasing its target) or passively (by approaching and standing close to the supportee but without physical involvement) during or after the initial agonistic interaction in which it interfered.

Inter-observer reliability

Behavioural observations for the group of 2005 were done by C.S. After the breeding season in 2006, two more observers, R.S and D.G., were engaged. To assess inter-observer reliability two 30 min video-sequences of the birds, recorded in October 2006 and March 2007, were coded by each of the three observers independently. To calculate inter-observer reliability for this "tutor-student" situation (Haccou and Meelis, 1994) we compared records between C.S. and R.S. and between C.S. and D.G. Inter-observer reliability was excellent: between C.S. and R.S.: $p_o = 0,89$, Cohen`s Kappa = 0.871 and also, between C.S. and D.G.: $p_o = 0,92$, Cohen`s Kappa = 0.905. Therefore, observational records of all three observers were pooled for analysis.

Observation periods and analysis

Jackdaws reach sexual maturity already in their first year and form pair bonds at about 8 months of age (Lorenz, 1931). Hence, each year of observations, 2005 and 2006, was divided into two periods, juvenile and adult. The observational juvenile periods lasted from June 2005 to December 2005 and from July 2006 to December 2006 when pair bonding started at the end of each year. Observations in the adult periods lasted from January 2006 to April 2006 and from January 2007 to April 2007 when breeding season had already started. Results for juvenile birds were obtained by analysing both juvenile periods together and results for adult birds were obtained by analysing both adult periods together.

In the juvenile period we compared behavioural parameters with regard to interactions of the focal individuals with nestmates and with non-nestmates. In 2005 data from 20 juvenile individuals were analysed. In 2006 only data from 14 juveniles were analysed because 2 individuals were handraised as singletons in their nests and therefore, did not have nestmates for comparison. In sum, for the juvenile period we used data from 34 individuals for analysis.

In the adult period we compared interactions of the focal individuals with their pair partner and with non-pair partners. Because paired jackdaws are territorial only in the immediate proximity of their nest sites (Haffer and Bauer, 1993), two birds were considered being a pair when they had successfully occupied a nestbox and defended it together during breeding season, regardless of breeding attempts or breeding success. Unfortunately, in December 2005 seven juveniles fell victim to predation. Therefore, only 13 birds reached adulthood in this year. Out of these 13 individuals 12 birds formed six pairs, five heterosexual and one male-male pair. One heterosexual pair consisted of unrelated nestmates, the other five pairs were unrelated non-nestmates. Therefore, 12 individuals were considered in the analysis. Adults

from 2006 formed five heterosexual pairs. Two pairs consisted of biological siblings, the other three pairs were unrelated non-nestmates. Therefore, data from 22 adult and paired individuals were analysed in total.

To compare the focal individuals` interactions with nestmates and non-nestmates (juvenile period) and with pair and non-pair partners (adult period) we first summed up durations or frequencies of parameters for each individual separately. To obtain these sums we only used individual values which were recorded when the individual was the focal individual to avoid pseudoreplication. Second, we divided these sums through the number of actual nestmates and non-nestmates (juvenile period) or pair and non-pair partners (adult period), respectively. Then, we corrected for the number of observations for each individual (apart from agonistic support and food-sharing data, note that food-sharing data only exist for juveniles from 2006, which were collected via *ad libitum* sampling). Thus, we obtained one average data point per individual per condition (standardised frequency, standardised duration). Although during 2006, the 29 birds of both years were kept together in one social group, and were therefore available as potential interaction partners, there were hardly any interactions between the two age groups with regard to the analysed parameters. Hence, corrections for the number of actual nestmates and non-nestmates or pair and non-pair partners were restricted to the corresponding age group of the focal individual.

We furthermore compared frequencies and durations of the focal individuals` interactions with their nestmates in the juvenile period and with their pair partners in the adult period to see whether frequencies and durations of parameters differed between the two periods, i.e. if intensities of parameters changed between periods. Note that food-sharing data only exist for 8 paired birds from 2006 that also had nestmates as juveniles.

To investigate how exclusively individuals applied behaviours towards particular conspecifics we compared the number of interaction partners for each behavioural parameter in the juvenile and in the adult period. We again first summed up the number of actual interaction partners, regardless of their relation to the focal individual, within the corresponding age group for each focal individual separately. To avoid pseudoreplication we only used the observations form the focal individual. Second, we divided these sums through the number of available interaction partners, in the corresponding age group of the focal individual. We then compared these corrected values between the juvenile and the adult period for each parameter for the 22 adult and paired individuals.

Whenever data were not normally distributed we used Wilcoxon signed-ranks tests and when data were normally distributed we used paired t-tests for comparisons. All tests were

calculated with SPSS 11.5. All test results are given two-tailed and considered significant when $p < 0.05$.

Results

Adult period

In adult birds frequencies and durations of interactions between pair partners compared to non-pair partners differed significantly in physical distance, sociopositive physical contact, object-related interactions, food-related interactions and agonistic support. Interaction frequencies and durations were significantly higher between pair partners than between non-pair partners in all nine parameters considered (Tab. 2a), clearly indicating bonding and valuable relationships between pair partners but not between non-pair partners. This was true for the focal bird`s nearest neighbour at the beginning of an observation which was more often the pair partner than it was a non-pair partner. Also sitting close (Fig.1a, left panel) and allopreening bouts lasted longer with the pair partner than with a non-pair partner. Touching (Fig.1b, left panel), approaching a bird that was manipulating an object (Fig.1c, left panel) or a food item (Fig.1d, left panel), joint manipulation of an object, food-sharing and agonistic support (Fig.1f, left panel) occurred significantly more often between pair partners than between non-pair partners. However, the frequency of severe aggression between pair partners did not differ significantly from the frequency between non-pair partners. The same applied to pecking (Fig.1e, left panel).

Juvenile period

Juvenile birds showed similar interaction patterns as adults, but with nestmates and non-nestmates. Frequencies and durations of interactions were significantly higher between nestmates than between non-nestmates in all nine parameters of physical distance, sociopositive physical contact, object-related interactions, food-related interactions and agonistic support (Tab. 2b), again indicating bonding and valuable relationships between nestmates but not between non-nestmates. The focal bird`s nearest neighbour at the beginning of an observation was more often a nestmate than it was a non-nestmate. Sitting close (Fig.1a, right panel) and allopreening bouts lasted longer between nestmates than between non-nestmates. Touching (Fig.1b, right panel), approaching a bird that was manipulating an object (Fig.1c, right panel) or a food item (Fig.1d, right panel), joint manipulation of an object, food-sharing and agonistic support (Fig.1f, right panel) occurred significantly more often between

nestmates than between non-nestmates. As the case in adult pairs, the juvenile birds also did not direct significantly different rates of agonistic interactions towards nestmates and non-nestmates. Nestmates did not differ significantly in their internal frequencies of severe aggression from non-nestmates. The same applied to pecking (Fig.1e, right panel).

Intensity of behavioural parameters in juvenile and adult period

When adult, 21 birds were paired which also had nestmates as juveniles. Comparing interaction frequencies and durations with their pair partner when adult and with nestmates when still juvenile showed that interactions were significantly more intense between adult pair partners than between juvenile nestmates (Tab. 3a). This included nearest neighbour, sitting close (Fig.1a), touching (Fig.1b), allopreening, approaching a bird that was manipulating a food item (Fig.1d) and agonistic support (Fig.1f). However, object-related interactions, agonistic interactions and food-sharing did not differ significantly between pair partners and nestmates. This was true for approaches to subjects that were manipulating an object (Fig.1c), joint manipulation of objects, severe aggression, pecking (Fig.1e), and food-sharing.

Exclusiveness of interaction partners in the juvenile and adult period

The number of interaction partners of 22 adult and paired focal individuals significantly decreased in some parameters from the juvenile to the adult period (Tab. 3b), indicating increasing exclusiveness of interaction partners. This was true for the number of individuals that were nearest neighbours (means±se: juvenile: 13.59±0.38, adult: 8.23±0.38), the number of subjects that were approached when manipulating an object (juvenile: 14.77±0.38, adult: 5.82±0.49), the number of interaction partners in joint manipulations (juvenile: 3.68±0.36, adult: 0.86±0.14), and the number of pecked subjects (juvenile: 7.68±0.75, adult: 3.05±0.47). The number of subjects that were touched by the focal individuals or approached when they were manipulating a food item also tended to decrease from the juvenile to the adult period. Touching decreased from 3.64±0.31 to 2.0±0.22 and approaches decreased from 9.77±0.45 to 5.91±0.53. However, there was no significant difference in the number of interaction partners in the juvenile and in the adult period with regard to sitting close (means±se: juvenile: 4.05±0.57, adult: 3.23±0.32), allopreening (juvenile: 1.36±0.25, adult: 1.45±0.4), severe aggression (juvenile: 1.86±0.35, adult: 1.09±0.29), food-sharing (juvenile: 1.3±0.21, adult: 1.14±0.14, note that data only exist for juveniles from 2006), and agonistic support (juvenile: 1±0.25, adult: 1.32±0.28). The number of interaction partners in these five parameters was

already low when the birds were still juveniles and did not show a significant decrease in the adult period, indicating a considerable degree of exclusiveness already in juvenile birds.

Discussion

Our results indicate that relationships between adult pair partners as well as between juvenile nestmates in jackdaws meet major characteristics of valuable relationships in primates (sensu van Schaik & Aureli, 2000). All interaction categories which are considered expressing valuable relationships, such as physical distance, sociopositive physical contact, object-related and food-related interactions and agonistic support, were more pronounced between pair partners than between non-pair partners and also between nestmates in comparison to non-nestmates. Hence, pair partners and nestmates exhibited similar qualitative patterns of interactions. When comparing behavioural parameters, indicative of interaction intensity, our results showed an increase in some parameters from the juvenile to the adult birds. Also, adult birds had less interaction partners outside their dyadic partnership as compared to juveniles, indicating exclusiveness of interactions. These differences in intensity and exclusiveness of interactions between juvenile and adult birds may reflect quantitative differences in valuable relationships between nestmates and pair partners.

However, frequencies of agonistic conflicts neither differed between pair partners and non-pair partners, nor between nestmates and non-nestmates, which was unexpected for dyadic partners of potentially valuable relationships. Although affiliated partners tend to be animals with similar ecological interests their interests probably never coincide completely, therefore, aggressive conflicts between valuable partners may be unavoidable, although they may be rare (van Schaik and Aureli, 2000). Even when agonistic interactions occur at a similar frequency between individuals that spend greater amounts of time close to each other as between individuals that are rarely in proximity, interactions may be regarded as more `serious` in the latter case by causing the victim to be more fearful of his aggressor (Colvin and Tissier, 1985). Hence, agonistic conflicts between valuable partners in this study, may be attributed as `unavoidable` and/or less `serious`, and may additionally be compensated by other `friendly` behaviours and agonistic support which are significantly more directed towards nestmates and pair partners.

In contrast to our jackdaw results, rooks, *Corvus frugilegus*, showed little or no acts af aggression between valuable partners (Emery et al., 2007). Also, jackdaws did not show higher rates of food-sharing between siblings (von Bayern et al., 2007) and between nestmates (de Kort et al., 2006) compared to other conspecifics. These differences may be explained by

species differences, but also by methodological differences of the studies. Observations of the social interactions between individuals in all three studies mentioned above were recorded while the experimenter provided each bird food pieces in turn which were not part of the maintenance diet. In the present study the human observer did not interact with the birds and food was available to all birds at any time. Highlighting one bird as the only possessor of a piece of highly valuable food at a given time is more likely to result in exchanging ´friendly´ behaviours than engaging in agonistic conflicts (Emery et al., 2007) or in harassing the possessor through begging which then leads to food-sharing between individuals, regardless of their relationships (de Kort et al., 2006). Additionally, methodological differences in handraising may have further contributed to the different results. In the von Bayern et al. (2007) study `birds were taken from their original nests and hand-raised as a single group from a young age` which makes it `likely that sibling recognition learning had been disturbed` (von Bayern et al., 2007, p.726). Current evidence from studies dealing mainly with cooperative breeding species suggests that associative learning is the most likely mechanism of kin recognition in avian societies (Komdeur and Hatchwell, 1999; Sharp et al., 2005). If we assume that an associative learning mechanism also accounts for kin recognition in jackdaws this would explain the lack of higher rates of food-sharing between siblings (von Bayern et al., 2007) when raised in a single group.

When comparing intensities of interactions between nestmates and pair partners and exclusiveness of interactions between juvenile and adult birds and then combining these results for valuable partners (nestmates and pair partners), we find some distinct patterns that may be explained through different functions they could play in establishing and/or maintaining affiliate relationships.

A significant increase in intensity from nestmates to pair partners and a simultaneous significant increase in exclusiveness of interaction partners was found with regard to nearest neighbour only. Indeed, mated jackdaws spend most of their time together (Röell, 1978). Proximity measures are often used to initially determine the character of relationships (Colvin and Tissier, 1985; von Bayern et al., 2007; Wechsler, 1989) and especially nearest neighbour measures are regarded most helpful to describe social preferences (Bashaw et al., 2007) which is confirmed by this study.

Food-sharing and both parameters of object-related interactions did not significantly differ in intensity between nestmates and pair partners, but the former also showed no significant difference in exclusiveness, whereas object-related interactions showed a significant increase in exclusiveness between juvenile and adult birds. Food-sharing was proposed to serve to

establish or reinforce social bonds between individuals even outside a courtship feeding context (Craig, 1987). Establishing strong bonds as the function of food-sharing was also used to explain the significant decrease in the number of food-sharing partners in juvenile jackdaws (von Bayern et al., 2007). This is not supported by our results but can be explained by methodological differences in hand-raising and observational procedure. Results of the present study showed that sharing of food with only a low number of partners occurred in both, in juvenile (mainly with nestmates) and in adult (mainly with the pair partner, see also Wechsler, 1989) birds and would therefore indicate that this behaviour rather serves to maintain, than to establish strong bonds. As a behaviour serving to establish bonds between individuals we would rather suggest object-related interactions, as a form of object play. Juvenile birds approached virtually all potential interaction partners when they were manipulating an object (14.77±0.38 interaction partners on average, the highest score of all analyzed parameters) but the number of interaction partners decreased significantly in adult birds, limiting object-related interactions to only certain other individuals, mainly the pair partner. Also the number of interaction partners in joint manipulation was significantly higher in juvenile than in adult birds. This meets the suggestion that play is a necessary step in the development of strong bonding by representing a low risk interaction (Colvin and Tissier, 1985) and makes object-related interactions a promising candidate to become acquainted with and to establish social relations with conspecifics.

Significantly increasing intensities but no significant differences with regard to exclusiveness of interaction partners from the juvenile to the adult period were found in behavioural parameters sitting close, touching, allopreening, approach food and agonistic support. This pattern indicates that these behaviours already in juvenile birds are quite exclusively directed towards certain other individuals, mainly the nestmates, but gain importance when birds are adult and paired. The significant increase of these five behaviours, reflecting main characteristics of valuable relationships, indicates that they may mainly serve to maintain the pair bond and potentially, also as a social signal to conspecifics about this relationship. We may conclude that pair bonds, as highly valuable relationships, require particular care of maintenance by the pair partners. These behavioural interactions are already manifest in less intensity between fledged juvenile nestmates.
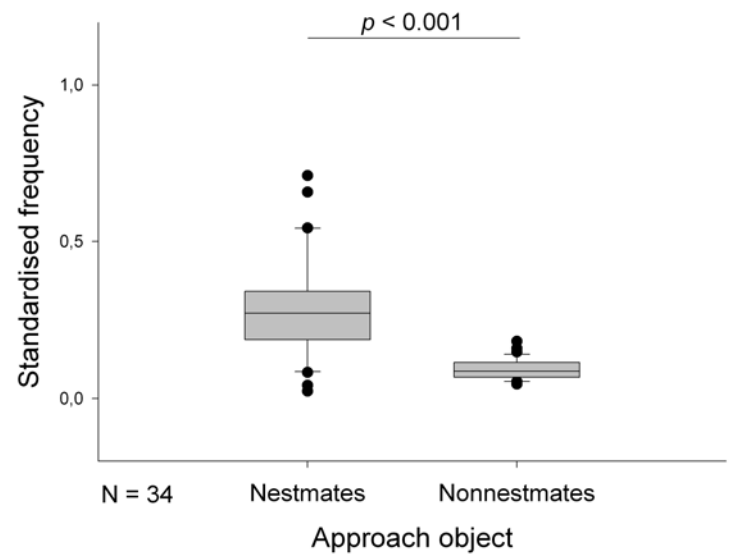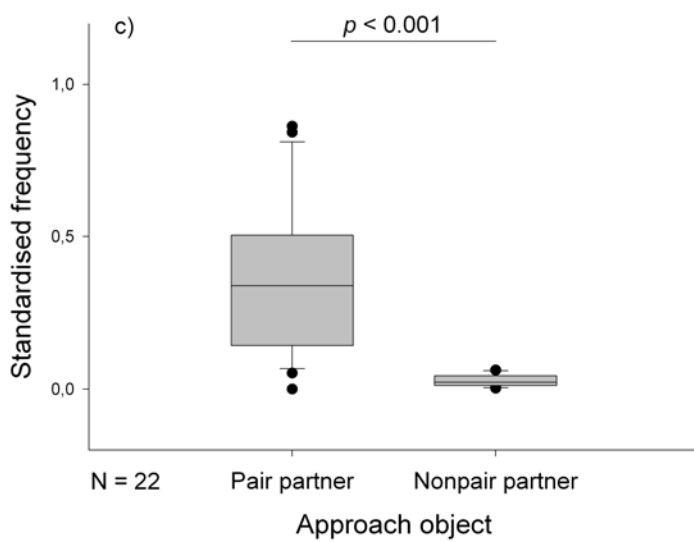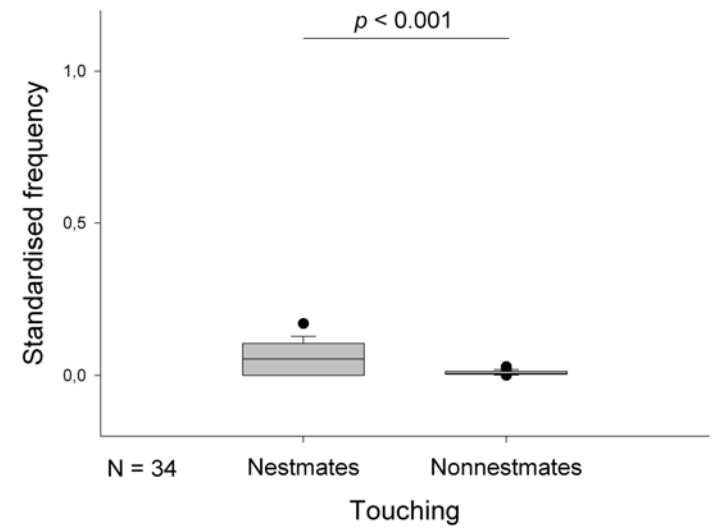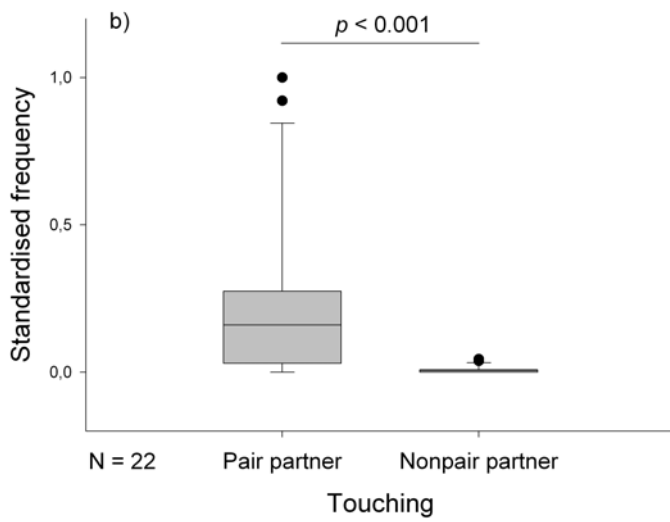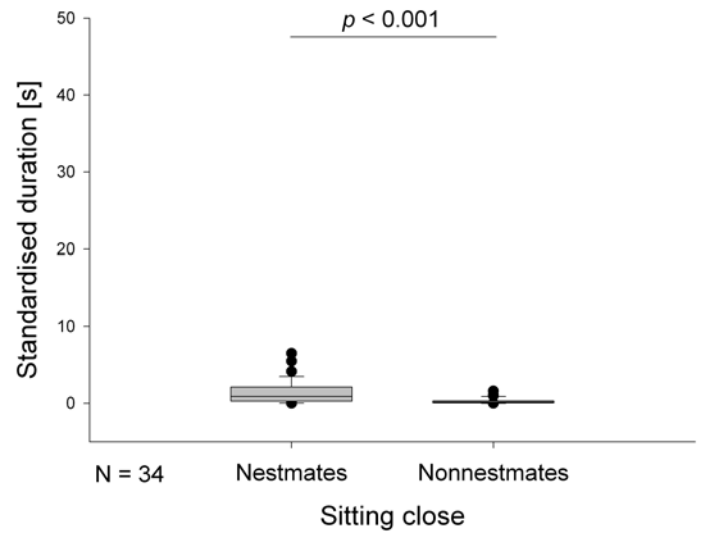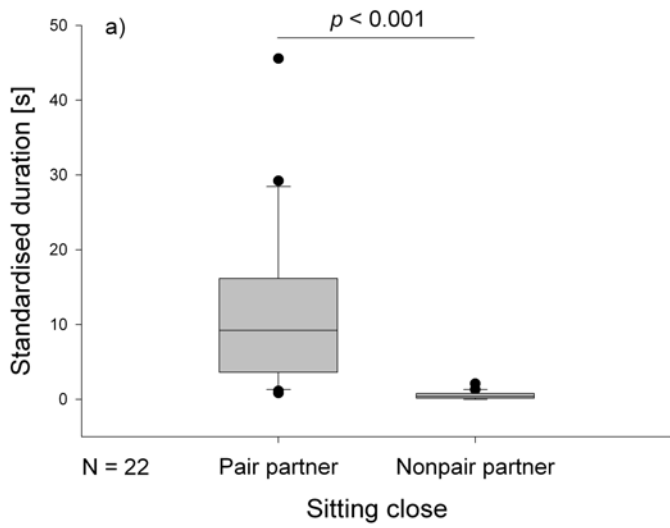
In conclusion, jackdaws engage in valuable relationships as fledged juveniles and in a similar, but more intense way, as adult pair partners. Comparative observations in our free-flying jackdaw group will show whether these birds maintain the same relationships found in hand-raised captives also when living unrestrained and non-hand-raised.

Acknowledgements

Table 1: Data from 36 birds of both years, 2005 and 2006. "Subject" contains abbreviations of subjects` names, "Sex" indicates f for females and m for males, same numbers in "Nest" indicate that birds have been handraised together in one nest, same letter in "Siblings" indicate that birds are genetically related siblings.

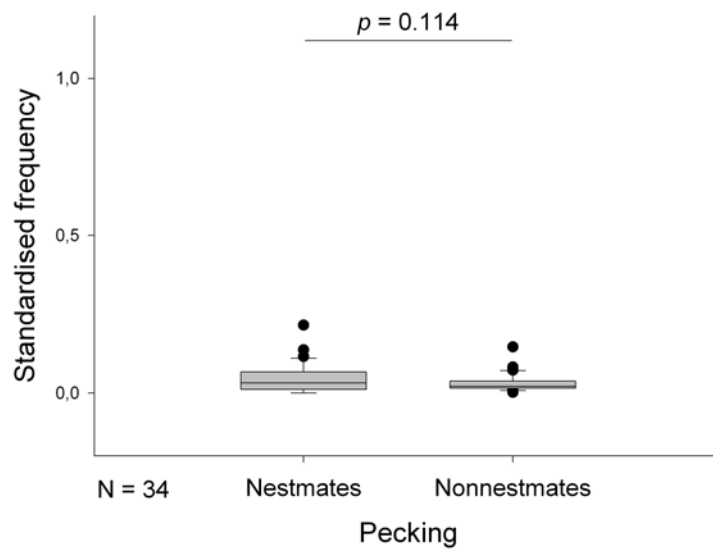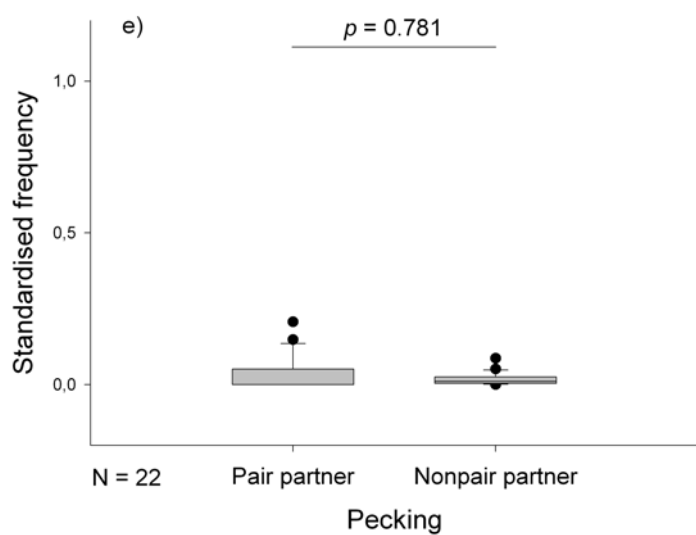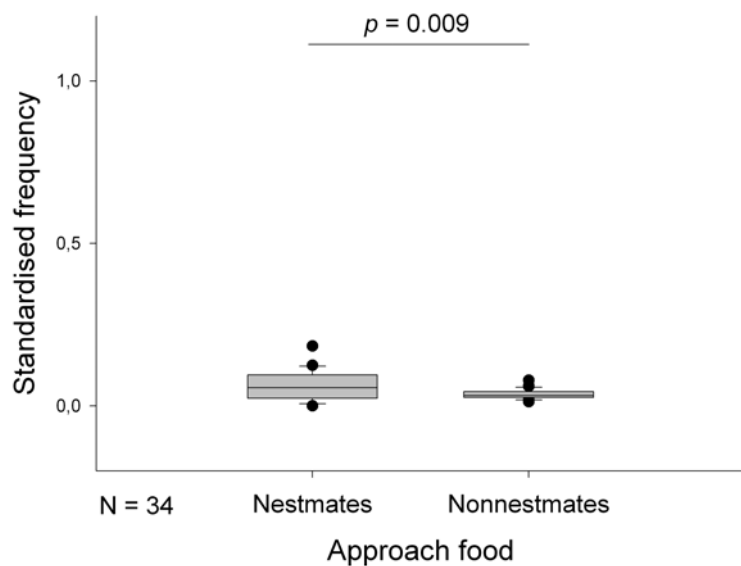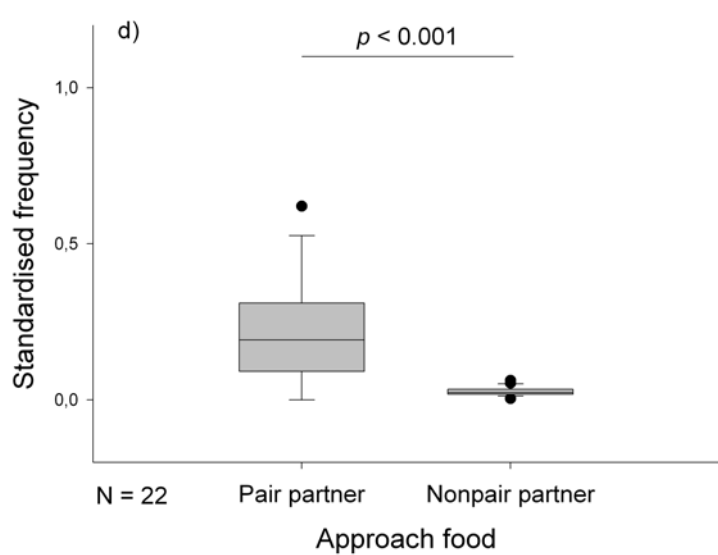| Year	Subject	Sex	Nest	Siblings	Year	Subject	Sex	Nest	Siblings
2005	K	f	1	A	2006	V	m	1	A
	A	f	1	A		T	f	1	A
	F	f	1	A		G	m	1	A
	W	f	1	A		N	m	2	B
	R	m	2	B		O	f	2	B
	S	m	2	B		Y	f	2	B
	C	m	2	B		Q	f	3	C
	B	f	2	B		S	m	3	C
	G	m	3	C		H	f	4	D
	N	m	3	D		M	m	4	E
	X	m	4	E		Z	m	4	F
	U	m	4	F		C	f	5	G
	J	m	4	G		P	m	5	G
	L	f	5	H		K	m	5	H
	O	m	5	H		D	m	6	I
	P	m	5	I		R	f	7	J
	D	m	5	I					
	E	m	6	J					
	M	m	6	J					
	I	m	6	K					

Figure 1. Comparisons of durations [s] or frequencies of analysed behavioural parameters between adult pair partners and non-pair partners (left panels) and between juvenile nestmates and non-nestmates (right panels) in jackdaws. Parameters recorded via focal sampling were corrected for the number of actual conspecifics per condition per individual and the number of observations per individual and given as standardised duration or standardised frequency: a – sitting close; b – touching; c – approach object; d - approach food; e – pecking. Parameters recorded via ad libitum sampling were corrected for their frequency per actual conspecifics per individual: f – agonistic support. For definitions of parameters please see methods. Boxes represent mean durations and frequencies of 22 (f, left panel: 16) adult and 34 (f, right panel: 23) juvenile birds. Boxes indicate median, 25th and 75th percentiles, whiskers indicate 10th and 90th percentiles and dots indicate outliers. *P*-values give the results of Wilcoxon signed-ranks or paired t tests.

Table 2: Statistical analysis of behavioural parameters comparing durations or frequencies of behaviours between a) adult pair partners and non-pair partners and between b) juvenile nestmates and non-nestmates in jackdaws. Cat. indicates category of social interactions to which parameters were assigned. A: physical distance, B: sociopositive physical contact, C: object-related interactions, D: food-related interactions, E: agonistic interactions, F: agonistic support. Columns state applied statistical tests, test statistics and *p*-values. Bold *p*-values indicate significant differences.

	Comparison	a) **Pair – non-pair partners adult period (22 birds)**				b) **Nestmates – non-nestmates juvenile period (34 birds)**			
Cat.	Parameter	Test	*N*, d*f*	*T, Z*	*p*	Test	*N*, d*f*	*T, Z*	*p*
A	Nearest neighbour	Paired t	21	7.714	**< 0.001**	Paired t	33	5.512	**< 0.001**
A	Sitting close	Wilcoxon	22	-4.042	**< 0.001**	Wilcoxon	34	-4.026	**< 0.001**
B	Touching	Wilcoxon	21	-3.597	**< 0.001**	Wilcoxon	33	-4.208	**< 0.001**
B	Allopreening	Wilcoxon	17	-3.29	**= 0.001**	Wilcoxon	27	-3.027	**= 0.002**
C	Approach object	Paired t	21	5.986	**< 0.001**	Wilcoxon	34	-4.864	**< 0.001**
C	Joint manipulation	Wilcoxon	16	-3.363	**= 0.001**	Wilcoxon	33	-5.012	**< 0.001**
D	Approach food	Paired t	21	5.037	**< 0.001**	Wilcoxon	34	-2.607	**= 0.009**
D	Food-sharing	Wilcoxon	20	-3.81	**< 0.001**	Wilcoxon	13	-2.763	**= 0.006**
E	Severe aggression	Wilcoxon	12	-0.471	= 0.638	Wilcoxon	21	-1.825	= 0.068
E	Pecking	Wilcoxon	21	-0.278	= 0.781	Wilcoxon	33	-1.581	= 0.114
F	Agonistic support	Wilcoxon	15	-3.412	**= 0.001**	Wilcoxon	21	-3.043	**= 0.002**

Table 3: Statistical analysis of behavioural parameters comparing a) durations or frequencies of behaviours between adult pair partners and juvenile nestmates and comparing b) number of interaction partners between adult and juvenile birds in jackdaws. Cat. indicates category of social interactions to which parameters were assigned. A: physical distance, B: sociopositive physical contact, C: object-related interactions, D: food-related interactions, E: agonistic interactions, F: agonistic support. Columns state applied statistical tests, test statistics and *p*-values. Bold *p*-values indicate significant differences.

| | **Comparison** | **a) Pair partner – nestmates** | | | | **b) Number of interaction partners** | | | |
| | | **adult – juvenile period (21 birds)** | | | | **adult – juvenile period (22 birds)** | | | |
Cat.	Parameter	Test	*N*, d*f*	*T, Z*	*p*	Test	*N*, d*f*	*T, Z*	*p*
A	Nearest neighbour	Paired t	20	6.923	**< 0.001**	Paired t	21	3.425	**= 0.003**
A	Sitting close	Wilcoxon	21	-4.015	**< 0.001**	Wilcoxon	20	-0.598	= 0.55
B	Touching	Wilcoxon	21	-2.798	**= 0.005**	Paired t	21	1.998	= 0.059
B	Allopreening	Wilcoxon	16	-2.999	**= 0.003**	Wilcoxon	18	-0.96	= 0.337
C	Approach object	Paired t	20	0.891	= 0.384	Paired t	21	8.319	**< 0.001**
C	Joint manipulation	Paired t	20	0.101	= 0.921	Wilcoxon	21	-4.02	**< 0.001**
D	Approach food	Wilcoxon	21	-3.632	**< 0.001**	Paired t	21	1.953	= 0.064
D	Food-sharing	Wilcoxon	7	-0.254	= 0.799	Wilcoxon	5	-0.137	= 0.891
E	Severe aggression	Wilcoxon	9	-0.059	= 0.953	Wilcoxon	16	-1.087	= 0.277
E	Pecking	Wilcoxon	18	-1.067	= 0.286	Paired t	21	4.819	**< 0.001**
F	Agonistic support	Wilcoxon	18	-3.293	**= 0.001**	Wilcoxon	18	-1.592	= 0.111

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Enhanced social learning between siblings in common ravens,

Corvus corax

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Enhanced social learning between siblings in common ravens, *Corvus corax*

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It has been suggested that social dynamics affect social learning but empirical support for this idea is scarce. Here we show that affiliate relationships among kin indeed enhance the performance of common ravens, *Corvus corax*, in a social learning task. Via daily behavioural protocols we first monitored social dynamics in our group of captive young ravens. Siblings spent significantly more time in close proximity to each other than did nonsiblings. We subsequently tested birds on a stimulus enhancement task in model–observer dyads composed of both siblings and nonsiblings. During demonstration the observer could watch the model manipulating one particular object (target object) in an adjacent room. After removing the model, the observer was confronted with five different objects including the former target object. Observers from sibling dyads handled the target object for significantly longer periods of time as compared with the other four available objects, whereas observers from nonsibling dyads did not show a preference for the target object. Also, siblings matched the model's decision to cache or not to cache objects significantly more often than did nonsiblings. Hence, siblings were likely to attend to both, the behaviour of the model (caching or noncaching) and object-specific details. Our results support the hypothesis that affiliate relations between individuals affect the transmission of information and may lead to directed social learning even when spatial proximity has been experimentally controlled for.

Social learning, i.e. learning that is influenced by observation of, or interaction with, other individuals or their products (Galef 1988; Heyes 1994), has been found in a variety of animals including common ravens, *Corvus corax* (Fritz & Kotrschal 1999). Social dynamics, the distribution of social interactions within a group, could be critical for the pattern and type of social learning and for the spread of new behaviours in a group (Coussi-Korbel & Fragaszy 1995; Fritz & Kotrschal 2002).

Social dynamics may be characterized by social spacing and behavioural coordination in space and time (Coussi-Korbel & Fragaszy 1995). Social spacing has been defined as the 'differences in the frequency and degree of spatial

proximity sought and tolerated between individuals' (Coussi-Korbel & Fragaszy 1995, p. 1446) and behavioural coordination in space and time involves that 'an individual approaches the same site as another and engages in a similar activity simultaneously with the other at that site' (Coussi-Korbel & Fragaszy 1995, p. 1443). Therefore, the quality of social learning may vary between dyads depending on their social relations, whereby social dynamics may affect the salience of individuals for each other and the likelihood of preferential (Hatch & Lefebvre 1997) or directed social learning (Coussi-Korbel & Fragaszy 1995). For preferential or directed social learning to occur it is necessary that animals live in socially structured groups (e.g. kin and nonkin, familiar and unfamiliar) to provide individuals with opportunities to choose from alternative sources of information (Hatch & Lefebvre 1997). Furthermore, preferential or directed social learning indicates that particular models will be more influential for certain individuals than others (Coussi-Korbel & Fragaszy 1995; Laland 2004).

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In the present study we aimed to investigate preferential or directed social learning based on affiliate relations in juvenile common ravens. A number of variables have been shown to direct social learning, such as dominance (Nicol & Pope 1994, 1999), sex (Mason & Reidinger 1981; Benskin et al. 2002; Katz & Lachlan 2003), age (Galef & Whiskin 2004), kinship (Hatch & Lefebvre 1997), familiarity (Lachlan et al. 1998; Swaney et al. 2001; Benskin et al. 2002) and pair bonding (Wechsler 1988). Still, studies on the effects of affiliation (Russon & Galdikas 1995; Bonnie & de Waal 2006) on social learning are rare.

Ravens are well capable of learning socially from both, attached conspecifics (Fritz & Kotrschal 1999) and heterospecifics (M. Loretto, T. Bugnyar, K. Kotrschal, unpublished data). After becoming independent from their parents at about 100 days after hatching, they spend their first years in a nonbreeder-group until they form long-term monogamous pairs and establish territories at 3–4 years of age (Haffer & Bauer 1993). Such groups of juvenile nonbreeders provide the opportunity for developing diverse social relations with conspecifics. They are essentially fission–fusion societies with individuals assembling at overnight roosts and splitting into variable groups during daytime foraging (Heinrich et al. 1994; Ratcliffe 1997). Ravens of these groups recruit conspecifics via food calls to rich food sources (Heinrich 1988; Bugnyar et al. 2001), mainly to overcome defence by territorial pairs (Heinrich 1988; Marzluff & Heinrich 1991).

If those nonbreeder-groups would be just aggregations at carcasses or overnight roosts one could expect that the social relations are qualitatively similar between all individuals. But if the members of these groups would show some social ties (Heinrich 1988; Huber 1991; Parker et al. 1994) or even form socialized subgroups (Huber 1991) it could be expected that the social relations show different qualities between certain individuals. There would be the opportunity for individuals to develop different social relations, if they consistently interact with certain other individuals, and to use different sources of information provided by other individuals. Hence, the social ontogeny of ravens suggests that testing for preferential learning should be most promising during this nonbreeder period when individuals need to acquire information about the world.

Affiliate social relations can be characterized on a number of levels (Bonnie & de Waal 2006), such as high levels of sociopositive and low levels of agonistic behaviours. Thereby, sociopositive behaviours are measured as social support, food sharing or allopreening and agonistic behaviours as approach–retreat interactions or fights. Because of our short focal period (four months) in this study we concentrated on spatial proximity as an integrative measure (Bonnie & de Waal 2006) for determining social dynamics between individuals. Close social spacing and behavioural coordination in space and time do not only need social tolerance between individuals but also include actively seeking spatial proximity of others and can therefore, be regarded as basic measures of affiliation. We first examined the social dynamics within our group of hand-raised ravens via behavioural observations. We then experimentally tested for the influence of social dynamics on social learning performance in a stimulus enhancement task. Following Zentall's (1996, p. 229) definition 'the term stimulus enhancement is used when the activity of the demonstrator draws the attention of the observer to a particular *object*' and it is considered to involve relatively low cognitive capacities (Galef 1988). Unlike previous experiments on ravens (Fritz & Kotrschal 1999) model–observer dyads were tested in physical separation to control for effects of spatial proximity on social learning. Following the ravens' life history in nonbreeder-groups we expected that the social dynamics would not be randomly distributed in our group of juvenile hand-raised ravens. We predicted enhanced social learning performance when individuals in a model–observer dyad maintain affiliate relationships as compared with socially more distant dyads.

METHODS

Subjects and Keeping

Subjects were 12 juvenile common ravens, *C. corax*, that had been hand-raised in four sibling groups from 12 to 40 days after hatching to fledging at the Konrad-Lorenz-Research Station in Gruenau, Austria, in spring 2004. At the beginning of this study, birds were in their second month postfledging (fourth month of age). Seven birds (three males, four females) were zoo-bred (München, Wuppertal) and five birds (four males, one female) were taken out of wild nests with permission. At the time of the study birds were housed together in one social group in an aviary in the Cumberland game park in Gruenau, Austria, together with two adult male birds. They will remain in captivity until the end of their natural life span. The aviary consisted of three outdoor compartments (80, 80 and 35 m², maximum height of 7 m) and of experimental compartments, consisting of a central room (16 m²), two lateral chambers (left and right, each 6 m²) and two pathways (left and right, each 4 m²) which could all be divided by wire-mesh doors. Except of the experimental compartments the aviary was equipped with natural vegetation, wooden perches and rocks. In addition birds were provided with leafs, twigs and plastic toys for behavioural enrichment. Birds had ad libitum access to water and were fed three times a day with various kinds of meat, milk products, vegetables and fruits. They were marked with coloured rings for individual identification.

Behavioural Observations

We carried out behavioural observations twice a day, morning and afternoon, for 30 min. Observations consisted of 5-min focals and were counterbalanced for order of observations for each individual. We recorded all social interactions between the focal individual and any other conspecific. The observation period lasted from fledging of the birds, beginning of May 2004 to the end of the experimental trials, end of August 2004, resulting in an average number of focal observations of 65.6 ± 3.9 (range: 58–71) and an average total observation time of

327.9 ± 19.5 min (range: 290−350 min) per individual. Because of the short observation period we determined affiliation through social spacing and behavioural coordination in space and time. To determine social spacing, we used two variables, the duration of sitting close, that is within 20 cm, to each other, and the nearest neighbour of each focal individual at the beginning of every observation. To determine behavioural coordination in space and time we measured the frequency of approaches to a conspecific which was manipulating an object (inedible item like a stone, leaf, twig, or plastic toy) and the frequency of two or more birds handling such an object together.

For analysis we first summed up durations for sitting close, frequencies for nearest neighbour, approaches and handling together bouts with its siblings and nonsiblings for each individual separately. To obtain these sums we only used individual values which were recorded when the individual has been the focal individual during observation to avoid pseudoreplication. Second, we divided these sums through the number of actual siblings and nonsiblings and corrected for the number of observations for each individual to obtain one average data point per individual per condition. Differences within paired values were normally distributed. We therefore used t tests for paired samples to compare relations between siblings and nonsiblings. Test results are given two tailed and considered significant when $P < 0.05$.

Composition of Experimental Model−Observer Dyads

Because kinship and affiliation covaried in our group of hand-raised ravens, we opted for testing sibling dyads versus nonsibling dyads. For composing the latter, we chose birds that showed low levels of affiliation (i.e. proximity and behavioural coordination scores). As the number of siblings per bird varied between one and three, we assembled 13 possible sibling dyads and we controlled for the same number of trials in the sibling and in the nonsibling condition for each observer bird. Furthermore, we controlled for sex and composed dyads with the same number of pairs with same (five pairs) and different (eight pairs) sex in the sibling and in the nonsibling condition. Finally, we calculated average values of observer birds for the sibling and the nonsibling condition, so that each bird provided only one data point to the sample.

Experimental Procedure

Experimental trials

Dyads were tested in physical and visual separation from the rest of the group in the experimental compartments. Experimental dyads were physically separated from each other by a wire-mesh partition, but remained in visual contact. Note that this physical separation prohibited siblings to be in closer proximity than nonsiblings. Experimental trials consisted of a demonstration phase and a test phase for the observer. Each pair was tested twice with model and observer roles reversed and with the use of different sets of objects.

Demonstration phase

During the demonstration phase, the model was in the central experimental room and the observing bird was able to watch the model through the wire-mesh door either from the left or the right pathway. After the birds had been put in their respective compartments the experimenter (C. Schwab) placed one single object (the target object for this particular trial) in the middle of the central experimental room and left the room. The model was allowed to handle this single object. There was no time restriction to the demonstration phase, but if the model had not touched the target object for more than 20 s the bird was removed from the experimental compartment. We used a total of 20 different objects (four sets of five objects each, see Fig. 1) which we obtained from Kinder-Überraschungseier®. Objects were approximately 4 cm in diameter and chosen for balanced item dissimilarity and categorical similarity. By using inedible objects we wanted to avoid any influence on the performance of the birds through food. Furthermore, young ravens are known to extensively manipulate various small objects and even show play-caching of objects (Drack & Kotrschal 1995; Kabicher 1996; Heinrich & Smolker 1998), indicating that they are highly interested also in nonfood items. To identify the target object in the test phase the observers had to watch the model bird carefully because objects were chosen for limited dissimilarity. Each set was used a similar number of times. In case the model handled the target object less than 5 s the trial was terminated and started once again on another day.

Test phase

After removing the model bird the experimenter (C. Schwab) temporarily blocked the view of the observer with her body during removal of the target object. Then she arranged all five objects of a certain set, including the target object, on the floor of the experimental room. Objects were placed 30 cm apart, all at the same distance from the separating door between central experimental room and pathway where the target object had been placed in the demonstration phase. Then the experimenter touched all objects again in reverse order to avoid enhancement effects by the human. Finally, the observing bird was allowed into the central experimental room. Locations of the target objects were equally balanced throughout trials to avoid the development of site preferences by the birds.

As in the demonstration phase there was no time restriction for observers to manipulate objects. Trials were terminated 3 min after the last touch of any object by the bird. If a bird did not handle any object, the trial was finished after 5 min. The order of conditions was semirandomized, interspersing sibling and nonsibling trials, depending on the willingness of the birds to participate. Intertrial intervals were 4−20 days for a given dyad.

Figure 1. Objects. We used four sets (columns) of five objects (4 cm in size) each.

Analysis

Measured parameters were time (s) observers spent next to the wire-mesh partition in the demonstration phase, models' handling time (s) during demonstration, observers' handling time (s) for different objects in the test and frequency of caching behaviour (sticking an object into the ground substrate and/or digging a pit with the beak for this purpose, and covering the object with substrate) of the model and the observer. To take into account differences in lengths of demonstration and test phases, we calculated time spent observing the model as percentage of the models' actual handling time and handling times of objects by observers as percentage of the total handling time of the test phase. Handling time for all objects was set 100% and percentages of handling time for the target object and average objects were calculated accordingly. Parameters were compared between the sibling and the nonsibling condition. To obtain average values for those objects that had not been presented and handled by the models in the demonstration phase (average object), we calculated the observers' handling time for all objects minus the handling time for the target object and divided this result by four. With regard to caching behaviour, the observer bird received a score of 1 if its decision to cache or not to cache matched the model's behaviour and a score of 0 if it did not. Individual scores were summed over experimental trials

and compared between the sibling and the nonsibling condition.

To test for influences of the two individuals within a tested dyad on each other's behaviour we calculated an intraclass correlation for tested dyads. Neither in the sibling (single measure intraclass correlation: $r = -0.065$, $F = 0.878$, $df = (11,12)$, $P = 0.582$) nor in the nonsibling condition (single measure intraclass correlation: $r = -0.039$, $F = 0.925$, $df = (11,12)$, $P = 0.548$) was there a significant correlation within dyads with regard to percentage of time observers handled the target object. After finishing its sibling tests, one of the males had to be separated from the group for medical treatment. Therefore, only 11 birds were considered in the analysis of the experimental tests. Trials were videotaped (Sony DCR-TRV14E, Digital Video Camera Recorder). Because data were not normally distributed we used Friedman test and Wilcoxon signed-ranks tests. Because of the small sample size all Wilcoxon signed-ranks tests were calculated by hand according to Siegel & Castellan (1988). Results of tests are given two tailed and considered significant when $P < 0.05$.

Control trials

In another series of experiments we controlled for object preferences. These control trials were conducted 5

months after finishing the experimental trials. This time delay was chosen to avoid the development of preferences for certain objects before the experimental trials and to reduce the probability that the birds remembered their object choices from the experimental trials. Control trials were carried out identical to experimental trials, but the demonstration phase was omitted and every bird was tested alone. So every bird was tested for the same number of trials, with the same sets of objects and with the target objects placed at the same locations as in the experimental trials. Unfortunately, two males died because of predation from a marten in the time period between experimental and control trials. So only nine birds participated in the control trials. As with the experimental trials, all control trials were conducted by C. Schwab. We analysed percentage of observers' handling time as in experimental trials. Furthermore, we compared overall handling times and percentage of time birds were handling the target object in the sibling and the nonsibling condition between experimental and control trials. Because data were not normally distributed we used Wilcoxon signed-ranks tests. Because of the small sample size they were calculated by hand according to Siegel & Castellan (1988). Results of tests are given two tailed and considered significant when $P < 0.05$.

RESULTS

Behavioural Observations

The nearest neighbour of the focal individual at the beginning of an observation was significantly more often a sibling than it was a nonsibling (paired t test: $t_{12} = 7.552$, $P < 0.001$) and siblings sat significantly longer close to each other than did nonsiblings (paired t test: $t_{12} = 2.899$, $P = 0.014$, Fig. 2a, b). Furthermore, siblings showed significantly higher levels of behavioural coordination in space and time than did nonsiblings when objects (such as stones, leaves, twigs, or plastic toys) were involved in the interactions (Fig. 2c, d). Ravens handled objects significantly more often together with a sibling than with a nonsibling (paired t test: $t_{12} = 4.583$, $P = 0.001$) and also approached another sibling that was handling an object more often than a nonsibling (paired t test: $t_{12} = 6.031$, $P < 0.001$).

Experimental and Control Trials

After experiencing a sibling handling a certain object in the demonstration phase of an experimental trial, ravens manipulated this particular target object significantly
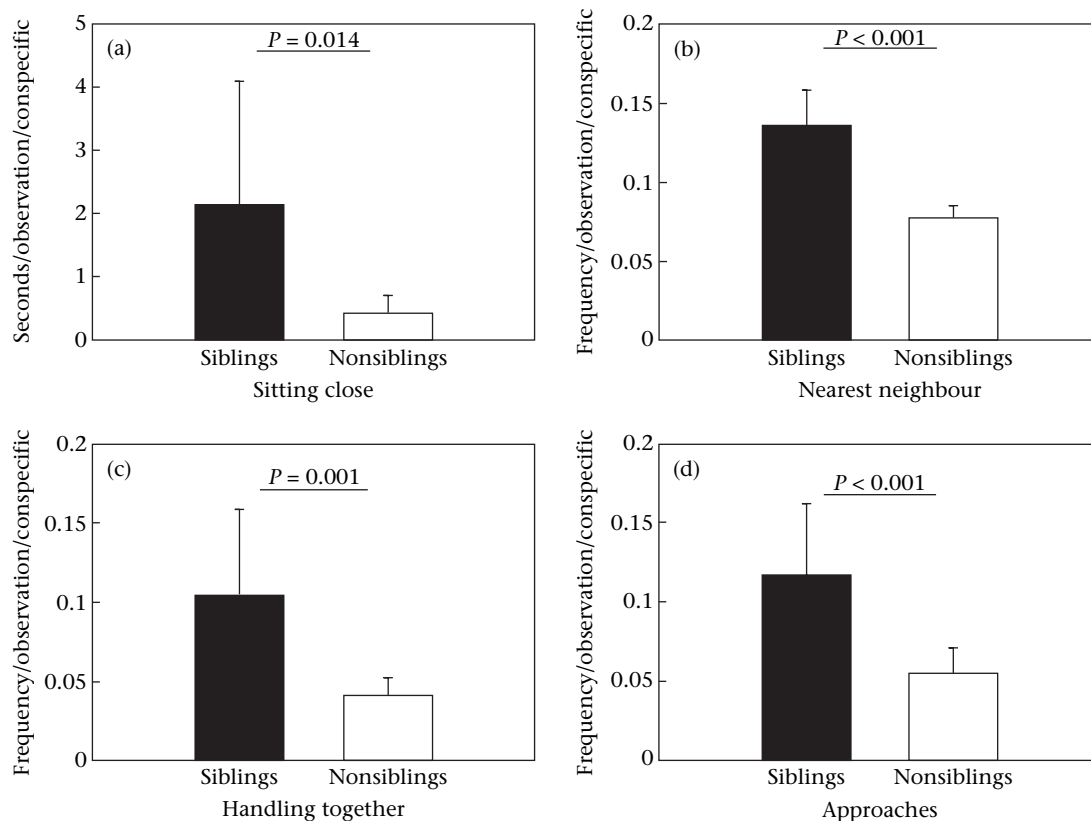

Figure 2. Behavioural observations of social interactions of birds in their social group. (a) Duration (s) birds sit close to each other, (b) frequency of being the nearest neighbour at the beginning of each observation, (c) frequency of birds handling an object together and (d) frequency of one bird approaching another bird which is manipulating an object. All graphs are corrected for the number of siblings and nonsiblings and for the number of observations for each individual. Bars represent mean durations and frequencies of 12 birds plus standard deviation. P values were derived from t tests for paired samples.

longer than any other average object in the subsequent test phase (Wilcoxon signed-ranks test: $T^+ = 56$, $N = 11$, $P = 0.042$, two tailed). Such a preference for the target object could not be found when the model was a nonsibling (Wilcoxon signed-ranks test: $T^+ = 34$, $N = 11$, $P = 0.9658$, two tailed, Fig. 3a). In control trials without a model, no differences were found in handling time of the target object relative to the other four objects, neither in the sibling condition ($T^+ = 12$, $N = 9$, $P > 0.5$, two tailed) nor in the nonsibling condition ($T^+ = 19.5$, $N = 9$, $P > 0.5$, two tailed, Fig. 3b). Directly comparing handling times of the target object between sibling and nonsibling conditions revealed no significant results (experimental trials: $T^+ = 51$, $N = 11$, $P = 0.123$; control trials: $T^+ = 18$, $N = 8$, $P > 0.5273$, two tailed). However, comparison between experimental and control trials showed a significant effect of overall handling time ($T^+ = 44$, $N = 9$,

$P = 0.0078$, two tailed) and a tendency for a longer relative handling time of the target object ($T^+ = 37$, $N = 9$, $P = 0.0976$, two tailed) in the sibling condition, but not in the nonsibling condition (overall handling time: $T^+ = 29$, $N = 9$, $P = 0.1484$; % handling time of target object: $T^+ = 27$, $N = 9$, $P = 0.6524$, two tailed, Fig. 3a, b).

Moreover, the pattern how observers acted towards objects in the test was affected by the previous behaviour of sibling and nonsibling models. Observers engaged in playful caching of objects only if the sibling models had cached the target object before in the demonstration phase. If sibling models did *not* cache the object in the demonstration phase, none of the observers cached any object afterwards (Fig. 4). The opposite was found for the nonsibling condition. Observers in the experimental trials cached mainly when the nonsibling model had *not* cached its target object in the demonstration phase beforehand (Fig. 4). When calculating a score of behavioural matching (see Methods), we found that the caching behaviour of models and observers was significantly more similar in the sibling than in the nonsibling condition (Wilcoxon signed-ranks test: $T^+ = 21$, $N = 6$, $P = 0.0312$, two tailed).

Neither sibling observers (Friedman test: $N = 11$, $\chi^2 = 7.083$, $df = 4$, $P = 0.132$) nor nonsibling observers ($N = 11$, $\chi^2 = 4.442$, $df = 4$, $P = 0.349$) showed any preferences concerning the locations of the five objects in the trials. Also, there was no significant difference between the sibling and the nonsibling observers in overall handling time of all objects (Wilcoxon signed-ranks test: $T^+ = 35$, $N = 11$, $P = 0.8984$, two tailed). Yet there was a tendency of the model handling the target object longer in the sibling than in the nonsibling condition of experimental trials (Wilcoxon signed-ranks test: $T^+ = 52$, $N = 11$, $P = 0.1016$, two tailed). Still, sibling and nonsibling observers did not differ in the percentage of time spent next to the separating wire-mesh door while the model was handling the target object
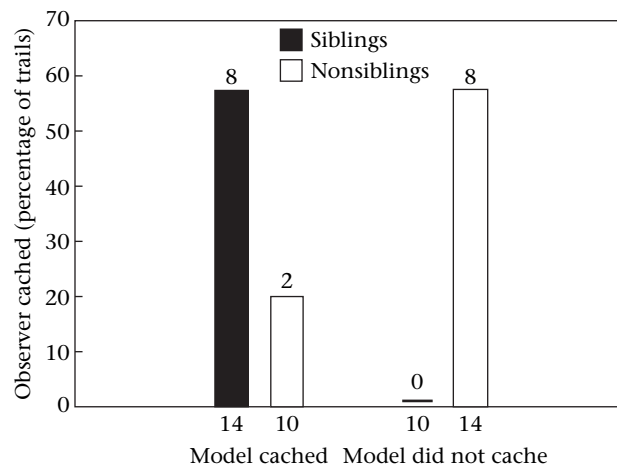

Figure 3. Percentage of time birds were handling the target object and an average of the other four available objects, both, in the sibling and in the nonsibling condition in test trials (a) and control trials (b). Black bars indicate birds' handling time of the target object while open bars indicate the average handling time of the other four available objects. *P* values were derived from Wilcoxon signed-ranks tests calculated by hand. (a) Bars represent mean percentage of handling times of 11 observers plus error bars. (b) Bars represent mean percentage of handling times of nine birds plus error bars.

Figure 4. Caching behaviour of models and observers. Bars indicate the percentage of trials in which observers cached any object. Numbers below (models) and above (observers) bars represent the number of trials in which caching behaviour of models and observers occurred. Caching behaviour of the models (14 and 10 caching trials and 10 and 14 noncaching trials) was set 100%.

(Wilcoxon signed-ranks test: $T^+ = 30$, $N = 11$, $P > 0.5171$, two tailed).

DISCUSSION

Our study confirms that young ravens are capable of learning socially from same aged peers (Fritz & Kotrschal 1999). Social learning, however, was clearly influenced by the social relationships between the birds. Behavioural observations showed that siblings maintained higher levels of social spacing and higher levels of behavioural coordination in manipulating standard aviary equipment than did nonsiblings. In the experiment, observers handled the target object significantly longer than any of the other four available objects when the model was a sibling and matched their decision to cache or not to cache objects with their siblings but not with nonsiblings. Finally, in the sibling but not in the nonsibling condition, the overall handling time of objects by the observers was significantly longer in experimental trials compared with control trials without a model.

Only a limited number of studies have dealt with the influence of affiliate relations on social learning performance (Laland 2004). In contrast to our findings, Wechsler (1988) reports no difference in socially learning a new food producing technique in paired jackdaws, *Corvus monedula*, in comparison with unpaired ones, even though paired jackdaws, like our ravens, showed close social spacing. Hatch & Levebvre (1997) found that within a flock of ringdoves, *Streptopelia risoria*, juveniles learned as readily from their fathers as they did from unrelated adults in foraging tasks. The authors link their results with the ecological context of scramble competition. Thus, our study is one of the first to provide supporting results to Coussi-Korbel's & Fragaszy's (1995) suggestion that the social dynamics within a group could be the crucial factor in social learning between individuals.

As predicted, in our group of hand-raised ravens affiliation was not evenly distributed among dyads but showed an asymmetry between dyads. Juveniles maintained affiliate relations mainly with their siblings, indicating that kinship and affiliate relations covary during the first half year of life. Behavioural observations on this raven group over the course of 1 year (M. Loretto, T. Bugnyar, K. Kotrschal, unpublished data) and preliminary data from wild ravens (W. I. Boarman, personal communication) are in support of these findings. Being close to siblings could provide birds with opportunities to learn, and to scrounge, from them more often than from nonrelated/nonaffiliated individuals. Spatial proximity itself could thus be confound for directed social learning. However, this possibility did not apply in our experiment since both siblings and nonsiblings were prevented from physical contact by a wire-mesh partition. The weak tendency of the model's longer handling time of the target object in the sibling condition might indicate that sibling models could have provided more information about the target object than did nonsibling models. In addition, sibling observers might have valued the provided information differently than nonsibling observers.

This interpretation would be in accordance with the idea that 'an intrinsic motivation to copy others' is 'guided by social bonds rather than material rewards such as food' (Whiten et al. 2005, p. 739) and may result in behavioural conformity among subsets of individuals.

Interestingly, nonsiblings did not simply show no behavioural coordination, as could be expected, but tended to show complementary coordination (Coussi-Korbel & Fragaszy 1995) in caching behaviour as compared with siblings. Obvious examples of complementary coordination are producer—scrounger phenomena where the scrounger shows different behavioural patterns to exploit the activities of the producer (Coussi-Korbel & Fragaszy 1995). Complementary coordination is often connected with dominance structures and competitive relationships and could involve an inhibition of transmission of a particular behaviour pattern as has been shown by Giraldeau & Lefebvre (1987).

Generally, the nonfood context of our study could have increased the importance of social relations on social learning performance because food might be considered as a powerful stimulus, attracting the attention of others, regardless of the relationship between the animals. Avoiding the food context could help to reveal the influence of social relations on social learning. The objects used in our experiment were chosen to look very much alike so the birds would have to watch carefully to be able to differentiate between them. Possibly, observer birds in the nonsibling condition could have been just paying attention to the model bird and its behaviour but not to the specific details of the presented objects, as has been found in pinyon jays showing good social learning abilities in a motor task but worse in a discrimination task (Templeton et al. 1999). Hence, different levels of affiliate relations could lead to different intensities of paying attention, which in turn may affect the degree/likelihood of using information provided by the model.

In respect to the observed differences in overall handling time between test and control trials in the sibling condition, two mutually not exclusive interpretations are possible. First, there could have been a general social facilitation effect on the observers by seeing the sibling models handling an object in the experimental trials. Second, it could have been an effect of age with the ravens being 5 months older and thus potentially less manipulative in control trials compared with experimental trials.

Taken together our results support the hypothesis that social dynamics influence social learning performance in ravens. Siblings maintaining high levels of affiliate relations showed better and also more specific information transfer between each other than did nonsiblings who hardly showed any sociopositive interactions. This might not only be because of close spatial proximity between siblings but also to more directed attention towards them and a higher motivation to copy their behaviours. The choice of models may thus be critical for studying the social transmission of information in corvids and generates testable predictions for the spread of behavioural traditions.

Acknowledgments

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Preferential learning from non-affiliated individuals in jackdaws, *Corvus monedula*

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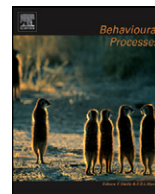
Preferential learning from non-affiliated individuals in jackdaws (*Corvus monedula*)

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ABSTRACT

It has been suggested that affiliated social relations may facilitate information transfer between individuals. We here tested this rarely examined hypothesis with juvenile and adult jackdaws (*Corvus monedula*) in three stimulus enhancement tasks, both in a non-food context (experiment 1) and in a food context (experiments 2 and 3). We first show that siblings and pair partners maintain stronger bonded social relations than do non-siblings and non-pair partners. We therefore tested individuals in sibling and non-sibling dyads and, later in ontogeny, in pair and non-pair dyads. Jackdaws either did not learn from any other conspecific (experiment 1), or they learned from non-affiliated individuals (non-siblings, non-pair partners in experiments 2 and 3). This may be related to two main characteristics of jackdaws' affiliated relationships. First, affiliates share food at a high rate and may rely on their knowledgeable partners to secure food rather than learning from them. Second, affiliates spend most time in close spatial proximity to each other which increases the probability that they simultaneously experience occurrences in their environment. Hence, spatially more distant individuals, which are more likely to be non-affiliated, face different foraging situations and may therefore provide more relevant information which may lead to selective social learning.

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Paying attention to conspecifics and monitoring their behaviours and skills may depend on the conspecific B's value and function for a certain individual A (Kummer, 1978). This value may be expressed as certain qualities of B such as sex, age or skills, its tendencies towards A such as fighting against, or caring for, A and its availability for A, influenced by physical distance and presence of third parties (Kummer, 1978). Differences in paying attention to, and monitoring of, others will affect social learning strategies, as well as performance in social learning. Individuals may either copy the majority, successful or older individuals, good social learners, kin or friends (Laland, 2004). Moreover, public information, cues that are provided inadvertently by efficiently performing individuals that share similar environmental requirements (Danchin et al., 2004), potentially affects the decision of observers about when, where, what and how to forage (Galef and Giraldeau, 2001; Templeton and Giraldeau, 1995).

Strategies from whom to learn are based on social dynamics within a group which are best characterized through differences in the frequency and degree of spatial proximity that is sought and tolerated between individuals (Coussi-Korbel and Fragaszy, 1995). The less evenly social dynamics are distributed within a group, the more likely directed social learning (Coussi-Korbel and Fragaszy, 1995) or preferential learning (Hatch and Lefebvre, 1997) will occur, meaning that particular individuals are more influential models for certain individuals than are others (Coussi-Korbel and Fragaszy, 1995). Close spatial proximity may enhance the probability of social learning (Coussi-Korbel and Fragaszy, 1995; Wechsler, 1988a). Among other behaviours the time individuals spend in close spatial proximity to each other is regarded as an important parameter characterizing social bonding and affiliate relations (Bonnie and de Waal, 2006; de Kort et al., 2003; van Schaik and Aureli, 2000; Wechsler, 1988a). Using spatial proximity between individuals in non-experimental situations as an indicator for affiliate relations, we tested the hypothesis that affiliated individuals learn more readily from each other than non-affiliated individuals.

A number of variables have been shown to affect social learning. Learning performance was enhanced when the model was dominant to the observer (Nicol and Pope, 1994, 1999), of different sexes (Benskin et al., 2002; Katz and Lachlan, 2003; Mason and

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Reidinger, 1981), older (Choleris et al., 1997; Galef and Whiskin, 2004), kin (Hatch and Lefebvre, 1997; Valsecchi et al., 1996) or familiar (Benskin et al., 2002; Lachlan et al., 1998; Swaney et al., 2001; Ward and Hart, 2005). There are some observational studies on the enhancing effects of affiliation (Bonnie and de Waal, 2006; Russon and Galdikas, 1995) on social learning but experimental studies are still rare.

We previously showed that observers in ravens, *Corvus corax*, manipulated a particular object for a longer period of time than other objects when it had been handled by a sibling model beforehand. However, this was not the case when the model was not a sibling (Schwab et al., 2008). In our group of ravens, siblings showed significantly higher levels of affiliated relations than did non-siblings (Schwab et al., 2008), supporting the hypothesis that socio-positive relations between individuals may enhance social learning. In contrast, pair bonding in jackdaws, *Corvus monedula*, neither accelerated learning of new food producing techniques nor did pair partners learn the same food producing technique (Wechsler, 1988b). This is interesting, considering that Wechsler's jackdaws showed strong bonds similar to our juvenile ravens (Schwab et al., 2008).

Relating to both studies, we first determined social dynamics within our group of hand-raised jackdaws via daily behavioural observations. Second, we carried out three social learning experiments. For reasons of comparability the first experiment was identical to that done in ravens, in which juvenile sibling and non-sibling dyads were tested in a non-food stimulus enhancement task. Experiment 2 was a colour discrimination task, carried out with the same juvenile birds, but now in a food context. Experiment 3 was identical to experiment 2 and the same birds were used as test subjects. However, in experiment 3, the juveniles from experiment 2 had reached adulthood and had formed pairs. Pair and non-pair dyads were tested to allow comparisons with Wechsler's 1988 study.

Jackdaws are socially living in groups throughout their lifes. They mainly breed in colonies and forage together in flocks which vary seasonally in size (Haffer and Bauer, 1993; Röell, 1978) depending largely on food availability and quality. Social dynamics within the group are not evenly distributed between individuals (Röell, 1978) which provides the basis for directed social learning (Coussi-Korbel and Fragaszy, 1995). Jackdaws maintain within-male and within-female hierarchies, with males generally being more dominant than females (Röell, 1978; Tamm, 1977; Wechsler, 1988a). Life-long pair bonds are usually monogamous (Henderson et al., 2000) and pair partners remain together throughout the year (Röell, 1978). They spend most of the time in close spatial proximity, allopreen each other (Wechsler, 1989) and support each other in agonistic interactions (Wechsler, 1988a). Recent studies indicate that also juvenile jackdaws maintain strongly bonded relations (Schwab et al., submitted; von Bayern et al., 2007). Therefore, if social dynamics determine preferential social learning in jackdaws, the birds should learn more readily from affiliated than from non-affiliated individuals. However, another main characteristic of affiliated relationships in jackdaws is a high rate of food-sharing between strongly bonded individuals. Food-sharing was found between adult pair partners (Wechsler, 1989) as well as between juvenile affiliated birds (Schwab et al., submitted; von Bayern et al., 2007). If following a definition of scrounging as benefiting from the food discoveries of others (Giraldeau and Lefebvre, 1987), food-sharing between individuals could be considered as a special case of scrounging (tolerated theft, co-feeding) (Giraldeau and Caraco, 2000). There are conflicting results dealing with the influence of scrounging opportunities on social learning, sometimes having an inhibiting (Giraldeau and Lefebvre, 1987; Giraldeau and Templeton, 1991), sometimes a facilitating effect (Caldwell and Whiten, 2003; Fritz

and Kotrschal, 1999). Taking both possible outcomes of scrounging into account, we could expect two scenarios. First, that individuals learn more readily from affiliated than from non-affiliated individuals if scrounging (in the sense of sharing) facilitates social learning. Second, individuals should learn more readily from non-affiliated than from affiliated individuals if scrounging opportunities inhibit social learning.

1. Methods

1.1. Subjects and keeping

Subjects were 20 juvenile jackdaws (*C. monedula*) that had been hand-raised from 13 to 20 days after hatching to fledging at the Konrad Lorenz Research Station in Gruenau, Austria in spring 2005. The 14 males and 6 females were taken out of wild nests with permission. Until fledging birds were kept in an indoor room in six separate nestboxes. Nests one and two consisted of four biological siblings each, nest three consisted of two single nestmates, nest four was composed of three single nestmates, nest five consisted of two biological sibling pairs and nest six was composed of one biological sibling pair plus one single bird. Because behavioural observations showed that nestmates maintained the same relation patterns to their conspecifics than did biological siblings we refer to all nestmates as siblings, even when the individuals are not genetically related. After fledging, the birds were transferred to an outdoor aviary and from then on housed together in one social group. The aviary consisted of one outdoor compartment (100 m², maximum height of 5 m) which was equipped with wooden perches, breeding boxes, rocks and natural vegetation. Outdoor experimental compartments, 2.5 m high, consisted of a central room (20 m²) and two pathways (left and right, each 7 m²) which could all be divided by wire mesh doors and which were equipped with wooden perches. When not being tested, birds could move around freely in all areas. Birds had *ad libitum* access to water and were fed three to four times a day with a mixture of shredded meat, dry insects, cottage cheese and eggs and various kinds of fruits, grain, milk products and vegetables. Jackdaws were individually marked with coloured metal rings.

1.2. Behavioural observations

We made behavioural observations on average every second day, alternating at morning and afternoon feedings. These 30-min observations consisted of 5-min focal observations from six birds and were counterbalanced for frequency and order of observations for each individual. We recorded all social interactions between the focal individual and any other conspecific. To determine affiliate relationships, we used two parameters: the duration that birds sat within 10 cm to each other, and the frequency with which each conspecific was the focal individual's nearest neighbour at the beginning of each 5 min focal observation. The observation period lasted from fledging of the birds, beginning of June 2005 to the end of the experimental trials, middle of April 2006 and resulted in 3.23 ± 0.3 (range: 0–7) 30 min observations per week.

To assemble dyads for the first and second experiments which were conducted in short succession, we analysed behavioural data from the beginning of June 2005 until the end of July 2005 when we started experiment 1. Experiment 2 was started at the middle of September 2005 right after experiment 1 was finished. To determine dyads for the third experiment we analysed data from the end of December 2005, when birds reached sexual maturity and pair bonding started, until the end of March 2006, when this final experiment started. Unfortunately, seven birds died between

experiments 2 and 3 due to predation. Therefore, behavioural observations for experiment 3 were based on 13 birds. For analysis we first summed up durations of sitting close and frequencies for nearest neighbours for each individual separately. To obtain these sums we only used individual values which were recorded when the individual was the focal individual to avoid pseudoreplication. Second, we divided these sums through the number of actual siblings and non-siblings or pair and non-pair partners, respectively, and corrected for the number of observations for each individual to obtain one average data point per individual per condition. Because these data were not normally distributed we used Wilcoxon signed-ranks tests to investigate whether siblings and pair partners spent significantly more time sitting close to each other, and were significantly more frequently observed as the nearest neighbour at the start of each focal observation, than non-siblings and non-pair partners. Tests were calculated by hand according to Siegel and Castellan (1988) when the number of individuals was <16, i.e. in adult birds. Test results are given two-tailed and considered significant when $P < 0.05$.

1.3. Composition of experimental model–observer dyads

We assembled nine sibling dyads, consisting of 12 males and 6 females. From the two nests with an uneven number of nestmates (three individuals each) we excluded one bird per nest to obtain one dyad out of each nest for testing. Whenever possible we tested biological siblings in a dyad, but three out of the nine tested dyads were in fact nestmates. For composing non-sibling dyads we at random chose individuals which were non-nestmates. Due to increasing shyness of two sibling birds we tested only 16 individuals (11 males, 5 females) in experiment 2 but otherwise dyads were composed as in experiment 1. The sex of most juvenile birds was unknown when they were tested but dyads turned out to result in 7 and 5 same sex dyads in the sibling and non-sibling conditions, respectively, in experiments 1 and 2. At the end of December 2005 individuals entered sexual maturity and pair bonding started being six pairs which were tested in experiment 3. For composing non-pair dyads we again chose individuals at random out of those 12 which were non-pair partners and of different sexes.

1.4. General experimental procedure

Dyads were tested in physical and visual separation from the rest of the group in the experimental compartments. The order of conditions was semi-randomized, interspersing sibling and non-sibling trials and pair and non-pair trials, respectively. As a principle, birds are never caught or grabbed, therefore, the experimenter waited for the test subjects to fly into the corresponding experimental compartments and then closed them off via wooden doors or wooden windows to the rest of the group. Birds were well habituated to this procedure and initially rewarded for flying into compartments and being separated from other individuals. If an individual chose not to participate in experiments on a given day, it was simply tested the next day. The experimental dyads themselves were physically separated from each other by wire mesh, but were in visual contact. Each pair was used twice, with model and observer roles reversed. Experimental trials consisted of a demonstration phase and a test phase.

During the demonstration phase the model was in the central experimental room, while the observing bird was able to watch the model through the wire mesh door either from the left or the right pathway. The model was allowed to handle one object (target object—experiment 1) or to eat mealworms from a coloured filmbox (rewarded colour—experiments 2 and 3). Handling was defined

as manipulation of objects by the bird with its beak and/or feet. There was no time restriction to the handling time of the model in the demonstration phase, but if the model had not touched the object for more than 20 s or had eaten five times from the coloured box it was removed from the experimental compartment.

After removing the model bird, the experimenter (C.S.) temporarily blocked the view of the observer bird with her body while collecting the item. In experiment 1 (juveniles, non-food context) she then arranged all five objects of a certain set, including the target object, on the floor of the experimental room. She then touched all objects again in reverse order to avoid enhancement effects by the human. In experiment 2 (juveniles, food context) and 3 (adults, food context) she placed both boxes (rewarded and unrewarded colour) of a certain set simultaneously on the ground. Then, in all three experiments, she opened the separating wire mesh door and the observer bird was allowed to enter the central experimental room which started the test phase. As in the demonstration phase there was no time restriction for observers to manipulate objects or boxes. Trials were terminated 2 min after the last touch of any object or box by the bird. If a bird did not handle any of the objects or boxes at all, the trial was finished after 5 min. All trials were video-taped (Sony DCR-TRV14E, Digital Video Camera Recorder).

1.5. Experiment 1: juveniles, non-food context

Experiment 1 was carried out from end of July 2005 until beginning of September 2005. For reasons of comparability C.S. conducted the experiment in exactly the same way as she did with the ravens (Schwab et al., 2008). In the demonstration phase the model bird was allowed to handle one object (target object) out of a set of five. We used 20 different plastic objects (four sets of five objects each), 2–3 cm in diameter, which were novel to the birds but small enough not to provoke a neophobic reaction. Objects were differently coloured but arranged into sets for categorial similarity (size, shape). Sets of objects were equally distributed between observers and each set was used only once with each tested dyad. In case the model handled the target object less than 5 s the trial was terminated and started once again on another day. For the test phase objects were placed 30 cm apart, all at the same distance (1 m) to the door separating experimental room and pathway. Locations of the target objects were equally balanced between trials.

We first compared models' handling times of the target objects in the sibling and in the non-sibling condition. Second, we measured observers' handling time of objects and compared the handling times of the target object and any other object in both the sibling and the non-sibling condition. To obtain average values for those objects that had not been presented and handled by the models in the demonstration phase (average object), we calculated the observers' handling time for all objects minus the handling time for the target object and divided this result by four. Because data were not normally distributed we used Wilcoxon signed-ranks tests to compare conditions. Results of tests are given two-tailed and considered significant when $P < 0.05$.

1.6. Experiment 2: juveniles, food context, and experiment 3: adults, food context

In the demonstration phase, the model bird was allowed to eat two mealworms five times out of a coloured filmbox (rewarded colour) attached to a similarly coloured wooden block. After baiting, the box was put onto the ground and the model bird was free to approach. The box was covered with its lid upside-down so the lid could be easily pushed away or lifted by the birds. Only the model

bird was allowed to watch the baiting process of the box. We used eight differently coloured boxes randomly combined into four pairs (yellow-blue, grey-violet, green-red, brown-white). To overcome the jackdaws' neophobia we habituated the birds to the boxes by leaving the boxes firmly closed in the aviary for 1 week before starting the tests but otherwise the birds did not have any experience nor did they receive any training with the boxes. We controlled for smell by keeping mealworms in each box before starting the tests. In all demonstration phases the model birds readily ate the mealworms. For the test phase, both boxes (rewarded and unrewarded colour) of the particular pair were placed simultaneously on the ground, 1 m apart and at the same distance to the separating door between central experimental room and pathway. Boxes were covered with upside-down lids. We avoided giving spatial cues, by placing the rewarded box in the demonstration phase somewhere else than the boxes in the test phase. Furthermore, both the rewarded and unrewarded box in the test were not baited with mealworms to avoid affecting the handling time by the observer bird through contents of the boxes. Each pair of boxes was used only once with each tested dyad. Model birds that had fed from a certain coloured box in experiment 2 were tested with the same pair of boxes in experiment 3 when used as observers. But in experiment 3 the previously non-rewarded colour of the pair became the rewarded one to control for the possibility that the birds remembered their experiences from experiment 2 with regard to feeding from a certain coloured box. We controlled for possible colour preferences by counterbalancing the rewarded colour of each pair of boxes between trials. We furthermore controlled for possible side effects by counterbalancing the placement of the rewarded box (left or right with regard to the entering bird) between trials and within individuals.

We measured the observers' handling time of rewarded and unrewarded box and the number of visits to each of the boxes. A visit was counted either when a bird was manipulating a box or approaching a box within 10 cm and looking inside the already open box with either one or two eyes. Both parameters could be determined without ambiguity and the latter would additionally express a checking behaviour of the individual to reconfirm about the content of an already open box. Because data were not normally distributed we used Wilcoxon signed-ranks tests to compare handling times of and visits to boxes in the sibling and non-sibling and in the pair and non-pair conditions. Tests were calculated by hand according to Siegel and Castellan (1988) when the number of individuals was <16, i.e. in adult birds. Test results are given two-tailed and considered significant when $P < 0.05$.

Experiment 2 (juveniles, food context) was carried out from middle of September 2005 until end of October 2005. To the end of the experiment daily behavioural observations showed that the birds manipulated objects (like leafs, twigs, stones or plastic toys which were provided for behavioural enrichment) in the aviary on average for 12.89 ± 0.38 s per manipulation bout. In the test we used two differently coloured boxes. Therefore, we repeated the average manipulation time for objects and added a few seconds for the bird to switch position between objects. This calculation results in 30 s. Hence, we analysed the first 30 s of each trial starting with the observer's first touch of any object. Experiment 3 (adults, food context) was carried out from end of March 2006 until middle of April 2006 after pairs had formed. At that time the birds were starting to build nests and became easily distracted when separated from their pair partners in the non-pair condition. Therefore, we did not leave the partners with the rest of the group but brought them in the second pathway where their vision was blocked by opaque curtains. Nevertheless, the tested birds often hesitated to manipulate the boxes. Therefore, in experiment 3 we analysed the entire time until the bird did not touch any box anymore for 2 min (mean duration was 95.38 ± 15.53 s).

2. Control trials

In October 2006 we carried out control trials with 12 juvenile birds being naïve to the task to check for colour preferences of the birds. Those birds were hand-raised in spring 2006 and were kept in the same way as the tested birds. These seven males and five females out of five sibling groups were housed together with four more juveniles and the tested birds in one social group since fledging in June 2006. Each bird was tested alone in four trials, physically and visually separated from the rest of the group. In each of the four trials a different colour set of boxes was presented with upside-down lids for easy removal. The experimenter placed both boxes simultaneously at locations in the central experimental room were they had been placed in the experimental trials while the bird was in one of the pathways. Then the experimenter opened the wire mesh door and the bird was free to enter and to manipulate. As in the experimental trials there was no time restriction to the control trials but the trial was terminated 2 min after any of the boxes had been touched by the bird. If no box was handled, the trial was finished after 5 min. Placing of boxes was counterbalanced with regard to left–right location of colours between trials. For habituation to the boxes they were left in the aviary with firmly closed lids for 1 week before starting the control trials.

Although control birds were well habituated to the test situations and to the experimental compartments, they hardly manipulated any of the boxes. In only 5 out of 48 control trials did a bird manipulate at least one of the boxes (three individuals). In six more trials a bird visited a box without touching it (three individuals). Six individuals neither manipulated nor visited any of the boxes in any of the trials. In 37 control trials there was neither a manipulation nor a visit by any of the birds, resulting in insufficient data for statistical analysis. In the experimental trials we controlled for the same number of left and right locations of rewarded boxes within individuals and trials and also controlled for counterbalancing the colour of the rewarded box to left and right location between trials. This enabled us to calculate possible colour or side preferences out of the experimental trials.

3. Results

3.1. Behavioural observations on affiliation

Juvenile jackdaws showed higher affiliate relations between siblings than between non-siblings. Siblings sat within 10 cm to each other for significantly longer than non-siblings ($N = 17$, $Z = -2.012$, $p = 0.044$, Fig. 1a, sitting close). Also, the nearest neighbour of the focal individual at the beginning of each observation was significantly more often a sibling than it was a non-sibling ($N = 20$, $Z = -2.203$, $p = 0.028$, Fig. 1b). Adult jackdaws showed similar results but with their pair partners. Pair partners sat within 10 cm to each other for significantly longer than non-pair partners ($N = 12$, $T^+ = 78$, $p = 0.0004$, Fig. 1c, sitting close) and the nearest neighbour of the focal individual at the beginning of each observation was significantly more often the pair partner than a non-pair partner ($N = 12$, $T^+ = 78$, $p = 0.0004$, Fig. 1d).

3.2. Experiment 1: juveniles, non-food context

Following the social dynamics hypothesis we predicted for this stimulus enhancement task that observers would handle an object (target object) longer than any of four other available objects if a sibling model had been handling this object before, but not if the model had been a non-sibling. However, juvenile
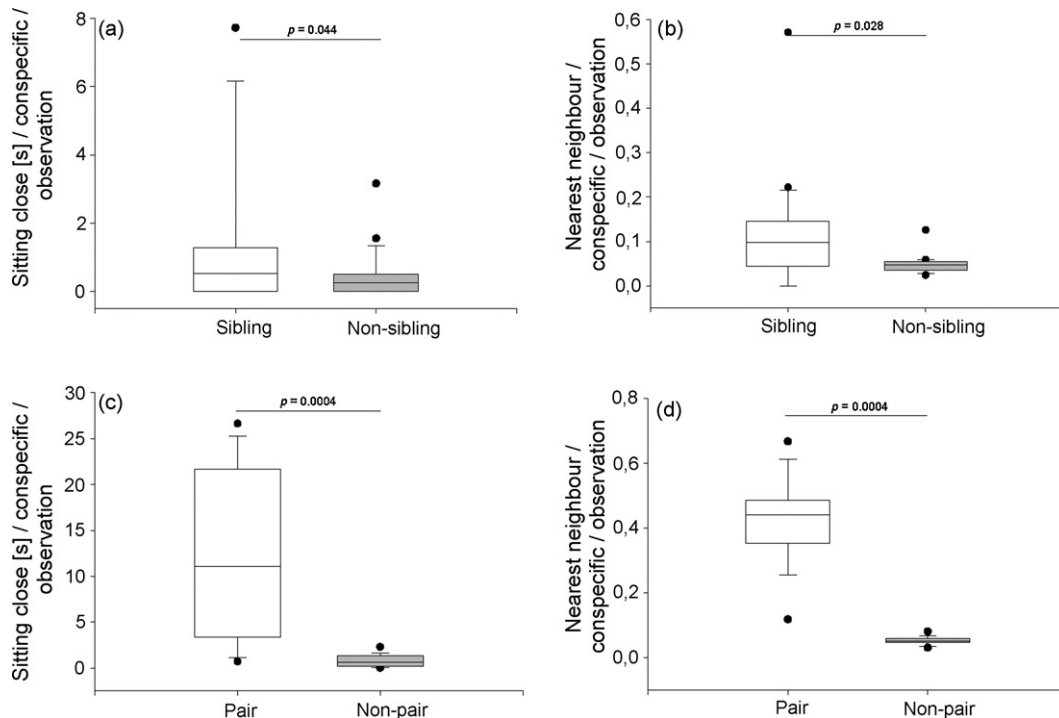
Fig. 1. Behavioural observations of social interactions of jackdaws in their social group. Duration (s) birds sit close to each other in (a) juvenile and (c) adult jackdaws. Frequency of nearest neighbours at the beginning of each observation in (b) juvenile and (d) adult jackdaws. (a) and (b) show comparisons between siblings and non-siblings and (c) and (d) show comparisons between pair and non-pair partners. All graphs are corrected for the number of actual siblings and non-siblings and pair and non-pair partners and for the number of observations for each individual. Boxes represent mean durations and frequencies of 20 juvenile and 13 adult birds. Boxes indicate median, 25th and 75th percentiles, whiskers indicate 10th and 90th percentiles and dots indicate outliers. Wilcoxon signed-ranks tests.

observer birds did not handle the target object significantly longer than any other object (Fig. 2). This was true both for the sibling ($N = 14$, $Z = -0.754$, $p = 0.451$) and the non-sibling condition ($N = 13$, $Z = -0.315$, $p = 0.753$). We also tested the probability that a bird copies the behaviour of a conspecific depending on the behaviour of the model. But comparing the time the model was manipulating the target object in the sibling and in the non-sibling condition did not reveal a significant difference between conditions (Wilcoxon signed-ranks test: $N = 16$, $Z = -1.138$, $p = 0.255$).

Fig. 2. Comparison of handling time (s) of the target object and average objects in the sibling and non-sibling condition of experiment 1. Boxes represent mean handling times of 18 juvenile jackdaw observers. Boxes indicate median, 25th and 75th percentiles, whiskers indicate 10th and 90th percentiles and dots indicate outliers. Open boxes indicate observers' handling time of the target object while black boxes indicate the average handling time of the other four available objects. Wilcoxon signed-ranks test.

3.3. Experiment 2: juveniles, food context

For this colour discrimination task, we again predicted that observers would handle and/or visit the former rewarded colour of the demonstration longer and/or more often if the model bird had been a sibling, but not if it had been a non-sibling if the existence of food-sharing between affiliated individuals faciliates social learning. On the contrary, if food-sharing inhibits social learning, observers should handle and/or visit the former rewarded colour of the demonstration longer and/or more often if the model bird had been a non-sibling, but not if it had been a sibling.

Juvenile observer birds that had previously seen a model bird feeding from a certain coloured (rewarded) box showed significant differences with regard to handling time only in the non-sibling but not in the sibling condition. Non-sibling observers manipulated the previously rewarded coloured box significantly longer than the unrewarded one ($N = 15$, $Z = -2.359$, $p = 0.018$, Fig. 3a) and there was a trend towards visiting the rewarded colour more often than the unrewarded one ($N = 12$, $Z = -1.89$, $p = 0.059$, Fig. 3b). On the contrary, in the sibling condition there was no significant difference neither with regard to handling time ($N = 14$, $Z = -0.976$, $p = 0.329$, Fig. 3a) nor to visits ($N = 12$, $Z = -0.577$, $p = 0.564$, Fig. 3b) to the rewarded coloured box in comparison to the unrewarded one.

Juvenile birds did not show any significant preference for a certain colour of a pair of boxes or a certain side (left–right). Comparisons of paired colours did not result in significant differences neither with regard to handling time (colour pair 1: $N = 8$, $T^+ = 30$, $p = 0.109$; colour pair 2: $N = 6$, $T^+ = 14.5$, $p = 0.563$; colour pair 3: $N = 8$, $T^+ = 24.5$, $p = 0.461$; colour pair 4: $N = 7$, $T^+ = 19$, $p = 0.469$) nor with regard to number of visits (colour pair 1: $N = 6$, $T^+ = 14$, $p = 0.563$; colour pair 2: $N = 6$, $T^+ = 17.5$, $p = 0.219$; colour pair 3: $N = 5$, $T^+ = 7.5$, $p > 0.999$; colour pair 4: $N = 7$, $T^+ = 17.5$, $p = 0.688$). Also, juvenile birds did not show a significant preference for left or right boxes,
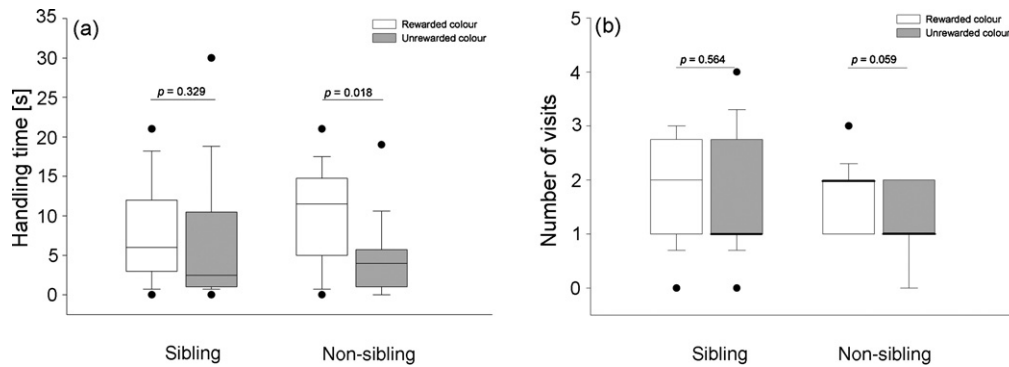
Fig. 3. Comparison of (a) handling time (s) and (b) number of visits of rewarded and unrewarded coloured filmboxes in the sibling and non-sibling condition of experiment 2. Boxes represent mean handling time and number of visits of 16 juvenile jackdaw observers. Boxes indicate median, 25th and 75th percentiles, whiskers indicate 10th and 90th percentiles and dots indicate outliers. Open boxes indicate observers' handling time and number of visits of the rewarded colour while black boxes indicate observers' handling time and number of visits of the unrewarded colour. Wilcoxon signed-ranks test.

either with regard to handling time ($N = 15$, $Z = -0.313$, $p = 0.754$) or with regard to number of visits ($N = 11$, $Z = -0.549$, $p = 0.552$).

3.4. Experiment 3: adults, food context

For this colour discrimination task, we predicted the same outcome as for experiment 2 but now for pair and non-pair partners instead of siblings and non-siblings. Adult birds showed a less pronounced, but similar pattern than the juveniles in experiment 2. In the non-pair condition they did not differ significantly with regard to handling time of the previously rewarded coloured box ($N = 8$, $T^+ = 21.5$, $p = 0.742$, Fig. 4a). However, non-pair partners tended to visit the rewarded colour more often than the unrewarded one ($N = 11$, $T^+ = 54$, $p = 0.067$, Fig. 4b) as did juvenile observer birds. On the contrary, in the pair condition there was no significant difference between the rewarded and the unrewarded coloured box neither with regard to handling time ($N = 9$, $T^+ = 23$, $p > 0.999$, Fig. 4a) nor with regard to number of visits ($N = 9$, $T^+ = 24$, $p = 0.91$, Fig. 4b).

Adult observer birds did not show any significant preference for a certain colour of a pair of boxes neither with regard to handling time (colour pair 1: $N = 5$, $T^+ = 9$, $p = 0.812$; colour pair 2: $N = 3$, $T^+ = 0$, $p > 0.999$; colour pair 3: $N = 4$, $T^+ = 7$, $p = 0.625$; colour pair 4: $N = 5$, $T^+ = 12$, $p = 0.313$) nor with regard to number of visits (colour pair 1: $N = 6$, $T^+ = 13$, $p = 0.688$; colour pair 2: $N = 5$, $T^+ = 5$, $p > 0.999$; colour pair 3: $N = 5$, $T^+ = 10.5$, $p = 0.625$; colour pair 4: $N = 4$, $T^+ = 5$, $p > 0.999$). Adult birds handled boxes to the left for longer ($N = 10$, $T^+ = 53.5$, $p = 0.006$) and visited them more often ($N = 12$, $T^+ = 76$, $p = 0.001$) than boxes to the right.

4. Discussion

In our social learning experiments jackdaws either did not show any significant behavioural modification in response to the performance of a model bird (experiment 1: juveniles, non-food context), or they learned from non-affiliated rather than affiliated individuals (experiment 2: juveniles, food context, and experiment 3: adults, food context). To our knowledge, this is the first study showing enhancement effects of non-affiliated individuals on social learning because other studies dealing with affiliation patterns and social learning found positive effects between affiliated individuals (Bonnie and de Waal, 2006; Russon and Galdikas, 1995; Schwab et al., 2008).

Contrary to our prediction for experiment 1, observers did not handle an object for a longer period of time than any of four other available objects if a sibling model has been handling this object before in experiment 1 (juveniles, non-food context). These non-significant results were not due to a general avoidance of handling objects. Juvenile jackdaws did manipulate the presented objects in experiment 1, but did not prefer to handle the demonstrator's object over the other objects presented. Hence, a lack of interest in artificial objects per se, or neophobic reactions to the test objects, can be excluded as explanations for our results.

In the same experimental set-up, hand-raised juvenile ravens handled objects significantly longer when they had been manipulated by sibling models before, whereas non-sibling models produced no such effect. Furthermore, ravens also matched their decisions to cache or not to cache with their siblings but not with
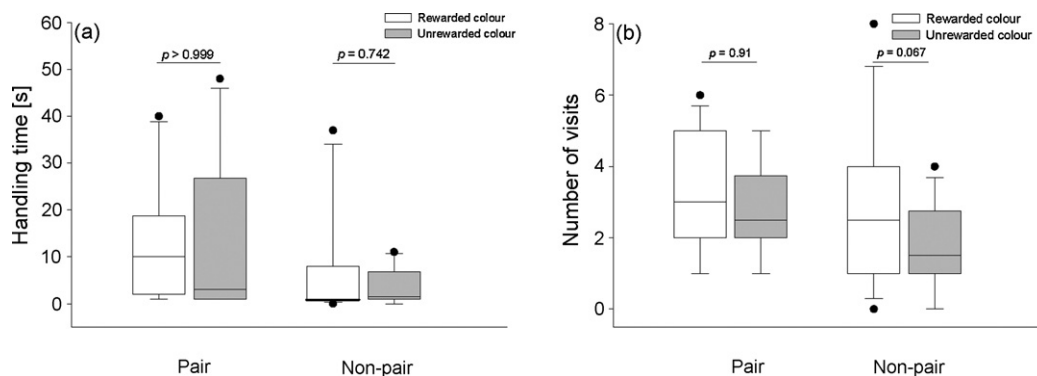

Fig. 4. Comparison of (a) handling time (s) and (b) number of visits of rewarded and unrewarded coloured filmboxes in the pair and non-pair condition of experiment 3. Boxes represent mean handling time and number of visits of 12 adult jackdaw observers. Boxes indicate median, 25th and 75th percentiles, whiskers indicate 10th and 90th percentiles and dots indicate outliers. Open boxes indicate observers' handling time and number of visits of the rewarded colour while black boxes indicate observers' handling time and number of visits of the unrewarded colour. Wilcoxon signed-ranks test.

non-siblings (Schwab et al., 2008). We suggest two not mutually exclusive explanations for these different results in the two studies. First, raven models showed a tendency of handling the target object longer in the sibling than in the non-sibling condition (Schwab et al., 2008), which was not true for jackdaw models. Hence, the quality of demonstration may have been different in ravens than in jackdaws, enhancing potential effects on social learning in the former but not in the latter. Second, because social relations of juvenile jackdaws and juvenile ravens showed the same pattern with siblings maintaining closer affiliated relations than non-siblings, differences between jackdaws and ravens in this non-food experiment could be caused by differences in caching behaviour. Jackdaws hardly, if ever, cache and if, they do it superficially (Henty, 1975). Ravens on the other hand intensely cache food (Bugnyar and Kotrschal, 2002; Heinrich, 1999; Heinrich and Pepper, 1998) and even show play-caching of objects (Bugnyar et al., 2007; Heinrich and Smolker, 1998). Caching of objects may be important for ravens to develop cache protection strategies (Bugnyar et al., 2007). Therefore, caching ravens generally may be more interested in objects than non-caching jackdaws. This could result in ravens being more attentive to an object handling conspecific and learning socially in this non-food context experiment as opposed to jackdaws.

Experiments 2 (juveniles) and 3 (adults) were conducted in a food context. When paired with a non-affiliated model, juvenile observers handled the rewarded coloured box for significantly longer than the unrewarded one and observers tended to visit the rewarded box more often in both non-sibling and non-pair conditions. There was no negative carry-over effect from experiment 1 to experiments 2 and 3, indicating that jackdaws could be motivated to learn by a change in the set-up. Wechsler (1988b) also found no enhanced learning from pair partners in adult jackdaws. However, the latter study was conducted in a group context with several potential models being present at the same time. In the present study, birds were tested in dyads with only one model present. Furthermore, Wechsler used a feeding apparatus which had to be manipulated in certain ways, while in the present study birds had to manipulate boxes without engaging in any sophisticated manipulation techniques. These methodological differences could explain the difference in results to our present study.

Naïve birds which did not observe a model, did not manipulate the boxes sufficiently to allow statistical analysis. It is unlikely that this was due to neophobia because naïve birds received an identical habituation phase to the boxes as observer birds and they did not show any behavioural signs of neophobia. More likely, the absence of conspecifics attenuated their interest in the objects as has been found in other species (Fragaszy and Mason, 1978). Therefore, we used test trials to calculate colour and side preferences, which were all non-significant with the exception of adult jackdaws who had developed a left-side preference. Although this may have influenced the birds' performance and may have made our results more conservative, adults nevertheless tended to visit the rewarded colour more often. This result supports the clear results of juvenile observers in experiment 2.

All models readily ate the mealworms in all demonstrations of the experiments. The time they spent at the food source did not differ significantly between conditions, indicating that demonstration quality did not have an effect on the results of observer birds. Furthermore, one could argue that jackdaws, typically pairing in their first year (Lorenz, 1931), might have paid more attention to non-siblings as potential future pair partners. Although this might be generally true, none of the tested non-sibling dyads paired later on. Even more importantly, this could not explain the results of the birds in experiment 3, when they were already adult and paired.

Measuring the frequency and duration of looks of observer individuals in an independent experiment and testing dyads of

jackdaws in a food and in a non-food context showed that the percentage of watching was higher for non-affiliated than for affiliated models in jackdaws, whereas the pattern was reversed in ravens (Scheid et al., 2007). This corroborates our current results and suggests that they may have been caused by paying different attention to affiliated and non-affiliated conspecifics.

Taken together, our results indicate that social relations do affect social learning in jackdaws, but differently than predicted by the social dynamics hypothesis (Coussi-Korbel and Fragaszy, 1995). Birds learned more readily from non-affiliated than from affiliated individuals. One outstanding characteristic of affiliation in jackdaws is that birds show high tolerance at food and even the active sharing of food (de Kort et al., 2006; von Bayern et al., 2007). Although the birds did not have the opportunity to share food, in the sense of tolerated scounging, during the current experiments they could have relied on their knowledgeable affiliated partners to secure food as has been proposed for female zebra finches (Beauchamp and Kacelnik, 1991). To interpret the lack of directed social learning expected between pair partners in jackdaws, Wechsler (1988b) suggested that pair partners might preferentially profit from each other's food findings. Hence, non-affiliated individuals might be more important with regard to information about food than affiliated individuals, because food could be more likely shared with the latter than with the former. Furthermore, affiliated individuals spend most time in close spatial proximity to each other, which increases the probability that they simultaneously experience occurrences in their environment. On the contrary, spatially more distant individuals, which are more likely to be non-affiliated, may face different foraging situations and therefore provide different and/or more relevant information. Hence, physical distance, as an outcome of social relations, may increase the value of non-affiliated individuals because they might provide most useful discoveries based on the greater distance to the subject (Kummer, 1978). This may result in high attention towards non-affiliated individuals (Scheid et al., 2007) and preferential learning from them.

In sum, our results support the view that the choice of models in social learning experiments might be crucial and that it may depend on the social system and the quality of social relations between individuals. Interestingly, non-affiliated models were probably more valuable sources of information than affiliated conspecifics to the jackdaws of our study. In our experiments jackdaws were tested in dyads. Testing them in a more naturalistic setting, a group context, could show if the spread of a behaviour follows the same patterns as have been found here, or if other effects determine its transmission within the group.

Acknowledgements

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"We don`t have to name names,
point fingers, or,
name names."
Seinfeld, Season 8, Episode 4

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Nationality:	Austria

Current Occupation: PhD-student and project assistant in the FWF-project P 18920-B17: "Cooperative and Competitive Cognition in Corvids"

Education:

Since WS 2004/05	PhD project in Zoology
	Working title of thesis: "Effects of ecological constraints and social factors on cognitive abilities in ravens (*Corvus corax*) and jackdaws (*Corvus monedula)*", University of Vienna
SS 1995 – WS 2003/04	Master study of Zoology, main research area: Ethology Master thesis: "The reaction of dogs to different degrees of attention of their owners", University of Vienna
SS 1990 – WS 1997/98	Master study of Ethnology in combination with Sociology, Philosophy, Spanish Master thesis: "Construction of identity of Hungarians in the Burgenland: political, cultural and ethnical aspects of a historical process", University of Vienna
09 / 1981 – 05 / 1989	Grammar school BG & BRG XXII, Vienna
09 / 1977 – 06 / 1981	Primary school, Vienna

Awards:

Bischof DDr. Stefan László-Preis 2000. Applied by the AKV (Arbeitsgemeinschaft katholischer Verbände Österreichs) for the master thesis in ethnology. (ATS 10.000).

Grants:

Nine months PhD-grant from the AÖU (Aktion Österreich-Ungarn) for Budapest, Hungary. (€3.600). Working on dogs together with Ass. Prof. Dr. Ádám Miklósi from the Ethology Department at ELTE (Eötvös Loránd Tudományegyetem) University in Budapest.

Project-Collaboration:

2006- present	PhD position in the FWF-project P 18920-B17: "Cooperative and Competitive Cognition in Corvids"
2004-2006	PhD position in the FWF-project P 16939-B03: „Exploration and Neophobia in Ravens and Jackdaws"

Publications:

Schwab, Christine; Bugnyar, Thomas; Swoboda, Ruth; Gaede, Drew & Kotrschal, Kurt. Similarities and differences of relationships between adult pair partners and between juvenile nestmates in jackdaws (*Corvus monedula*). Subm.

Gaede, Drew; Kotrschal, Kurt; Bugnyar, Thomas & Schwab, Christine. Testing Problem Solving in European Jackdaws (*Corvus monedula*): The String-Pulling Task. In prep.

Schwab, Christine; Bugnyar, Thomas & Kotrschal, Kurt. Preferential learning from non-affiliated individuals in jackdaws (*Corvus monedula*). Behavioural Processes, in press.

Schwab, Christine; Bugnyar, Thomas; Schloegl, Christian & Kotrschal, Kurt. 2008. Enhanced social learning between siblings in common ravens, *Corvus corax*. Animal Behaviour, 75, 501-508.

Bugnyar, Thomas; Schwab, Christine; Schloegl, Christian; Kotrschal, Kurt & Heinrich, Bernd. 2007. Ravens Judge Competitors through Experience with Play Caching. Current Biology, 17, 1804-1808.

Schwab, Christine & Huber, Ludwig. 2006. Obey or not Obey? Dogs (*Canis familiaris*) Behave Differently in Response to Attentional States of Their Owners. Journal of Comparative Psychology, 120 (3), 169-175.

Schwab, Christine. Die Volksgruppe der burgenländischen Ungarn im historischen und sozio-kulturellen Wandel. In: Reif, Elisabeth & Schwarz, Ingrid (Hg.): Zwischen Ausgrenzung und Integration. Ein interdisziplinäres Friedensprojekt zum Thema „Interkulturelle Kommunikation" mit Ungarn. Mandelbaum Verlag, Wien, 2004, 170-188.

Schwab, Christine. Identitätsbildung der burgenländischen Ungarn. In: Csáky, Moritz & Stachel, Peter (Hg.): Mehrdeutigkeit. Die Ambivalenz von Gedächtnis und Erinnerung. Passagen Verlag, Wien, 2003, 123-131.

Conference contributions:

Talks:

Schwab, Christine; Bugnyar, Thomas & Kotrschal, Kurt. 4th European Conference of Behavioural Biology, ECBB. Dijon, France, July 18-20, 2008. "Similarities and differences of relationships between adult pair partners and between juvenile nestmates in jackdaws (*Corvus monedula*)".

Schwab, Christine; Bugnyar, Thomas; Swoboda, Ruth; Gaede, Drew & Kotrschal, Kurt. EG-Meeting. Regensburg, Germany, February 20-22, 2008. "Similarity of socio-positive relationships between adult pair partners and between juvenile nestmates in jackdaws (*Corvus monedula*)".

Schwab, Christine; Bugnyar, Thomas & Kotrschal, Kurt. XXX International Ethological Conference, IEC. Halifax, Nova Scotia, Canada, August 15-23, 2007. "Use of information provided by affiliated and non-affiliated conspecifics in ravens (*Corvus corax*) and jackdaws (*Corvus monedula*)".

Schwab, Christine; Bugnyar, Thomas & Kotrschal, Kurt. EG-Meeting. Social Organization and Cognitive Tools. General Patterns in Vertebrates? Gruenau, Austria, February 22-25, 2007. "Use of information provided by affiliated and non-affiliated conspecifics in ravens (*Corvus corax*) and jackdaws (*Corvus monedula*)".

Schwab, Christine & Huber, Ludwig. Joint East and West Central Europe. ISAE Regional Meeting. Tihany, Hungary, May 20-22, 2004. "Dogs discriminate the attentional states of humans".

Schwab, Christine. Südwind. Entwicklungspolitik NÖ Süd. „Von fremden und vertrauten Nachbarschaften. Ein interdisziplinäres Friedensprojekt zum Thema „Interkulturelle Kommunikation" mit Ungarn. 4. und 5. März 2004, Festsaal der Wirtschaftskammer NÖ, Herrengasse 10, 1014 Wien. „Die Volksgruppe der burgenländischen Ungarn im historischen und sozio-kulturellen Wandel".

Schwab, Christine. ÖAW – Österreichische Akademie der Wissenschaften. 3. Internationaler Kongress des Forschungsprogramms „Orte des Gedächtnisses". „Mehrdeutigkeit des kulturellen Erbes". 8.-10. November 2001, Theatersaal der Akademie, Sonnenfelsgasse 19/I, 1010 Wien. „Identitätsbildung der burgenländischen Ungarn".

Posters:

Schwab, Christine; Bugnyar, Thomas & Kotrschal, Kurt. EDICI Workshop: Evolution, Development and Intentional Control of Imitation. Vienna, Austria, March 5-7, 2008. "Learning through competition in hand-raised juvenile jackdaws (*Corvus monedula*)".

Schwab, Christine; Bugnyar, Thomas & Kotrschal, Kurt. 3rd European Conference of Behavioural Biology, ECBB. Belfast, Northern Ireland, September 4-6, 2006. "Learning through competition in hand-raised juvenile jackdaws (*Corvus monedula*)".

Schwab, Christine; Bugnyar, Thomas & Kotrschal, Kurt. XXIX International Ethological Conference, IEC. Budapest, Hungary, August 20-27, 2005. "Kinship Relations Affect Social Learning in Common Ravens (*Corvus corax*)".

Schwab, Christine; Bugnyar, Thomas & Kotrschal, Kurt. St. Andrews International Conference on Animal Social Learning. St. Andrews, Great Britain, June 15-18, 2005. "Kinship Relations Affect Social Learning in Common Ravens (*Corvus corax*)".