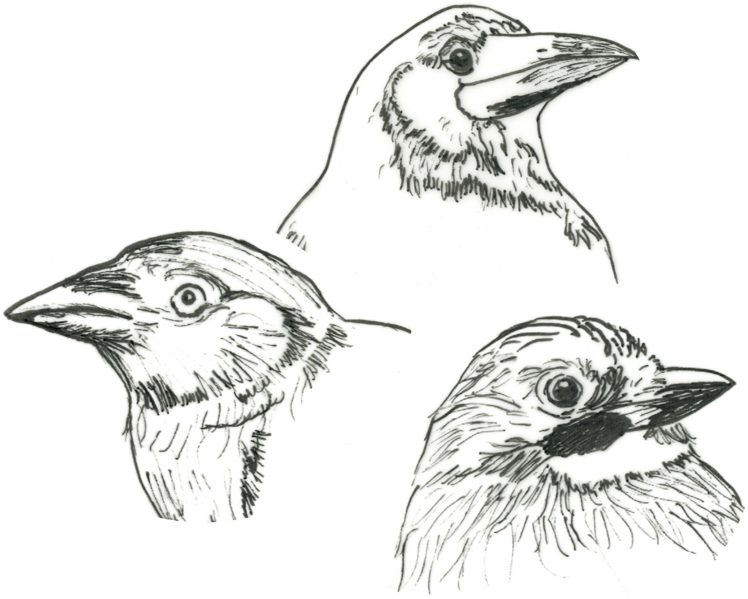
Sociality, Social Learning and Individual Differences in Rooks, Jackdaws and Eurasian Jays



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This dissertation is submitted for the degree of Doctor of Philosophy

Dedication

This thesis is dedicated to my grandmother, Ingeborg Heim, who was always an inspiration to me. As a 6 year old I enthusiastically informed her that I wanted to spend my time working with birds. My only wish now is that she were here to share this achievement with me.

Declaration

The following work was carried out at the Sub-Department of Animal Behaviour, Madingley, University of Cambridge, between October 2006 and March 2010, under the supervision of Dr. Nathan J. Emery and Professor Barry Keverne. I hereby declare that this dissertation has not been submitted, in whole or in part, for any other degree, diploma or qualification at any other university.

This dissertation is the result of my own work and includes nothing that is the outcome of work done in collaboration, except where specifically indicated in the text. I have attempted to reference appropriately any idea or finding that is not my own.

This dissertation does not exceed the limit of length specified by the Degree Committee for Biology.

Ira G. Federspiel

May 2010

Summary

Social intelligence is thought to have evolved as an adaptation to the complex situations group-living animals encounter in their daily lives. High levels of sociality provide individuals with opportunities to learn from one another. Social learning provides individuals with a relatively cheap and quick alternative to individual learning. This thesis investigated social learning in three corvid species: gregarious rooks (*Corvus frugilegus*) and jackdaws (*Corvus monedula*) and non-gregarious, territorial Eurasian jays (*Garrulus glandarius*). In addition to that, the species' social structure was analysed and individual differences between members of each species were determined. Introducing the field of social learning research, I presented a new framework for investigating social learning, combining ecology, ethology and evolution. Experiments were conducted within that framework.

I found that rooks and jackdaws develop social bonds and dominance hierarchies, whereas Eurasian jays do not. This is most likely related to their territoriality. In two experiments using two-action tasks, jackdaws learned socially. The underlying social learning mechanism was enhancement, which fits in with their feeding ecology. Rooks did not show social learning when presented with videos of conspecifics opening an apparatus. This might have been due to the difficulty of transferring information from videos or due to an ingrained 'affinity' to innovation and/or rapid trial-and-error learning overriding social learning processes. Individual differences along the bold/shy axis existed in all three species, but they were not stable across contexts. Thus, it seemed that the individuals perceived the two seemingly similar contexts that were designed to investigate neophobia and exploration (novel object in familiar environment; novel environment) as two different situations. The information may therefore have been processed by two distinct underlying mechanisms, which elicited different responses in each of the contexts. The implications of the findings of this thesis are discussed with regard to the new framework, integrating sociality, social learning and individual differences with the species' ecology.

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Nobody works well without a safety net of friends; thus I would like to dedicate the last two paragraphs to my friends both in Vienna and in Cambridge. In Vienna I would like to first of all thank the old crew – Jakob Achter, Flaum Blahacek, Oliver Brandl, Alex Grundorath, Stefanie Irsigler, Herwig Kovacic, Michael Ledl, Stefan Löffler, Tom Stockinger and Jakob Zwerger – for making me the person I am today and for decades of true friendship; Daniel Amesberger, Clemens Prerovsky and Anna Tampier for talking my life over with me every time I needed it (and when I did not); Valentin Sysel for playing an important role in my life, although he is so far away from me most of the time; Robert Bodnar, Moni Gassauer, Hans-Peter Fuehrer, Maria Marschler, Irene Meisel, Barbara Süssenbacher, Gerda Teichmann, Simon Tragust and Birgit Zendron for being part of this crazy journey through biology and zoology and for becoming close friends during that time; and to my truly amazing best friends Petra Kröpfl, Andras Lengyel, and Lukas Nespor for going through both the good and the bad times with me.

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Publications

To date, the following publication has arisen in whole or part from this thesis:

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Table of Contents

Chapter 1.

The 3E's approach to social information use in birds - integrating Ecology, Ethology and Evolutionary history

This chapter was published as a contribution to the book 'Cognitive Ecology II' (Federspiel, I. G., Clayton, N. S. & Emery, N. J. 2009; Ed. by R. Dukas & L. M. Ratcliffe).

1.1 Abstract

The field of social learning has attracted considerable attention over the last few years. Researchers from various fields, including psychologists, zoologists and ecologists, have been working on both the theoretical framework and the practical methods for studying social information use in animals, from mammals and birds to reptiles and fish. A significant obstacle for learning about how the mechanisms and functions of social learning may interact arises from the lack of communication between these fields, resulting in non-unified definitions, non-comparable results due to different methodologies and different ways of interpreting results. The aim of this opening chapter is to propose a new framework for the study of social learning in animals. This will lead us to obtaining a more complete picture of social learning processes and assist researchers when interpreting findings and designing future experiments. I will focus on birds and by presenting case studies on a few species give examples of how to apply the 3E's approach. This will set the stage for the experiments presented in this thesis.

1.2 Introduction

Kamil (1998, p.1) underlined the importance of integrating the different approaches to the study of animal behaviour that developed from two scientific revolutions: the cognitive revolution that stemmed from comparative psychology, and the behavioural ecology revolution that originated in biology. As discussed by Dukas (1998, p.405) in the first edition of 'Cognitive Ecology', the philosophy underlying cognitive ecology is that "cognition must be studied with regard to an animal's ecology and evolutionary history, and that knowledge of cognitive mechanisms can help us explain behavioural, ecological, and evolutionary phenomena".

In this chapter, I will evaluate the success of this integrative approach, focusing specifically on social information use by birds. I will argue that investigating the psychological mechanisms underlying social learning processes in the light of an animal's umwelt, in terms of the '3Es' - ecology, ethology and evolutionary history (as shown in Figure 1, but see also 'The 3E's approach and why it is important') - is critical for gaining a more complete, unified picture of social information use, not only for interpreting existing results, but also in designing new experiments with high ecological validity as well as rigorous experimental control.

Studying the psychological mechanisms of social learning in the light of the 3Es and drawing conclusions from such studies may help us to *define* the underlying mechanisms, whereas in reverse it is more difficult, and consequently, explaining an animal's ecology by examining its cognition is more complicated and more speculative. In this chapter, I shall largely concentrate on the former approach, but a good example of how a specific type of social learning can influence a species' ecology is the caching (i.e. food hording) behaviour of corvids. The sophisticated arms race between cachers and pilferers (i.e. thieves) would not be possible without the basic cognitive ingredient of observational spatial memory, in which pilferers can accurately locate the caches others have made, even when the cacher has left the scene (see 'The 3E's approach and why it is important').

As highlighted by Kendal et al. (2009), the successful use of social information is a matter of gaining benefits, i.e. fitness, and avoiding costs. Being part of a social group or a pair-bond appears to be a prerequisite for exploiting the knowledge of others, since only being in the company of others opens up opportunities to 'scrounge' information from knowledgeable conspecifics (i.e. 'information scrounging', Giraldeau et al. 2002, Laland 2004). Different types of social information and a varying number of opportunities to access that information are available, depending on the social and mating system (Lefebvre & Giraldeau 1996). For example, for territorial birds there may be fewer opportunities for picking up social information than for gregarious birds, and for pair-bonded birds there may be different types of information than for lekking birds.

Social learning, defined as "changes in the behaviour of one individual that result, in part, from paying attention to another" (Box 1984, p.213), involves various factors, ranging from 'low-fidelity copying mechanisms' (Whiten et al. 2004), which include mechanisms of social influence, such as social facilitation (i.e. the mere presence of another animal affects the motivation or arousal of the observer) and contagious behaviour (i.e. species typical behaviour is released by the sight of others engaged in that activity), to 'high-fidelity' social learning, such as imitation and emulation. Animals can learn from others using a variety of different mechanisms, such as local enhancement (i.e. facilitation of learning that results from drawing the observer's attention to a location or object with which the other individual is interacting), stimulus enhancement (i.e. attention is drawn to a certain stimulus) and observational conditioning (learning about the positive or negative reinforcement of an object or event). In Great Britain, a population of blue tits (*Parus caeruleus*), great tits (*P. major*) and coal-tits (*P. ater*) species learned how to open milk bottles to get to the cream off the top of the milk. Different bottle opening techniques were observed, indicating a social learning mechanism other than imitation (i.e. copying the exact action of another), most likely stimulus enhancement (Fisher & Hinde 1949, Hinde & Fisher 1951; Sherry & Galef 1984).

Imitation and emulation (i.e. copying the goal or result of an action sequence or learning about the operating characteristics of objects) are often considered more complex forms of social learning than those already discussed, although some authors argue against that view (Heyes 1999; for reviews and definitions see Custance at al. 1999, Galef 1988, Heyes 1994, Heyes & Galef 1996; Mineka et al. 1984, Thorpe 1956, Tomasello 1996, Whiten & Ham 1992, Whiten et al. 2004, Zajonc 1965, Zentall 2004, Zentall & Galef 1988). Well-known examples of imitation include vocal imitation, used to increase the repertoire size (Pepperberg 2007), and the imitation of human's greeting gestures (Moore 1992) in Grey parrots, *Psittacus erithacus*.

In addition to commonly described forms of social learning, the usage of other types of social information may play a role in decision-making (Bonnie & Earley 2007). Mechanisms for copying another's choice of mate and eavesdropping (the use of information in signals by individuals other than the primary target; Peake 2005), e.g., learning about the whereabouts of potential predators, are also important information resources. In eavesdropping, some authors distinguish between interceptive and social eavesdropping (Peake 2005). Interceptive eavesdropping is common when the eavesdropper is a different species from the signaller, e.g. prey detecting predator cues, or individuals from one species picking up information from individuals of another. For example, in a playback experiment it was found that black-casqued hornbills (*Ceratogyma atrata*) responded to alarm calls given by Diana and Campbell's monkeys (*Cercopithecus Diana* and *C. campbelli*, respectively) and could distinguish between calls that for these monkeys referred to crowned eagles and leopards (Rainey et al 2004). Within species, animals of the same sex may pick up information that was intended for the opposite sex (Mennill et al 2002; Peake 2005). Social eavesdropping takes place within a species when individuals intercept signals that were sent between conspecifics, such as female great tits (*Parus major*) gaining information about potential mates by listening to song interactions between neighbouring males (Otter et al. 1999) or domestic fowl (*Gallus gallus domesticus*; Hogue et al. 1996) and pinyon jays (*Gymnorhinus cyanocephalus*) inferring their own dominance rank after watching encounters between conspecifics (Bond et al. 2003, see also later in this chapter).

However, there are also good reasons not to use social information. Although 'less expensive' than information acquired via individual trial-and-error learning, information gained through social learning may come at a cost. Observing others performing an action involves forgoing other behaviours that could have been pursued in the meantime, such as watching out for predators, looking for food or finding a potential mate (McGregor & Dabelsteen 1996). Second, there is the possibility of learning incorrect or inefficient behaviours (Rieucau & Giraldeau 2009). Therefore, an animal should only employ social learning if it contributes to its survival or reproductive success (not a conscious decision) (see Kendal et al. 2009).

Another reason for suggesting that social learning might be costly is that social species often have large brains relative to their body size (Dunbar 1992), although this does not hold for all social species, and there are a number of positive correlations between brain size and various indices of sociality, such as grooming (Kudo & Dunbar 2001), forming coalitions (Shultz & Dunbar 2007) and deceiving others (Byrne & Corp 2004). Indeed, according to the *Social Function of Intellect* hypothesis (Humphrey 1976, 1988; see also Jolly 1966), it is the ability to survive the political dynamics of a complex social world that has been the primary driving force shaping primate intelligence. Keeping track of others' interactions and relationships in addition to their own in large social groups may be beneficial in future interactions, when it comes to deceiving others, knowing who to ask for support in a fight, or climbing up the dominance hierarchy. This imposes an additional burden, since a large amount of social information has to be processed every day, and may have lead to the development of social intelligence in animals living in large groups (Humphrey 1976, 1988).

In primates, relative neocortex volume (neocortex volume/brain volume remainder) increases with an increasing group size, indicating an effect of social complexity on the brain (Dunbar 1992). But also other indications of social complexity, such as size of grooming networks (Kudo & Dunbar 2001), whether the species forms coalitions (Dunbar & Shultz 2007a) and the rate of tactical deception (Byrne & Corp 2004) are all positively correlated with relative neocortex volume in many social primates.

Striking similarities between apes and corvids suggest that these social skills may not be unique to primates: for example, to stabilize their bonds in a group, birds engage in allopreening bouts, similar to grooming in apes (Emery et al. 2007). Furthermore, there is evidence for post-conflict affiliation (Seed et al. 2007) and deception in corvids (Bugnyar & Kotrschal 2004). The different types of mating systems, such as monogamy or promiscuity, seem to also have an impact on brains in birds (Dunbar & Shultz 2007b). Birds that form life-long pair bonds or are cooperative breeders were found to have the largest relative brain size (Emery et al. 2007). Similar to primate alliances, members of life-long pairs in birds spend a lot of time and energy on maintaining their relationship. The benefits of pair-bonding include, but are not limited to, food sharing, allopreening, support during fights, and reducing stress levels by initiating affiliative post-conflict behaviours such as bill-twining, the avian equivalent of chimpanzee kissing (von Bayern et al. 2007, Emery et al. 2007, Seed et al. 2007). These skills require high levels of coordination, and may have led to a certain form of intelligence, so-called relationship intelligence (Emery et al. 2007).

1.3 A comparative approach

Two main hypotheses for the development of social learning skills in social species have been proposed: social learning as an adaptive specialisation (Klopfer 1959) or social learning as a more general process (Lefebvre & Palameta 1988). Although difficult to interpret, a study with highly social, cooperatively breeding pinyon jays (*Gymnorhinus cyanocephalus*) and less social Clark's nutcrackers (*Nucifraga columbiana*) suggests the former: the jays and nutcrackers were provided with two tasks, a motor task (lifting a lid off a shallow well containing food) and a colour discrimination task (lifting a lid of a particular colour off a well containing food), which could be learned individually or socially (Templeton et al. 1999). The pinyon jays learned faster in the social compared to the non-social condition, whereas there was no difference in learning rate for the social and non-social learning tasks in Clark's nutcrackers. Thus, pinyon jays showed an enhanced performance under social conditions, whereas there was no such effect in the territorial nutcrackers. However, intra-specific competition over food between group members may have pushed the overall learning skills in social animals (Lefebvre & Palameta 1988, p.155), independent of whether socially or individually learned. In a study with gregarious pigeons (*Columba livia*) and territorial doves (*Zenaida aurita*), the birds had to find food and were provided with information about the location of the food by a demonstrator (social condition) or the apparatus that contained the food itself (non-social condition). The group-living pigeons performed better in both social learning and individual learning tasks, indicating a more general process underlying the enhanced learning skills found in social bird species, rather than a specialisation for social learning (Lefebvre et al. 1996, Shettleworth 1998). Both of those hypotheses seem to provide a sensible explanation, but they may not necessarily be mutually exclusive.

Templeton et al.'s (1999) results run contrary to Lefebvre & Palameta's (1988) study, because pinyon jays are significantly worse at the individual condition than the social condition compared to the pigeons, which displayed a more general learning ability. Although Templeton and colleagues (1999) suggest that their results support the idea of an adaptive specialisation for social learning, I believe these studies highlight the importance of taking other aspects of an animal's natural history into consideration when either designing cognitive ecological tasks and interpreting the findings from them. In a chapter on scrub-jay cognition, Emery & Clayton (2008) have recently suggested the importance of the 3E's approach for comparative cognition, extending Kamil's (1988) synthetic approach to animal intelligence to integrate information about the evolutionary history and ethology of an animal as well as its ecology.

1.4 The 3E's approach and why it is important

At the outset it is important to make a distinction between the ecological factors that affect an animal's behaviour, namely its diet, the habitat in which it lives, and its social system and mating system, from the ethology, by which I mean the natural behavioural repertoire, which also contributes to 'skilful' social information use. For example, knowing who associates with whom may play a major role for social birds, such as colonial, cooperatively breeding (ecology) pinyon jays (Marzluff & Balda 1992). As intense social cachers (ethology), they need to know who to protect caches from and who is safe as an observer, which they can infer from watching interactions between conspecifics coupled with an understanding of their social relationships. Transitive inference in social scenarios is defined as the ability to infer the relative dominance status of an individual based on observed interactions and should be an essential skill in this type of complex social environment. In a laboratory experiment designed to test this ability, three groups of pinyon jays with a linear hierarchy were formed: group 1 with birds A to F, the Push Group with birds 1 to 6, and group 3 with birds P to S. Group 1 was dominant to the Push Group, and the Push Group was dominant to group 3. An observer, bird 3, was allowed to compete with bird B. Bird 3 had never met bird B before, but he had watched encounters between bird A and B and between 2 and B. Also bird 2 was part of 3's group and therefore bird 3 would have information that bird 2 was dominant to him from their previous interactions. In the observed encounters, bird 3 could watch bird B being submissive to bird A, but dominant to bird 2. Bird 3 was then allowed to interact with bird B, and during their encounter, bird 3 demonstrated a greater number of submissive displays to bird B, suggesting that bird 3 had formed a representation of the relative dominance of those birds from their previous observations. All of the tested birds showed similar appropriate behaviours across different combinations of birds (Paz-y-Miño et al. 2004). It would be most informative to know whether these birds could also extrapolate this information about dominance relationships in order to know from whom they should protect their caches and when.

In tests of this transitive inference ability using arbitrary stimuli, pinyon jays outperformed the less social western scrub jays (western scrub jays live in very small, territorial groups and thus have fewer interactions with conspecifics than the pinyon jays; nest spacing is even in western scrub jays, but aggregated in pinyon jays; see Table 1, p. 36); however, the scrub-jays did learn (Bond et al.

2003). In an initial experiment involving discrimination learning between successive colour pairs that were implicitly ordered was tested. Social pinyon jays were faster at learning the dyadic relationships and made fewer errors. Whereas both species learned the first pair without problems, pinyon jays adapted more rapidly to reversals and thus made fewer errors in subsequent reversal trials, in which the previously rewarded pair was incorrect. When more pairs were included in the tests, pinyon jays learned and improved faster than the less social scrub-jays. In a second experiment, the birds were tested for transitive inference by intermixing familiar pairs with novel, non-adjacent pairs. Both species showed high accuracy and thus, transitive inference. However, differences were found in the responses to the position of the stimulus colour pair in the implicit rank order. Pinyon jays responded more slowly to low-ranking pairs, although no effect was found with the highest-ranking pair, whereas western scrub-jays displayed a first-item accuracy with almost no effects on latency. The authors concluded that the two species may have used different methods for representing the rank order, with pinyon jays using relational representations in which novel pairs can be inserted into a pre-existing structure, whereas western scrub-jays build a series of associative representations (Bond et al. 2003).

It therefore appears that differences in socio-ecology between these species may have driven them to develop different social information use skills. Pinyon jays are colonial birds living in large groups that breed in aggregated pairs of 50 and show cooperative breeding. By contrast, western scrub-jays are semi-territorial birds that breed in single pairs (Clayton & Emery 2007). Inferring the dominance status of conspecifics therefore seems to be much more important for the pinyon jays, since using social information to gain knowledge about one's own and others' relationships seems to be an (adaptive) advantage for species living in large, social groups.

Finally, considering the putative evolutionary history of the species under consideration is also important. Although a specific aspect of an animal's ethology or ecology may not be present in the extant species, it may have been present in the common ancestor of the group in question. For example, there is no evidence that jackdaws cache in the wild, but there are anecdotes that jackdaws do display proto-caching, by which I mean they are sometimes seen to place food in nooks and crannies without ever hiding it or leaving it for any length of time. A reconstruction of the evolution of caching in corvids has suggested that the common ancestor of corvids was a caching species (de Kort & Clayton 2006). Therefore, taking these points into consideration may aid in interpreting the results of cognitive ecological studies and help in the design of experiments comparing closely-related species which appear to differ in ecology and ethology, i.e. the challenges they face in their given environment and their natural behavioural repertoire.

In justifying the 3E's approach I have described a few studies on a small number of different species. In the following sections, I will discuss further why the 3E's approach - combining ecology, ethology and evolutionary history - is important, by focusing on social information use in birds (Fig. 1). By using detailed case studies of a small number of species, I hope to show how the 3E's determine when the solution to a problem is learned socially and what mechanism may be employed.

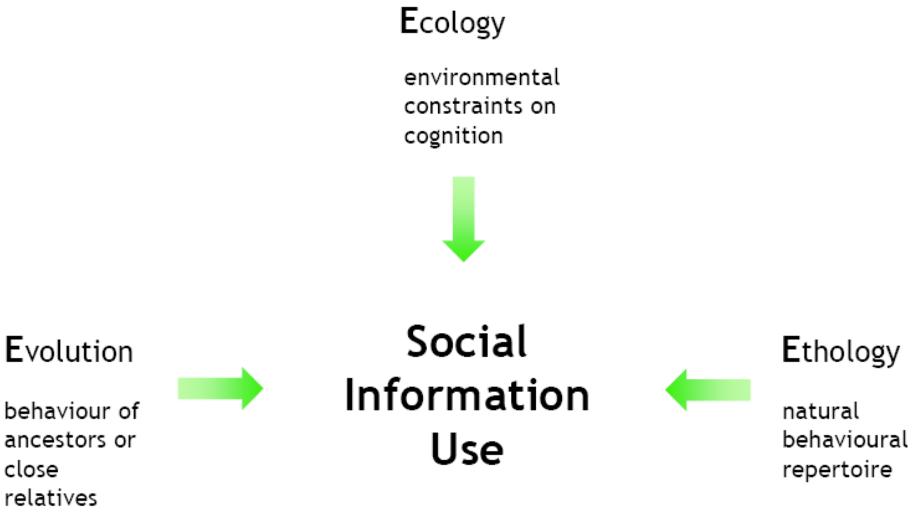


Figure 1. Diagram of the 3E's that influence social information use: Ecology, Ethology and Evolutionary history. Arrows represent the influence of the 3E's on social information use. (Drawing by I. D. Federspiel)

1.4.1 Case studies

1.4.1.1 Corvidae

Western scrub-jays & ravens

Many birds, including western scrub-jays and ravens, cache temporary surpluses of food for future consumption, which they recover days if not months later. Krebs (1990) argued there had likely been considerable selection pressure for them to have highly accurate and long lasting memories of where they hid the food for efficient cache recovery, and he argued that as a consequence, food caching birds had an adaptive specialisation in behaviour, in terms of this enhanced spatial memory, and an adaptive specialisation in brain, in terms of an enlarged hippocampus relative to the rest of the brain. The most striking example of an adaptive specialisation in caching, memory and the hippocampus comes from two populations of black-capped chickadees which live in very different environmental conditions, one in the harsh climatic conditions in Alaska and one in the milder conditions in Colorado, thereby highlighting the importance of ecology (Pravosudov & Clayton 2002). The Alaskan chickadees cache considerably more food than the Colorado ones, even when housed in identical conditions in the laboratory. Furthermore, the Alaskan birds were much more efficient at cache recovery and their performance of spatial but not non-spatial memory tasks was much more accurate. They also had much larger hippocampal volumes than the Colorado ones, both in terms of absolute size and in relation to the rest of the brain. Taken together, these findings support the hypothesis that population differences within a species reflect adaptations to ecological conditions.

The abilities needed for recovering food have been investigated in a study combining spatial memory and social learning and have been called observational spatial memory (Balda et al. 1997). Three corvids that differ in levels of sociality and the number of caches made were required to remember where a conspecific had hidden food (Bednekoff & Balda 1996a, 1996b). Clark's nutcrackers, territorial birds that are thought to be able to remember up to 30,000 food caches (Balda et al. 1997), were less accurate in finding another's caches and could not remember for as long as social pinyon jays and Mexican jays (*Aphelocoma ultramarina*), two species that cache much less food than Clark's nutcrackers. However, less social western scrub-jays (*Aphelocoma californica*) which also cache much less food than Clark's nutcrackers, remembered the location of the caches almost as accurately as the cachers themselves (Clayton et al. 2001). Ravens (*Corvus corax*) were more successful at raiding another's caches if the caches were made more than 3m away from them, suggesting that they were accurate in recovering caches when the cacher was not present to defend them (Bugnyar & Kotrschal 2002).

Although spatial memory is essential for the birds' accurate cache recovery, the birds also need to keep track not only of what they have cached but also what has been recovered, for cache sites may have been emptied, either by themselves or by pilferers. To protect against cache theft, cachers have to employ strategies to either distract others from their caches or to defend them when conspecifics approach them (Dally et al. 2006a). This may only be an issue for corvids, because there is little evidence that other caching species, such as parids (e.g. black-capped chickadees), can remember where another individual has cached (Hitchcock & Sherry 1995; but see Pravosudov 2008 for contrary evidence on the same species).

Most of the studies on social information use in caching experiments have been performed on two species of corvid: common ravens and western scrub-jays. These two species have similar ecologies, with both living in monogamous, territorial or semi-territorial pairs, respectively, or in flocks that include pairs (Clayton & Emery 2007). Although these species are not particularly social in the traditional sense, social information plays an important role for both species in their caching and pilfering. One striking fact is that each individual can play both the role of cacher and pilferer simultaneously, caching their own food, whilst at the same time watching others cache food and them attempting to pilfer those caches (Fig. 2).

Figure 2. A raven caching food in the snow (uncredited photographs are the author’s).

This ‘cognitive arms race’ between cachers and pilferers seems to have driven the food-caching corvids to excel when it comes to social skills (Bugnyar & Kotrschal 2002), such as keeping track of who was watching when and where. Applying the necessary tactics to the acquired knowledge would seem to be beneficial in such a highly competitive environment.

Western scrub-jays, a species also known for its skills in mental time travel (i.e. recollecting past experiences in terms of what they cached where and how long ago and planning for the future in terms of what to cache for tomorrow’s breakfast; Clayton & Dickinson 1998, Clayton et al. 2003, Correia et al. 2007, Raby et al. 2007), are also able to use various cache protection strategies in a flexible manner, choosing the technique most suitable to the context in which the caches were made (Fig. 3).

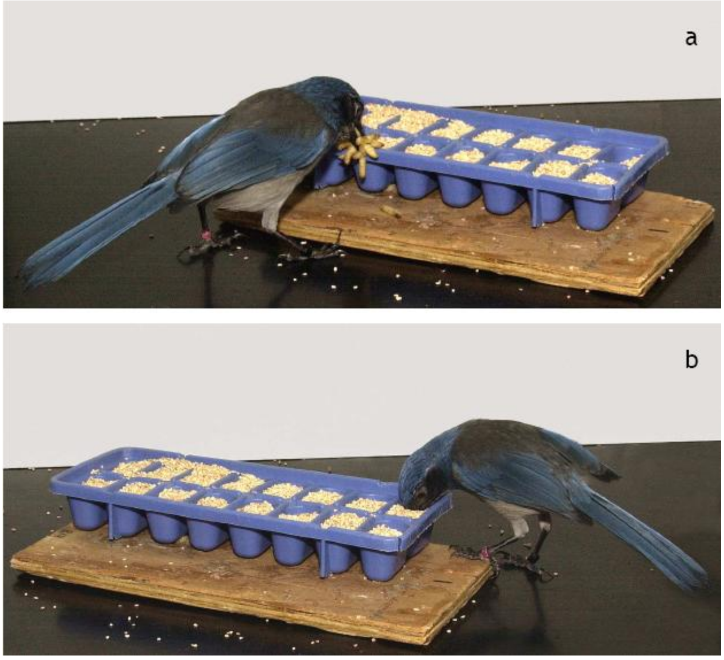


Figure 3. A western scrub-jay (a) carrying worms towards a caching tray and (b) caching a worm. (Photograph by C. R. Raby)

When given the opportunity to cache in full view of an observer or behind a barrier, the cacher chose to hide more food items behind the barrier (Dally et al. 2005; Fig. 4a). When given the opportunity to either cache close to or further away from an observing bird, they chose to cache at a distance, but showed no preference when they were visually isolated from the potential observer (Dally et al. 2005, Fig. 4b). When caching in view of the observer, they moved the food item around multiple times during the caching process. In recovery sessions, during which the food-hiding birds were allowed to approach the caches without being observed, they tended to retrieve the caches made either close to or in view of the observing conspecifics and re-cached them in new sites. When provided with the opportunity to choose between 'shady' and 'well-lit' sites for caching when observed, the jays showed a clear preference for the shady sites, whereas they cached equally at both sites when no observer was present (Dally et al. 2004, Fig. 4c). When recovering, they tended to re-cache those food items hidden in the 'well-lit' sites once the observer had left the scene.

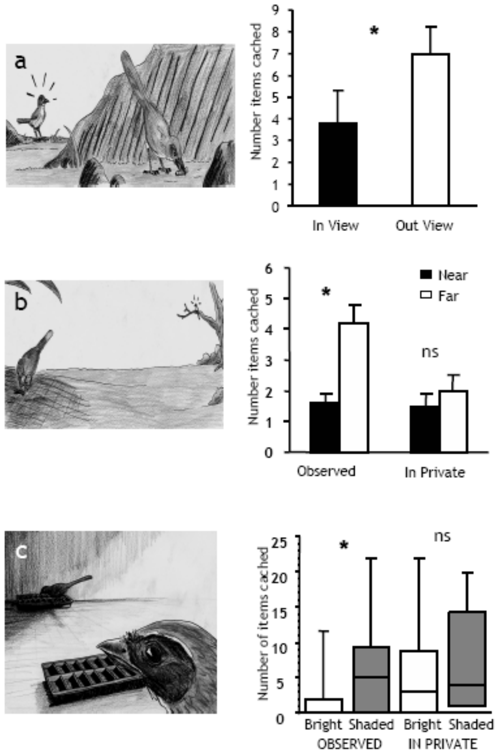


Figure 4. Cache protection strategies of western scrub-jays. (a) Drawing of scrub-jay caching behind a rock, out of view of a competitor. Number of food items cached either behind a barrier or in the open. * $p < 0.05$. Adapted from Dally et al (2005). (b) Drawing of scrub-jay caching as far as possible from another scrub-jay. Number of food items cached in private or when observed by another scrub-jay. In each condition the cacher could store food in two trays; one close to the observer, the other relatively further away. * $p < 0.05$. Adapted from Dally et al (2005). (c) Drawing of a scrub-jay caching in front of another scrub-jay in a shady part of their environment, compared to a well lit part. Number of food items cached in private or when observed by another scrub-jay. In each condition, the cacher could store in two trays; one in a darkened part of the cage, the other in a brightly lit part of the cage. * $p < 0.05$. Adapted from Dally et al. (2004). (Illustrations by S. Stevens)

The scrub-jays therefore appear to use different strategies in different caching contexts. Caching out of view clearly limits the information that can be gained by an observer. In addition to the strategies mentioned, the jays were often observed re-distributing the substrate after caching, making it almost impossible to tell where they had hidden their food (Dally et al. 2005). Increasing the number of caches made in view of the observer may have been used as a strategy to offset the risk of cache loss. Confronted by a single trial with a pilfering conspecific or a human experimenter taking away the caching trays after just having hidden food, jays switched from checking the caches to predominately eating them and caching in 'out of tray' sites that the human experimenter or conspecific could not get to

(Emery at al. 2004). Cachers also use combinations of at least two strategies, for example, when forced to cache in view of the observer, scrub-jays chose to cache at a distance and increase the number of caches, which they later re-cached if they had not been stolen. Especially the caches that were at high risk, i.e. those cached in the sight and/or close to the observer; were later re-cached during recovery (Dally et al. 2005). Scrub-jays also remember who was watching them when making caches in specific locations (Dally et al. 2006b). They were given the opportunity to re-cache food in private or in front of one of two observers, one of which had been present during caching. When in the presence of an observer, they moved more caches from the tray in which they had been watched making caches by that same observer. When re-caching in private, jays cached in 'out-of-tray' locations, whereas when re-caching in front of an observer the jays seemed to use a confusion tactic, moving the caches twice as often as during in private re-caching (Dally et al. 2006b).

Experience as a pilferer also appears to play an important role. Birds were allowed to cache either in private or whilst a conspecific was watching. Individuals given the chance to pilfer others' caches prior to the experiment re-cached only those caches that they had made in front of an observer. Jays without pilfering experience did not, suggesting some sort of experience projection (Emery & Clayton 2001; Emery & Clayton 2008). Social information use not only plays a role in the caching context, but also during foraging at a new food resource. In a field study, Florida scrub-jays (*Aphelocoma coerulescens*) learned to forage at a novel patch where conspecifics had already foraged successfully. Juveniles that watched others digging for peanuts and were able to scrounge learned more about the technique than control individuals. Watching the demonstrations increased the probability that the birds would approach the novel patch, and occasionally, demonstrators modified their behaviour 'in a way that suggested teaching' (Midford et al. 2000, p.1205).

Ravens have also demonstrated impressive performances in social information use, including caching and pilfering tasks. Recently, ravens have been found to learn about their competitors in caching bouts during play caching of objects (Bugnyar et al. 2007). In the wild, ravens were observed to hide themselves when caching food (Heinrich & Pepper 1998) and protecting their caches by retrieving the food or aggressively approaching others who come close to their caches (Heinrich 1999). Controlled experiments revealed that they appear to differentiate between birds that were present during a caching event and those that were not (Bugnyar & Heinrich 2005, 2006; Fig. 5).

Figure 5. Ravens during a caching experiment; the observer (top left) watches the storer (right) through a window. (Photograph by T. Bugnyar)

When released back into the caching area, storers retrieved more caches when they were accompanied by a knowledgeable conspecific (present during caching) than they did together with ignorant birds (absent at caching) (Fig. 6a). However, they only retrieved the caches, when the conspecific was moving towards them, suggesting that the ravens were acting upon the behaviour of the competitors (Fig. 6b). To rule out the possibility of the ravens acting on the basis of whom they had seen during a caching event, a second experiment was performed, this time with a human experimenter making the caches. A subject was able to observe the experimenter and could then enter the site, either with a co-observer, a non-observer or in private. The subjects delayed caching when given access to the site together with a dominant non-observer, but did not differentiate between dominant and subdominant co-observers, going straight to the cache with either observer. This led to the subjects being first at the cache in all but one of the cases with the non-observers, even though they delayed approaching the cache with the dominant non-observer. In cases in which the subject was dominant, it always reached the cache before the co-observer, but with a dominant co-observer, they almost failed (Bugnyar & Heinrich 2005). Approaching the cache as fast as possible with a co-observer therefore seemed to be the only potential method of getting the food.

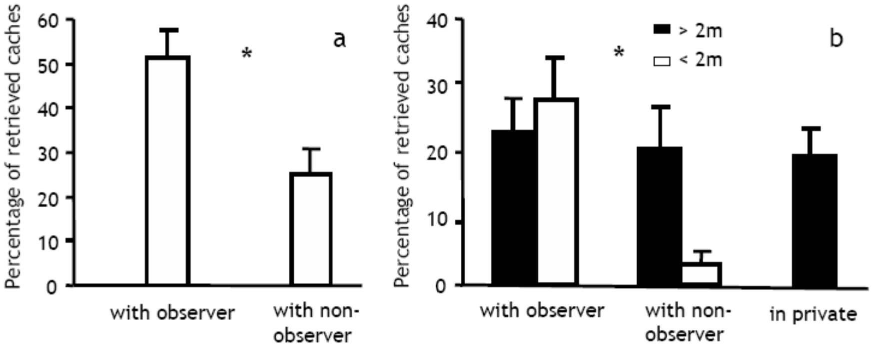


Figure 6. Mean percentage of caches retrieved by storers with previous observers and non-observers (a) and when competitors approached the caches (white bars) or did not come near them (black bars). * $p < 0.05$. Adapted from Bugnyar & Heinrich 2005.

Ravens adjust their behaviour in line with the social relationship and knowledge state of their opponent. As storers, they selectively retrieved caches that others were able to watch being made, and as pilferers they hurried to the cache with a co-observer, but delayed approaching with a dominant non-observer (Fig. 6). Similar to western scrub-jays, ravens demonstrate some understanding of another's perspective. Further evidence for this comes from an experiment in which a subordinate began to lead a dominant conspecific away from a food resource about which only the subordinate had knowledge of. Subsequently, the dominant bird learned not to stop following the knowledgeable subordinate bird and started searching for the food themselves (Bugnyar & Kotrschal 2004).

Ravens feed opportunistically on animal and plant material and are also carrion scavengers, feeding on road kill. Information about new food resources may be passed on at so-called information centres (Heinrich 1999), through food calls (Bugnyar et al. 2001) or via visual social information. Individuals accessing new food resources are thus an interesting stimulus for others. In an experiment with a small group of ravens, birds observing others opening a food box tended to open the box using the same technique (Fritz & Kotrschal 1999). A demonstrator was trained to open the box by pulling a flap to open the lid. Non-observer birds, i.e. the birds of the control group that did not watch demonstrations of how to open the box by pulling the flap, exclusively opened the box by pecking at a crevice in the middle and then levering the lid open. The observer birds, i.e. the birds that could watch demonstrations, were faster at approaching the box and also at opening it than the non-observers. They also initially used both possible opening techniques: pecking and pulling. It therefore seems likely that the observing birds were influenced in their choice of technique by the demonstrating birds. Whereas two of the three observers went on to almost exclusively open the box by pecking, the third retained the pulling technique. Due to the two different initial positions a bird had to assume in order to perform one of the two actions, the authors concluded that both imitation and stimulus enhancement could have accounted for the observers' performance (Fritz & Kotrschal 1999). Social information use seems to be somewhat enhanced between siblings. When they were able to watch a conspecific manipulate an object, ravens manipulated the same object (out of a choice of five), if the conspecific was their sibling (Schwab et al. 2008). This may have been due to socially biased learning (Fragazy & Visalberghi 2004), with individuals tending to learn from siblings rather than non-siblings.

Social learning was also found to have an effect on the spread of vocalizations by ravens (Enggist-Dueblin & Pfister 2002). Similar to other songbird species, ravens learn calls from other individuals in their group, and specific dialects spread within sub-populations via social learning (Gwinner 1964). Enggist-Dueblin and Pfister (2002) recorded the vocalizations of free-ranging ravens interacting with a captive pair and analysed the different types of vocalizations, their distribution and their differences and similarities. Interestingly, there seemed to be no difference in repertoire size between males and females, which contrasts with the majority of songbirds (Catchpole & Slater 1995). The calls were mainly transmitted within sex, and in a few cases, to the partner, leading to a sex-specific call repertoire. The authors were able to divide the study site into three different parts on the basis of the geographical distribution of the different call types, suggesting a cultural process.

In summary, although territorial, ravens need to be able to use social information to deal with a highly competitive environment. An additional selection pressure is their diet and heterospecific competitors, such as wolves (*Canis lupus*), at carcasses. It was observed that ravens adjust their behaviour to the presence of wolves, which occasionally kill ravens when defending food, but not adjust their behaviour to boars (*Sus scrofa*), which do not pose a threat to ravens. When at the carcass with wolves, ravens specialised on scrounging rather than approaching the food resource themselves (Bugnyar & Kotrschal 2002). Finding a new food resource, dealing with competition over food and also establishing a vocal repertoire and communicating with others require social information use in a raven's life.

For caching species in general, the ability to use social information seems to be vital in order to pilfer another's caches, remember who was watching during a caching event, and protecting one's own caches. Furthermore, the evolutionary history of the species must also be taken into account. As I described earlier, de Kort & Clayton (2006) concluded that the common ancestor of all corvids was a moderate cacher and that the emergence of specialised cachers evolved independently at least twice. It seems obvious that moderate and specialized species possess the skill of using social information for employing cache protection strategies, and since the ancestors of the western scrub jay were either moderate or specialized cachers and the ancestors of the raven were moderate cachers (de Kort & Clayton 2006), one can legitimately assume that the ancestors of both of these species were able to use social information.

Together these findings indicate that scrub-jays and ravens use flexible caching and recovery strategies when hiding and protecting their own caches from the risk that others might steal them, and also in their role as thief of another's caches. Their feeding ecology, social system and the evolution of caching behaviour has shaped their skills in social information use with respect to storing and stealing.

1.4.1.2 Jackdaws

In another corvid species, the jackdaw (*Corvus monedula*), social information may play a role during foraging. Jackdaws are gregarious birds which are especially attentive to their partner's behaviour (Fig. 7, Röell 1978, von Bayern & Emery, 2009). However, they are less attentive to conspecifics than ravens (Scheid et al. 2007). Jackdaws feed mainly on invertebrates, including opportunistically catching insects on the wing, but they also forage in flocks on the ground for seeds, etc., with single birds joining these flocks when searching for a food resource (Wechsler 1988a, see Chapter 2).

Figure 7. A jackdaw foraging (right) and a conspecific (left) paying close attention (a), then approaching and exploring at the identical location (b-d).

Although jackdaws are a non-caching corvid species, they can remember the location of food on the basis of spatial and object-specific information, whereas food-caching Eurasian jays (*Garrulus glandarius*) respond preferentially to spatial cues (Clayton & Krebs 1994). In a field study on the social influences on foraging, a jackdaw colony was presented with food hidden in nine containers (Röell 1978). The alpha male had been trained to find the food, and which individuals approached and explored the containers was also recorded. The jackdaws hardly ever approached the containers in the absence of others. However, when the alpha male was present and gaining food, other jackdaws immediately joined him, exploring the containers and so learned how to open them. Most of the birds learned by supplanting a bird exploring the food source, indicating local enhancement followed by individual learning as the underlying learning mechanism. Similar results were found in a study using two different food dispensers (Wechsler 1988b). The birds had to either press a lever or pull a plastic disc to gain food. The behaviour spread through the group within two months, and 22/28 birds learned to press the lever, 23/28 to pull the plastic disc, however the birds did not preferentially chose to copy the method of their social partner. These results could not rule out individual trial-and-error learning, and it appears that there was some general enhancement effect, because the birds' attention was drawn to the dispensers, but in the beginning of the study they did not seem to know exactly how to operate the mechanisms. A similar result was found in a recent experiment in which jackdaws that had the opportunity to watch a conspecific opening a food box and feeding from it, approached the box faster, stayed close to the box for longer and showed a higher persistency in exploring the box than birds that were tested without demonstrations (Federspiel & Emery, in prep).

In conclusion, social information seems to play a less vital role in jackdaws than ravens and western scrub-jays. Although jackdaws are a more social corvid species, their ecology does not require them to use social information to the same extent as scrub-jays and ravens. They feed on abundant types of food; jackdaws may therefore not need to learn much about food via social information. However, the fact that they learn where to find food from their conspecifics in an experimental context shows that they have the capacity to do so. Since their diet does not include hard-to-access or process foods (no evidence for extractive foraging), they only need to learn the location of the food, but not how to process it. Therefore, the relatively simple mechanism of local enhancement seems to be adequate for their requirements.

1.4.1.3 Psittacidae

Keas

In contrast to jackdaws, some birds that feed on hard-to-access foods may need more complex social learning mechanisms, such as imitation or emulation, to learn how to access the palatable part of the fruit, nut, meat, etc. One example of the influence of ecology on social information use is the kea (*Nestor notabilis*), New Zealand's mountain parrot. Little is known about the mating system of this species, but certain occasions, such as feeding, appear to bring them together in large gatherings. As juveniles, keas form large flocks and travel around exploring their environment together (Diamond & Bond 1999). A complex dominance network, a relatively long developmental period of the young and various forms of social and object play may have contributed to their social intelligence (Diamond & Bond 1999, Keller 1975). Furthermore, the lack of predators and the patchy distribution of food in the winter are thought to have led to their extreme neophilia (Diamond & Bond 1999). A group of captive keas demonstrated flexible use of different social techniques to gain food in cooperation tasks (Federspiel 2006, Werdenich 2006), and dominant birds were even found to manipulate lower-ranking birds to coerce them into producing a food reward (Tebbich et al. 1996). In social learning tasks, ambiguous results have been found. Whereas in some field and laboratory studies there is little or no evidence of social learning (i.e. in the field: tube-lifting, Gajdon et al. 2004; rubbish bin opening, Gajdon et al. 2006; lab: social learning apparatuses, Pesendorfer 2007), in others, indicators of imitation and emulation have been reported. In a task with an artificial fruit and three locking devices (a bolt, a pin and a screw), observers that observed a conspecific performing the opening sequence displayed shorter latencies to approach the apparatus, a greater persistence in manipulating the devices and a higher success rate at opening the apparatus compared with those that did not observe a demonstrator (Fig. 8, Huber et al. 2001).

Figure 8. A kea performing two of the three required actions: poking out the bolt (a), pulling out the pin (b). (Photograph by L. Huber)

A second experiment with just one opening mechanism revealed keas' use of imitation; a crank had to be rotated repeatedly to get to the food reward, and two of the six observers copied the model's actions rather than just the outcome (Huber 2002). Although generalization across the whole species cannot be drawn from just two individuals, there does seem to be an indication of the capacity to imitate. Why the keas did not use imitation in the more complex task with the three locking devices remains unclear. There may be an urge to employ individual learning once they have learned about the affordances of an object, i.e. what can be done with/to the object.

Ecology must be a strong factor in the keas' use of social information. With no predators around and the urge to always search for food, especially in winter, when the surroundings are covered in snow (Campbell 1976), keas have become a flexible, opportunistic and very curious species (Diamond & Bond 1991). They live in the Southern Alps of New Zealand between elevations of 700m and 2000m and in winter fly down to the coast to find food. They feed on at least 89 plant species and nine animal species, nectar and fruit, and turn over stones to get to invertebrates (Breejaart 1988). Foraging on hard-to-access foods is thought to result in the development of larger brains in primates (Gibson 1986), and so the same argument could be made for large-brain birds, such as keas, that feed on openly available food types. In general, habitat opportunists show lower levels of neophobia (Greenberg 1990) and island populations show more exploratory behaviour (Mettke-Hofmann et al. 2002). This may have led to their well-developed manipulation skills and their persistence on instrumental tasks (Kubat 1992), influencing their approach to solving technical problems and the development of an advanced form of technical intelligence. During object play, they train their manipulatory skills and gather information about the affordances of an object (Inglis 1983). They are also well known for their playfulness and destructiveness around human settlements (Forshaw 1977), exploring and tearing apart everything they can get to.

As mentioned earlier, the social component may have also contributed to the keas' skills in social information use. They experience an extended post-fledging period of dependency on the parents and join juvenile flocks in their second summer. Under these conditions there are plenty of opportunities to utilise social information (Porter 1974, Lint 1958, Jackson 1963). Furthermore, there is an intricate dominance hierarchy in kea groups (Diamond & Bond 1999), which resembles a network, rather than a linear hierarchy such as found in chickens. Keeping track of relationships in the group may have further driven their skills for picking up social information, similar to pinyon jays.

Evolution also suggests the presence of social information use in the ancestors of the kea. The Order Psittaciformes includes roughly 350 species, that are commonly grouped into two families, namely cockatoos (Cacatuidae) and true parrots (Psittacidae), although different systematics exist. One tribe of the sub-family of the typical parrots (Psittacinae) is the Nestorini, consisting of three species: the Norfolk kaka (Nestor productus), which became extinct in the first half of the 19th century, the kaka (Nestor meridionalis) and the kea (Pies-Schulz-Hofen 2004). The ancestor of the three species was a 'Proto-kaka', which is thought to have lived 15 million years ago, when New Zealand was still a single, large island. During the Pleistocene, New Zealand was dissected into two smaller islands, the climatic conditions changed, and the differences between the northern and southern environments became extreme. The population living under harsh conditions in the south became keas; the population in the north became kakas, which specialised on fruits and insects of the rain forest (Diamond & Bond 1999; to this date, as far as I know, there are no data on comparative genomics). During the Holocene, there was an increase in the growth of forests, and the kaka returned to the south island of New Zealand, pushing the keas out of their foraging niche and thus forcing them into the alpine habitat. Although little is known about the supposed behaviour of the ancestors of the kea, their habitat and the extreme changes in temperature and environment they experienced suggest that keas would have been at an advantage using social information use and thus benefiting birds that were already adapted to these new living conditions. The kaka's varied diet suggests something similar. Similarities in the complexity and diversity of social play in keas and kakas (Diamond & Bond 2004) also indicate pronounced social skills in the close relatives of the kea. The relatively solitary lifestyle and the less complex play of the kakapo (*Strigops habroptilus*; Diamond et al. 2006), a close relative of the kea belonging to the Psittacinae and the tribe Strigopini, indicates the kea's social information use as a relatively novel phenomenon in evolutionary terms. However, this is necessarily speculative as it is constrained by information on the number of species.

1.4.1.4 Anatidae

Geese

Another gregarious species, greylag geese, live in large flocks of families, pairs and unpaired birds and form life-long pairs from their 3rd or 4th year. Their diet mainly consists of roots, fruits, flower-heads, leaves and stems (Cramp 1977). Certain behaviours related to feeding, such as adopting a novel food into the diet, are transmitted via social information use within groups (Fig. 9).

Figure 9. A goose foraging in the grass (front) and another watching (back). (Photograph by I. Nedelcu)

One year after some individuals were first observed to bite through the stems of butterbur leaves (*Petasites hybridus*), almost all the individuals of a semi-tame flock of geese displayed that behaviour (Fritz et al. 2000). The behaviour spread particularly quickly between birds that spent most of their time together, such as related animals, suggesting social influence on the learning process (Coussi-Korbel & Fragaszy 1995). It was even observed that ganders left stems to goslings if the goslings approached them whilst the gander was biting on the stems. To gain an insight into the processes involved, Fritz and colleagues (2000) conducted an experiment with a food box that could be opened by sliding a lid open. A human demonstrator showed them how to open the box, and all seven observers learned the action, whereas only one of the seven control animals that had not received a demonstration managed to solve the task. The observers showed no imitation, but explored the location more often at which the demonstrators had touched the box, which facilitated individual trial-and-error learning. Thus, observing an experienced conspecific chewing through the stems of butterbur leaves and may have accounted for the spread of the behaviour through the group (Fritz et al. 2000, Fritz & Kotrschal 2002).

The social lifestyle of the geese provides them with numerous opportunities to use social information. They are gregarious, except when nesting, live in flocks made up of families, pairs and unpaired birds and come together during moulting and migration. Individuals in a group support one another actively (participation of a social ally) and passively (mere presence of an ally reduces stress) during agonistic encounters (Scheiber et al. 2005, Weiss & Kotrschal 2004). Life-long monogamy is the rule, with males and females associating all year round (Cramp 1977). Nevertheless, their diet suggests no particular need to learn from others. They feed on abundant food resources, such as plants on the ground or water surfaces, flower-heads and fruits. It seems that geese will pick up social information if they are able to, but do not rely on it. Similar to jackdaws, local enhancement may therefore be sufficient for their requirements.

Although numerous fossil species have been suggested as ancestral to this genus (Brodkorb 1964, Livezey 1986, Short 1970), little is known about the social life of the ancestors of geese and living close relatives share a similar ecology. Species of the genus *Anser* are largely herbivorous wetland species (Cramp 1977). Given the similar diet and environment, it is unlikely that the relatives and the common ancestor of the genus *Anser* employed more complex forms of social information use. Again, the phylogenetic group to which grouse belong would be good to know.

1.4.1.5 Tetraonidae

Black Grouse

A different form of social information use is employed by some families of the order *Galliformes*, such as certain game birds (Family Phasianidae) (for Japanese quail, *Coturnix japonica*, see Galef. & White 2000 and White 2004) and grouse (Family Tetraonidae). One example is the European black grouse (*Tetrao tetrix*). Black grouse tend to be gregarious throughout the year with stable lekking groups in the spring and less stable groups in the autumn and winter (Cramp 1977). At leks (i.e. mating areas), males gather within sight of each other to court and compete at the outset of the breeding season. They perform mating displays and thus attract females they subsequently mate with (Tomkins 2004).

At the leks, it was found that after being chosen by one female, a male is generally more likely to be chosen by other females. Further experiments with model females revealed that rather than just seeing a male close to other females, watching a male actually copulating with a female made him more attractive to other females (Höglund et al. 1995). Copying the choice of others seems to be an additional process from the normal mate choice process of females (Höglund et al. 1995). Since some females may not have the opportunity to copy others, mate choice copying may not always be employed. In particular, young, inexperienced animals may benefit from copying others' choices. Although a well-known phenomenon, it seems that the ultimate reasons for mate choice copying are not yet clear. There are several theories however, ranging from avoiding the costs of independently sampling mates, to managing information and filtering out the unimportant information and simply reducing the errors made during mate choice and learning from knowledgeable conspecifics about the quality of potential mates (White 2004). Furthermore, local adaptations of the population are transmitted to the next generation, possibly leading to epigenetic changes (Freeberg 1998).

When the birds come together to form leks every year, females repeatedly have the opportunity to copy others' mate choice. Although the costs and benefits of mate choice copying are altogether not clear, using the social information of a conspecific about a male's fitness seems to have an advantage over individual learning. Their diet consists predominantly of abundant plants, such as berries and grasses (Cramp 1977), suggesting no particular requirement for social information use when it comes to accessing or processing food. Their usage of social information may therefore be restricted to the context of mate choice, but more experimental work needs to be performed to draw firm conclusions.

In terms of the influence of evolutionary history on the existence and the type of social information use, the close relatives of the black grouse may provide an insight. The birds of the genus *Tetrao*, such as the Caucasian Black Grouse (*Tetrao mlokosiewiczi*), the Capercaillie (*Tetrao urogallus*) and the Black-billed Capercaillie (*Tetrao parvirostris*) all form leks to display and choose mates (Madge & McGowan 2002), and even earlier in the genealogy, within the family of Tetraonide, all but one species, the willow grouse (*Lagopus lagopus*), the males are polygamous. This suggests similar social information use in the common ancestor.

1.5 Conclusions

In this chapter I have argued that knowledge of the ecology (environmental pressures), ethology (natural behaviour) and evolutionary history of a species is essential for understanding how the mechanisms responsible for social information use have been shaped. However, to understand these mechanisms and to define in what ways, if any, they differ between species we must adopt an integrative approach, combining the 3Es with knowledge of Experimental Psychology, in order to obtain rigorous experimental validity. Only then can we hope to understand why two behaviours which, when taken at face value, appear identical, are in fact examples of convergent evolution resulting from similar ecological, but not evolutionary histories. Similarly, it is only by taking this integrated approach that we can hope to show that two 'different' behaviours share an evolutionary antecedent and components of the same underlying mechanisms. Instead of only analysing the psychological processes involved in social learning mechanisms, taking these other components into consideration provides us with a more complete picture. There are still obvious gaps in our knowledge that restrict our use of this approach when it comes to investigating the evolutionary history of social information use. For these cases, the 3E's approach may be a useful tool for making predictions about how to direct future research. To improve this approach, more knowledge on physiological constraints and adaptations is needed and has to be integrated in the framework. More comparative work is clearly needed to determine the influence of ecology and evolutionary history on social information use, and experiments using different tasks should shed light on whether the capacity to use social information is domain-specific.

For example, rooks and jackdaws both pair for life, yet rooks engage in extra-pair copulations (Røskaft 1983), whereas jackdaws do not (Henderson et al. 2000). Although very closely related, we might predict that rooks will copy the choice of another's sexual partner during acts of promiscuity, whereas we might also predict that it would be futile to test mate choice copying in jackdaws who do not appear to commit infidelity. Therefore, jackdaws' social information use may be restricted to certain domains (e.g. behavioural coordination within the pair bond, learning about the location of good food patches) and not others (e.g. choice of partners during extra pair relations, extractive foraging techniques). We can therefore use knowledge of how the 3E's have influenced a particular species' life history to drive the development of appropriate research questions and methods, but also provide post-hoc explanations of successes and failures in psychological experiments. This makes the 3E's approach a very powerful research tool for cognitive ecology, but one that is only as good as the information provided by ecologists, ethologists, evolutionary biologists and comparative psychologists.

It will be the challenge of this thesis to apply the 3E's approach to social learning experiments with corvids. Combining established knowledge on social structure, individual differences and feeding ecology, I will investigate social learning skills in light of this new framework. This thesis addresses four main questions: (1) How do social relationships develop and is there a difference in social complexity between rooks, jackdaws and Eurasian jays? (2) Do rooks and jackdaws learn socially or do they rely on individually gained information? (3) If they do learn socially, which mechanism do they employ and how do the findings relate to the species' sociality and feeding ecology? (4) Are there stable individual differences between individuals of each of the species?

1.6 Thesis overview

Chapter 2 sees investigation of social relationships in rooks, jackdaws and Eurasian jays, with additional focus on social bonds and dominance hierarchies. Lastly, I will determine the stability of existing relationships in adult birds and look at the development of relationships in young birds.

Chapters 3 and *4* provide insight into social learning skills of jackdaws. I then report findings from studies using two different methods: a classical 'one-on-one' setting, with one observer watching one demonstrator and individual test sessions after the initial observation sessions, and a group setting, with both observation sessions and test sessions conducted in a group of jackdaws. *Chapter 5* turns to rooks and their social learning skills, using a relatively new technique in social learning research - video playback. *Chapter 6* addresses individual differences between members of each of the three species. Finally, *Chapter 7* summarises the findings of the thesis, addresses the main questions this thesis set out to answer (see above) again and points to potential future directions for social learning research.

Chapter 2.

The development of social bonds and dominance hierarchies in rooks, jackdaws and Eurasian jays

2.1 Abstract

Sociality is thought to be the prerequisite for social learning, as it creates opportunities for individuals to learn from others. The social complexity of any given species can be investigated by analysing the structure of a group. Two main factors contribute to the structure of a social group: social bonds and dominance hierarchies. In this chapter, I will discuss findings of a long-term study on sociality in rooks (2 adult groups, 1 fledgling group), jackdaws (1 adult group, 1 fledgling group) and Eurasian jays (1 fledgling group). Social proximity (sitting within two body lengths of each other) and displacements (one individual retreats after having been approached by another) were observed. From this data, I determined social bonds and calculated dominance hierarchies and sociograms for each of the six groups. (It is hypothetically possible that social proximity is associated with socio-negative behaviour, but this is not applicable here.) Stable social bonds and dominance hierarchies were found for jackdaws and rooks, but not for Eurasian jays. Social bonds observed in the corvids fell into one of three categories: bonds between siblings, pair bonds between different-sex partners and pair bonds between same-sex partners. These bonds were present in birds that were already adult at the onset of the study; the birds that started the study as fledglings, developed pair bonds when they were approximately 8 to 10 months (jackdaws) or 6 to 8 months old (rooks). Findings are in line with the social systems of the three species.

2.2 Introduction

As mentioned in *Chapter 1*, with birds, social learning may be an adaptive specialisation to group-living (Klopfer 1959). In a social environment, information is available to individuals in various situations, ranging from foraging to vigilance towards predators. Social animals therefore have an advantage over solitary animals in that they are not limited to information acquired individually, but may also have access to socially transmitted information. Two main factors that contribute towards sociality and hence group structure are the dominance hierarchy (as a form of competition; deriving from agonistic encounters) and the bonds between group members (as a form of cooperation; developed through social proximity and affiliative behaviours).

The first main factor that influences the structure of a group is the bonds between group members. Such stable social bonds have been described in various species, ranging from chimpanzees (Muller & Mitani 2005) to the mouth-brooding cichlids of the genus *Tilapia* (Russock 1999) and ants of the genus *Myrmica* (Brian 1986). When two individuals meet for the first time, a conflict may arise, one individual might dominate the other, and a dominance relationship may thus be formed. Alternatively, affiliative actions could be exchanged, such as preening or food sharing, which could lead to the formation of an affiliative social bond. In a conflict situation, game theory predicts that group members are expected to use behavioural tactics to minimise costs (physical and social) and to maximise benefits, such as potential future cooperation (Baker & Aureli 2000). Mitigating aggressive tendencies and minimising escalation are beneficial for both opponents (Archer & Huntingford 1994) and, as mentioned above, can be based on different mechanisms. Reducing uncertainty and tension facilitates interaction and thus the establishment of a social relationship or even a bond (Baker & Aureli 2000).

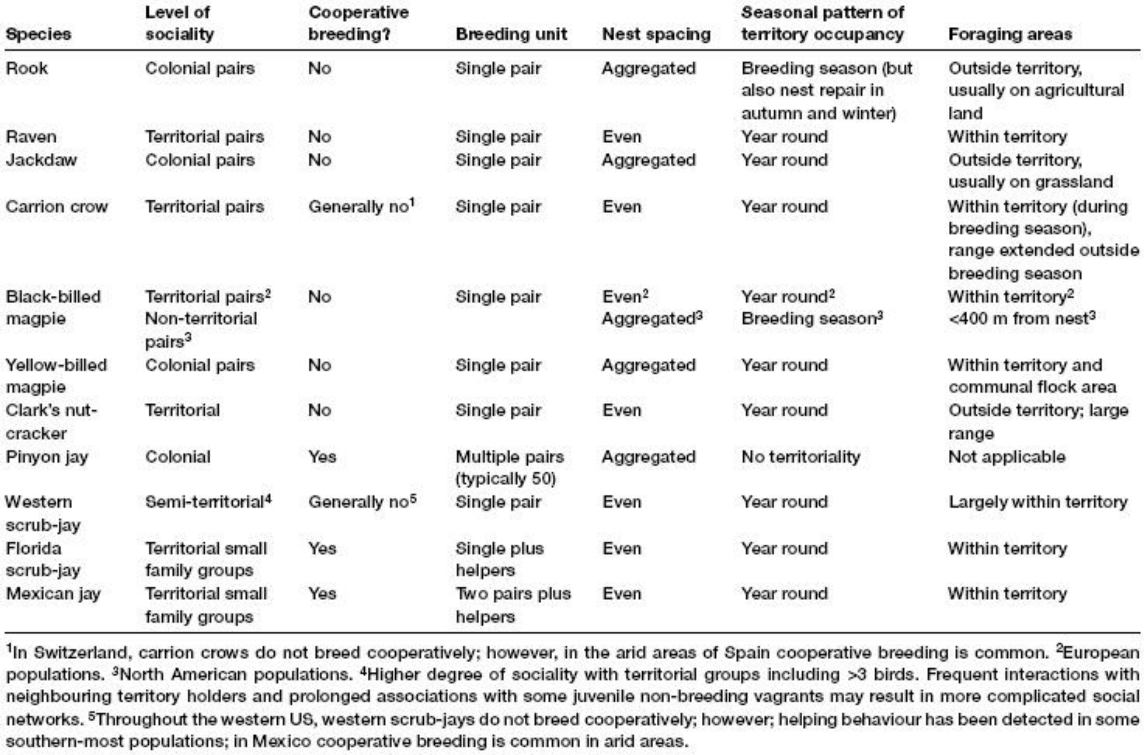
Two mechanisms are thought to be involved in the process of establishing a bond: ‘mutual shaping’ and a ‘species-typical etiquette’ (Mendoza 1993). In mutual shaping, individuals influence each other’s behaviour during an interaction, start predicting the outcome of actions (not necessarily consciously) and gradually arrive at a stage of shared expectations and tolerance. Species-typical etiquette, a strategy supposedly superior to mutual shaping due to lower costs involved, leads to the performance of a sequence of species-typical behaviours that quickly promote tolerance and affiliation (Baker & Aureli 2000). This sequence usually bears a remarkable regularity during the first few minutes of an encounter, as described for gelada baboons (*Theropithecus gelada*; Kummer 1974), hamadryas baboons (*Papio hamadryas*; Kummer 1995), crab-eating macaques (*Macaca fascicularis*; Welker et al. 1980), rhesus macaques (*Macaca mulatta*; Maxim 1976) and chimpanzees (*Pan troglodytes*; Baker & Aureli 2000).

In chimpanzees, grooming seems to be a crucial affiliative behaviour leading to the establishment of social bonds. Thus, it is often used as a measure for the quality of a social bond (Cords 1997, Mitani 2009). In birds, preening and food-sharing, the equivalent to primate grooming, play an important role in the establishment and maintenance of bonds, as well as other affiliative behaviours, such as synchronised displaying, bill twining, object play, caching food together or social support in agonistic interaction with others (de Kort et al. 2006, Emery et al. 2007, von Bayern et al. 2007). As an umbrella for all affiliative behaviours, social proximity (sitting in close contact) can be used as a measure of affiliation. The time individuals spend in close proximity to one another determines whether or not they will have opportunities to exchange affiliative behaviours and how many of those opportunities will arise. In a group, different amounts of time spent together between two individuals will lead to differential opportunities for dyads to form social bonds. Those bonds between group members contribute towards group cohesion (Baker & Aureli 2000) and are therefore expected to play an important role in social species.

The second factor that contributes to group structure is the dominance hierarchy. In a social group, where individuals interact with each other on a daily basis, dominance relationships will be established at a certain point during the animals' development (Katzir 1981, p. 1). By adopting places in a structured dominance hierarchy, individuals may save not only time and energy, but also avoid the risk that would occur if relative positions had to be established every time two or more individuals meet (Chase et al. 1974). These relationships will produce consistent outcomes over successive encounters without requiring the investment of high levels of energy (Drews 1993). Dominance within a group plays a major role in a social individual's life since it determines who gets access to food, mates and shelter (Huntingford & Turner 1978), however subordinate individuals may adopt alternative strategies to cope with their role within a group (Gross 1996).

Members of the corvid family vary greatly in their levels of sociality; some species are territorial with individuals spending the main part of their day on their own or with their partner in the breeding season, whereas others forage and roost in big groups (Clayton & Emery 2007, see Table 1). In carrion crows (*Corvus corone corone*), differences are even found between populations: generally territorial birds, they were observed to breed cooperatively in arid regions of northern Spain (Baglione et al. 2002).

Table 1. Levels of sociality in the family of Corvidae. Taken from Clayton & Emery (2007).



Species	Level of sociality	Cooperative breeding?	Breeding unit	Nest spacing	Seasonal pattern of territory occupancy	Foraging areas
Rook	Colonial pairs	No	Single pair	Aggregated	Breeding season (but also nest repair in autumn and winter)	Outside territory, usually on agricultural land
Raven	Territorial pairs	No	Single pair	Even	Year round	Within territory
Jackdaw	Colonial pairs	No	Single pair	Aggregated	Year round	Outside territory, usually on grassland
Carrion crow	Territorial pairs	Generally no[1]	Single pair	Even	Year round	Within territory (during breeding season), range extended outside breeding season
Black-billed magpie	Territorial pairs[2] Non-territorial pairs[3]	No	Single pair	Even[2] Aggregated[3]	Year round[2] Breeding season[3]	Within territory[2] <400 m from nest[3]
Yellow-billed magpie	Colonial pairs	No	Single pair	Aggregated	Year round	Within territory and communal flock area
Clark's nut-cracker	Territorial	No	Single pair	Even	Year round	Outside territory; large range
Pinyon jay	Colonial	Yes	Multiple pairs (typically 50)	Aggregated	No territoriality	Not applicable
Western scrub-jay	Semi-territorial[4]	Generally no[5]	Single pair	Even	Year round	Largely within territory
Florida scrub-jay	Territorial small family groups	Yes	Single plus helpers	Even	Year round	Within territory
Mexican jay	Territorial small family groups	Yes	Two pairs plus helpers	Even	Year round	Within territory

[1] In Switzerland, carrion crows do not breed cooperatively; however, in the arid areas of Spain cooperative breeding is common. [2] European populations. [3] North American populations. [4] Higher degree of sociality with territorial groups including >3 birds. Frequent interactions with neighbouring territory holders and prolonged associations with some juvenile non-breeding vagrants may result in more complicated social networks. [5] Throughout the western US, western scrub-jays do not breed cooperatively; however; helping behaviour has been detected in some southern-most populations; in Mexico cooperative breeding is common in arid areas.

In numerous studies, corvids have demonstrated impressive social skills in the past, ranging from behavioural coordination (Emery et al. 2007; Fig. 10) and post-conflict affiliation (Seed et al. 2007) in rooks (*Corvus frugilegus*), noticing who was watching while they were hiding food ('caching') and then adapting to it when retrieving the food or using various deception techniques already when hiding food in Western scrub jays (*Aphelocoma californica*; Dally et al. 2006a, Dally et al. 2006b; Dally et al. 2004, Dally et al. 2005, Emery at al. 2004) to similar cache protection skills and deception in ravens (*Corvus corax*, Heinrich & Pepper 1998, Heinrich 1999, Bugnyar & Heinrich 2005, 2006; Bugnyar & Kotrschal 2004) and transitive inference in pinyon jays (Paz-y-Miño et al. 2004).

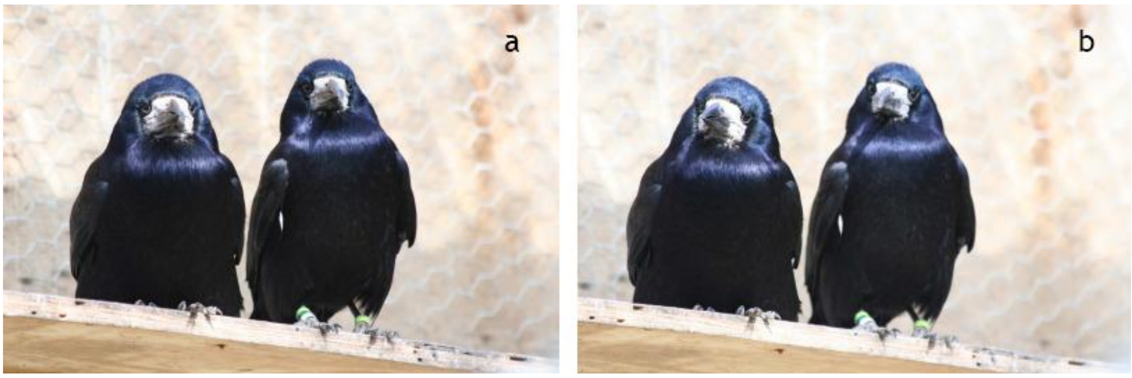


Figure 10. An example for behavioural coordination in rooks: members of a pair bond turn their heads to their right in a synchronised fashion.

Corvids are believed to be monogamous birds that form life-long pair bonds by mutual preening, bill twining and food sharing. This has been tested in jackdaws: a previous study revealed the importance of food- and object-sharing during the development of social bonds (von Bayern et al. 2007). Giving was directed towards a few conspecifics, but then became selective towards just one partner, which marked the dissolving of family bonds and the establishment of affiliative partnerships.

In this study, I will focus on social proximity (two individuals sit within two body lengths of one another) and displacements (one animal retreating after having been approached by another) as measures for the social structure within groups. I will investigate how those factors contribute to the establishment of bonds and hierarchies within six groups of corvids (comprising three different species) that were observed. In the following section, I will introduce the three species that I worked with for this study and the rest of my thesis: jackdaws (*Corvus monedula*), rooks (*Corvus frugilegus*) and Eurasian jays (*Garrulus glandarius*). They are all oscine passerine bird species belonging to the family of Corvidae, which includes more than 120 species, such as various crows and jays, magpies, ravens and nutcrackers. Jackdaws and rooks belong to the genus *Corvus*; Eurasian jays are part of the genus *Garrulus* (Fig. 11; for a phylogeny of the core-group Corvidae based on characteristics of tongue skeletons and the jaw apparatus see Manegold 2008; phylogenies are presented here for descriptive but not analytical purposes).

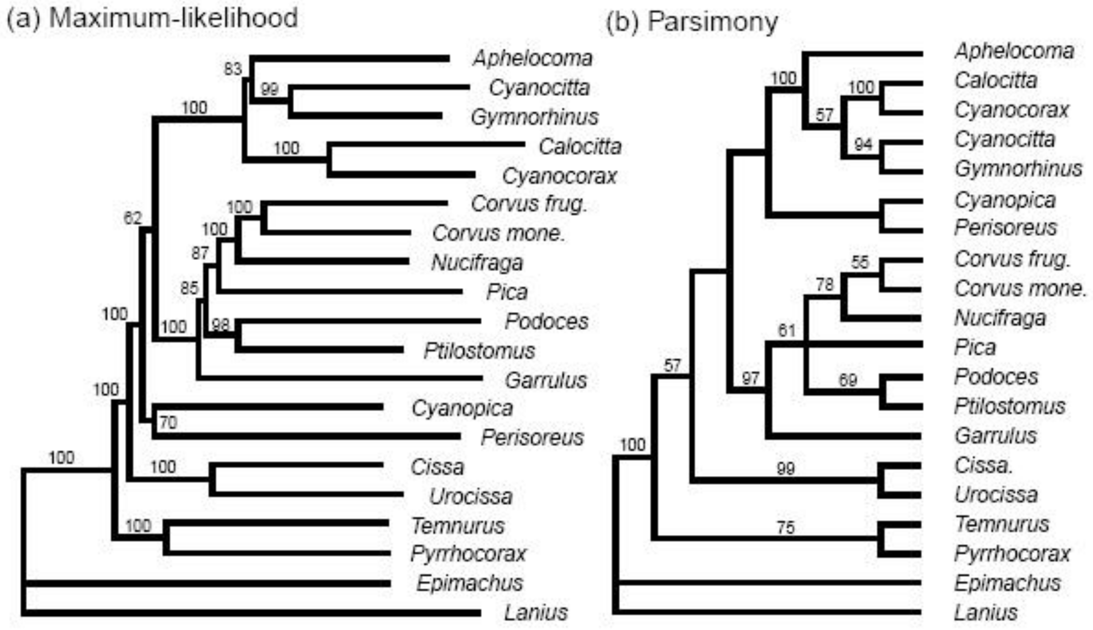


Figure 11. Phylogenetic trees for the Corvidae, based on the combination of three genes (cytochrome b, myoglobin, β-fibrinogen). The two trees represent different methods: (a) maximum-likelihood (best-fit tree) and (b) parsimony (strict consensus tree, based on the two shortest trees) (b). Numbers show posterior probabilities (>50%) estimated from Bayesian inference analysis. Taken from Ericson et al. (2005).

2.2.1 Western jackdaws (Corvus monedula)

Jackdaws are the smallest corvids in Europe. Their plumage is mainly black, with lighter grey areas on their nape (Fig. 12). Their eyes are light blue. The western European subspecies *spermologus* has a slightly darker nape plumage than the eastern subspecies *soemmerringii*, which sometimes has an obvious whitish collar (Madge & Burn 1994). Daurian jackdaws (*Corvus dauuricus*) are similar in size and appearance, but have a black-and-white plumage and a dark iris.

Figure 12. An adult jackdaw (a) and fledgling jackdaws (b).

Western jackdaws can be found almost everywhere in Europe, and even in parts of northern Africa and Russia (Snow & Perrins 1997). They prefer farmland, coasts and towns and can often be found nesting in chimneys (Madge & Burn 1994). In less urban areas, they breed in hollow trees, in rock crevices or even in rabbit holes. For foraging they fly to cropland where they feed on seeds and insects, often in close vicinity to rooks. Their diet also includes fruits and carrion (Snow & Perrins 1997). Described as ‘wary’ when in woodland, jackdaws become ‘relatively approachable’ in urban areas (Snow & Perrins 1997) and, as described by Konrad Lorenz (1931), can become tame when living with humans. In ‘King Solomon’s Ring’, Lorenz (1970) also illustrates the various postures and displays of jackdaws and provides a summary of the most distinct calls, such as the ‘kioo’ call that is heard when jackdaws fly over open areas. In general, vocalisations are complex calls that often intergrade, ranging from the rattling calls that are given in defence, to quiet social calls and even imitated sounds (Coombs 1978, Snow &

Perrins 1997). A typical jackdaw song consists of a mixture of various calls and is usually delivered with appropriate postures for each of the different parts (Coombs 1978).

Jackdaws often nest very close together. The pair is the basic unit within flocks, but they remain gregarious outside of breeding seasons (Snow & Perrins 1997). Several studies on jackdaw social behaviour have been carried out in the past, both in the wild (e.g. Roëll 1978) and in captivity (e.g. Wechsler 1989), and an extensive account of their social intelligence can be found in von Bayern's PhD thesis (2008).

2.2.2 Rooks (Corvus frugilegus)

Approximately 50cm in length, rooks are medium-sized, black corvids. Their glossy plumage appears metallic blue, green and purple, depending on the angle of light (Fig. 13). The diagnostic feature that distinguishes adults of the nominate form from carrion crows (*Corvus corone corone*) is their bare bill base which is not covered by their nasal bristles (as it is in carrion crows or common ravens, *Corvus corax*) (Madge & Burn 1994). The subspecies *pastinator* has a fully feathered face, but also a smaller bare bill base.

Figure 13. An adult (a) and a fledgling rook (b).

Rooks can be found everywhere in Europe and western Asia and have also been introduced into New Zealand (Madge & Burn 1994). They prefer agricultural areas with access to both grain and pasture (Coombs 1978). The diet is varied, but the main food sources are earthworms and fallen grain. Other foods include other invertebrates, such as molluscs (they were reported to drop mussels onto rocks to break them open) and crustaceans, potatoes and acorns (Madge & Burn 1994). Rooks are highly gregarious and forage together. Although their nesting territories are just a small part of the tree around their nest (Coombs 1978), they form massive communal roosts, and hence breed very close to each other (Madge & Burn 1994).

2.2.3 Eurasian jays (Garrulus glandarius)

Eurasian jays are slightly larger than jackdaws and have a pinkish-brown plumage, short black bill, a black ‘moustache’, black and white wings with an iridescent blue on the sides and a relatively long black tail (Snow & Perrins 1997; Fig. 14).

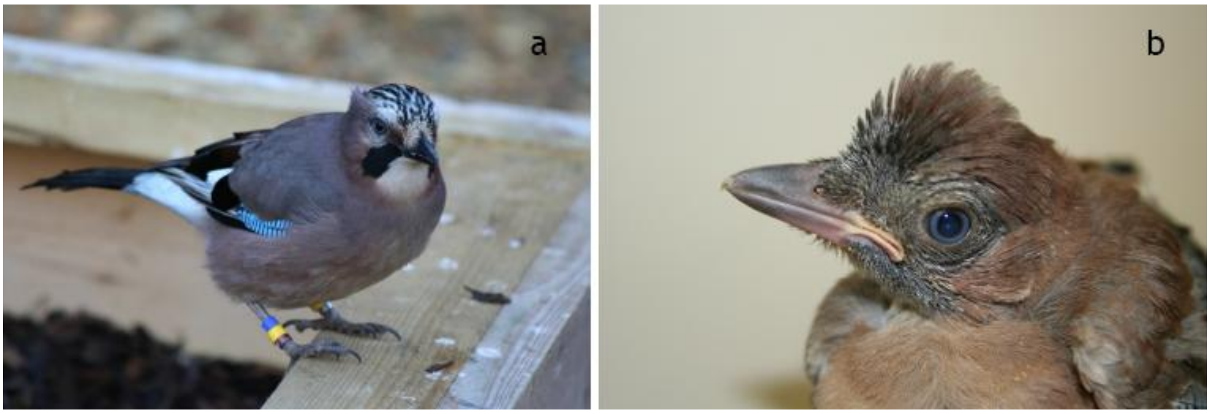


Figure 14. An adult (a) and a fledgling Eurasian jay (b).

Subspecies differ in appearance, with the European forms (nominate form) sporting a streaked crown (Madge & Burn 1994). Thirty-five subspecies falling into eight groups have been described (Madge & Burn 1994). Widespread in Europe, with exceptions of parts of Ireland, Scotland and north-west Scandinavia, jays are found even in North Africa and at the western shores of the Caspian sea (Coombs 1978). They mainly breed in continental temperate and Mediterranean regions and prefer areas with dense scrub and woodland, especially with beech *Fagus*, hornbeam *Carpinus* and oak *Quecus*, as they are acorn cachers (i.e. hoarders) (Bossema 1979, Snow & Perrins 1997). They were classified as 'specialised' cachers, hiding 'large numbers of items of predominantly one type of food' (*Quercus* acorns) and showing a 'seasonal peak of caching intensity which coincides with availability of that food'; they recover their caches 'often after long intervals' and live in areas of 'strong seasonal availability of food' (de Kort & Clayton 2006). In addition to acorns, they feed on other seeds, invertebrates (beetles, larvae), fruits, carrion and domestic scraps (Keve 1985, Goodwin 1986). Described as 'timid and wary', they show high levels of neophobia, but can habituate to humans in urban areas (Snow & Perrins 1997). Various displays and vocalisations have been described, with the most distinct one being their harsh, screeching alarm call (Snow & Perrins 1997, Goodwin 1949). Various incidents of vocal mimicry have been recorded for both sexes, which include mimicry of buzzards (*Buteo buteo*), kestrels (*Falco tinnunculus*), magpies (*Pica pica*) and starlings (*Sturnus vulgaris*) (Snow & Perrins 1997). In urban areas and captivity they have been heard mimicking barking dogs (Snow & Perrins 1997), lawnmowers (Goodwin 1956), the human voice and whistling (personal observation). Outside the breeding season jays usually do not flock; at the onset of the breeding season in spring birds become territorial and breeding pairs disperse at low density within their home ranges (Snow & Perrins 1997).

2.2.4 Predictions

For the sake of keeping this chapter condensed and to deliver a clear, straight-to-the-point message, I will focus on displacements as a measure of agonistic interactions and social proximity time spans as a measure of affiliative relationships in the analysis (additional data will be used when preparing this manuscript for publication).

Based on the different social systems of the three species, it is possible to predict bonding and dominance relationships in the fledging and adult groups. Both rooks and jackdaws form colonial pairs and breed and forage in large aggregations of animals. Thus, the same individuals are likely to interact with each other on a daily basis. A dominance hierarchy would enable them to save energy by determining relationships and acting upon those in subsequent encounters, thus avoiding the re-establishment of relative relationships every time those two individuals meet. I would therefore expect rooks and jackdaws to establish a hierarchy relatively early in their lives. Eurasian jays are territorial and therefore hardly ever interact with individuals other than their partner, apart from during the breeding season. I expect them to not form a dominance hierarchy. The importance of social bonds between group members in social species is obvious: social bonds facilitate group cohesion. As social bonds facilitate group cohesion, I predict the establishment of social bonds between partners and conspecifics in rooks and jackdaws, but not in the territorial Eurasian jays. In the three adult bird groups (two rook groups, one jackdaw group) I predict a relatively stable hierarchy and stable social bonds from the onset of the study, as those birds have been living together in the same group constellation for a few years.

2.3 Methods

2.3.1 Subjects

Seventy-two birds were observed for this study: 25 jackdaws, 33 rooks and 14 Eurasian jays (Table 2a-c). They were collected from nests as nestlings, hand-raised and then housed in four different aviaries (as fledglings). Birds were hand-raised so that they would be habituated to humans and thus be easier to work with in experiments. However, because corvids do not imprint (like e.g. geese do), this is not expected to influence results of experimental studies.

At the onset of the study, the fledglings were approximately 2 to 3 months old. Individuals of groups J2 and R2 were 4 years old; individuals of group R3 were 5 years old. All were banded with coloured rings for individual identification.

Table 2. Details for (a) jackdaws, (b) rooks and (c) Eurasian jays that took part in this study. The fledglings had not been sexed at the time this study took place, which is why the sex for almost all of them – with two exceptions – is unknown. Nest numbers indicate who shared a nest with whom when the birds were collected as fledglings; data for the year the birds hatched and which year of their life they were in at the onset of the study is given. Numbers in the last column show which studies each individual participated in (*Chapter 2* = bonds & hierarchies; *Chapter 3* = social learning in jackdaws, one-on-one setting; *Chapter 5* = social learning in rooks; *Chapter 6* = individual differences). *Chapter 4* (social learning in jackdaws, group setting) was conducted with a different group of birds in Germany. Details for that group can be found in the methods section of *Chapter 4*.

(a) Jackdaw Group 1

ID	Name	Sex	Nest	Hatched	Year	Chapter
Jo	Jo	?	1	2007	1	2, 6
Cl	Claude	?	1	2007	1	2, 6
Wi	Will	?	1	2007	1	2, 6
Iv	Ivo	?	2	2007	1	2, 6
Pe	Pedro	?	2	2007	1	2, 6
Ce	Celli	?	3	2007	1	2, 6
Ra	Raffa	?	3	2007	1	2, 6
Ga	Gaudi	?	4	2007	1	2, 6
Da	Dali	?	4	2007	1	2, 6
Pi	Picasso	?	4	2007	1	2, 6
Do	Dom	?	5	2007	1	2, 6
Va	Vasco	?	5	2007	1	2, 6
Es	Escher	?	6	2007	1	2, 6
Bl	Blake	?	6	2007	1	2, 6
Mu	Munch	?	6	2007	1	2, 6

Jackdaw Group 2

ID	Name	Sex	Nest	Hatched	Year	Chapter
Da	Daffy	f	?	2004	2	2, 3, 6
Be	Bert	m	?	2004	2	1, 2, 5
Wo	Woody	m	?	2004	2	1, 2, 5
Ca	Calimero	m	?	2004	2	1, 2, 5
Do	Donald	m	?	2004	2	1, 2, 5
Ph	Phoenix	m	?	2004	2	1, 2, 5
Tw	Tweety	m	?	2004	2	1, 2, 5
Al	Alex	m	?	2004	2	1, 2, 5
Or	Orville	m	?	2004	2	1, 2, 5
Ni	Nico	m	?	2004	2	1, 2, 5

(b) Rook Group 1

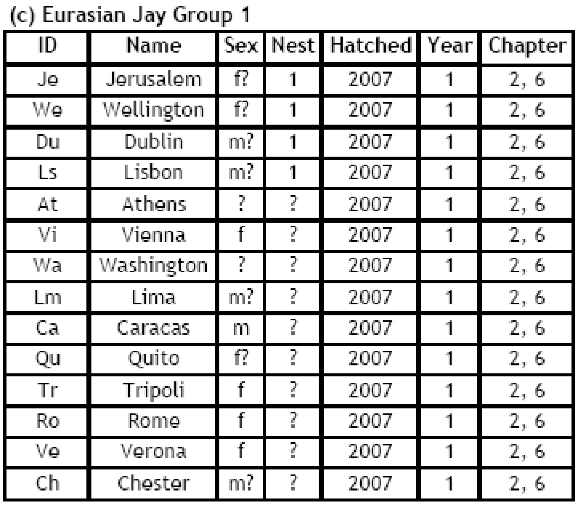
ID	Name	Sex	Nest	Hatched	Year	Chapter
Th	Thierry	?	1	2007	1	2, 6
Ar	Arthur	?	2	2007	1	2, 6
Lo	Loki	?	2	2007	1	2, 6
Me	Merlin	?	2	2007	1	2, 6
Be	Beowulf	?	2	2007	1	2, 6
Ro	Romulus	?	3	2007	1	2, 6
Re	Remus	?	3	2007	1	2, 6
Le	Leonidis	?	4	2007	1	2, 6
Ca	Cassandra	?	4	2007	1	2, 6
He	Hector	?	4	2007	1	2, 6
Ch	Chasca	?	5	2007	1	2, 6
Za	Zara	?	5	2007	1	2, 6
Ti	Ticci	?	5	2007	1	2, 6

Rook Group 2

ID	Name	Sex	Nest	Hatched	Year	Chapter
Mo	Monroe	f	?	2004	2	2, 5, 6
Bu	Bussell	f	?	2004	2	2, 5, 6
Fo	Fonteyn	f	?	2004	2	2, 5, 6
Fr	Fry	f	?	2004	2	2, 5, 6
Wo	Woody	f	?	2004	2	2, 5, 6
Nu	Nuryef	f	?	2004	2	2, 5, 6
Ca	Callas	f	?	2004	2	2, 5, 6
Gu	Guillem	f	?	2004	2	2, 5, 6
Cp	Cooper	f	?	2004	2	2, 5, 6
Ne	Newton	f	?	2003	3	2, 5, 6
Ck	Cook	m	?	2004	2	2, 5, 6
Co	Connelly	m	?	2004	2	2, 5, 6

Rook Group 3

ID	Name	Sex	Nest	Hatched	Year	Chapter
Vi	da Vinci	f	?	2003	3	2, 6
Da	Darwin	f	?	2003	3	2, 6
Hu	Huxley	f	?	2003	3	2, 6
Ei	Einstein	f	?	2003	3	2, 6
Ma	Mackintosh	f	?	2003	3	2, 6
Li	Linnaeus	m	?	2003	3	2, 6
Ar	Aristotle	m	?	2003	3	2, 6
Pl	Plato	m	?	2003	3	2, 6



(c) Eurasian Jay Group 1

ID	Name	Sex	Nest	Hatched	Year	Chapter
Je	Jerusalem	f?	1	2007	1	2, 6
We	Wellington	f?	1	2007	1	2, 6
Du	Dublin	m?	1	2007	1	2, 6
Ls	Lisbon	m?	1	2007	1	2, 6
At	Athens	?	?	2007	1	2, 6
Vi	Vienna	f	?	2007	1	2, 6
Wa	Washington	?	?	2007	1	2, 6
Lm	Lima	m?	?	2007	1	2, 6
Ca	Caracas	m	?	2007	1	2, 6
Qu	Quito	f?	?	2007	1	2, 6
Tr	Tripoli	f	?	2007	1	2, 6
Ro	Rome	f	?	2007	1	2, 6
Ve	Verona	f	?	2007	1	2, 6
Ch	Chester	m?	?	2007	1	2, 6

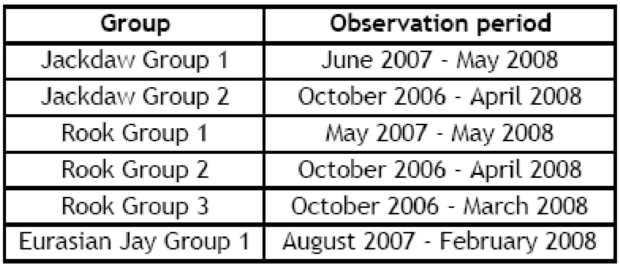
2.3.2 Housing

The birds were housed in outdoor aviaries containing perches, nest boxes and different types of enrichment at the Sub-Department of Animal Behaviour, Madingley. Jackdaw Group 1 (J1) and rook Group 1 (R1) were housed together (aviary measuring aviary: 6 m x 14 m x 3 m), as were jackdaw The Push Group (J2) and rook The Push Group (R2) (aviary: 20 m x 8 m x 3 m). The Eurasian jays (EJ1) and the rooks of Group 3 (R3) were kept in individual aviaries (6 m x 14 m x 3 m and 10 m x 8 m x 4 m, respectively). All aviaries but the one for rook Group 3 had runs adjacent to the main aviary area (6 m x 1 m x 3 m) leading to inside testing compartments, which allowed individuals to be visually and physically isolated from the rest of the group. Outside of testing times, the birds could access all areas of the aviary and fly in and out of the compartments. Water was provided *ad libitum* at all times. Subjects were fed once a day after experiments with a diet consisting of fruits, vegetables, eggs, bread, cheese, Mazuri pellets (Lillico), Insectivorous (Haiths) and a wild bird seed mix (Haiths).

2.3.3 Data collection

Data were collected during weekly behavioural observation sessions from October 2006 (adult birds) and spring/summer 2007 (fledglings) (see Table 3). Three individuals of the adult jackdaw group (J2; Daffy, Bert, Woody) had to be moved to a different aviary due to fights in the group from the 15th of January to the 4th of May, 2007. Data from this time span were therefore excluded from the analysis. One of the rooks of Group R3 (‘Newton’) was moved into Group R2 in January 2007. Data before and after the move were therefore analysed separately. No data were collected on July 2007.

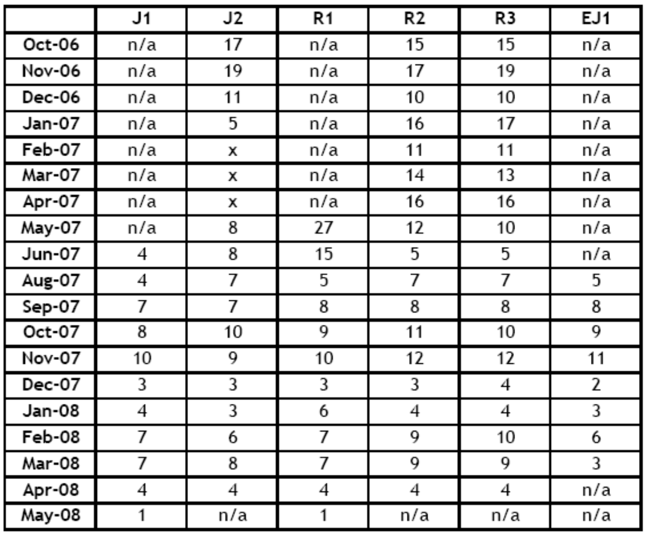
Table 3. Observation periods for the six bird groups.



Group	Observation period
Jackdaw Group 1	June 2007 - May 2008
Jackdaw Group 2	October 2006 - April 2008
Rook Group 1	May 2007 - May 2008
Rook Group 2	October 2006 - April 2008
Rook Group 3	October 2006 - March 2008
Eurasian Jay Group 1	August 2007 - February 2008

Each group was observed in their outdoor aviary for 20 minutes, usually three times a week and at random times during the day, but not under extreme weather conditions, such as heavy rain, as the birds were usually inactive during those periods (Table 4).

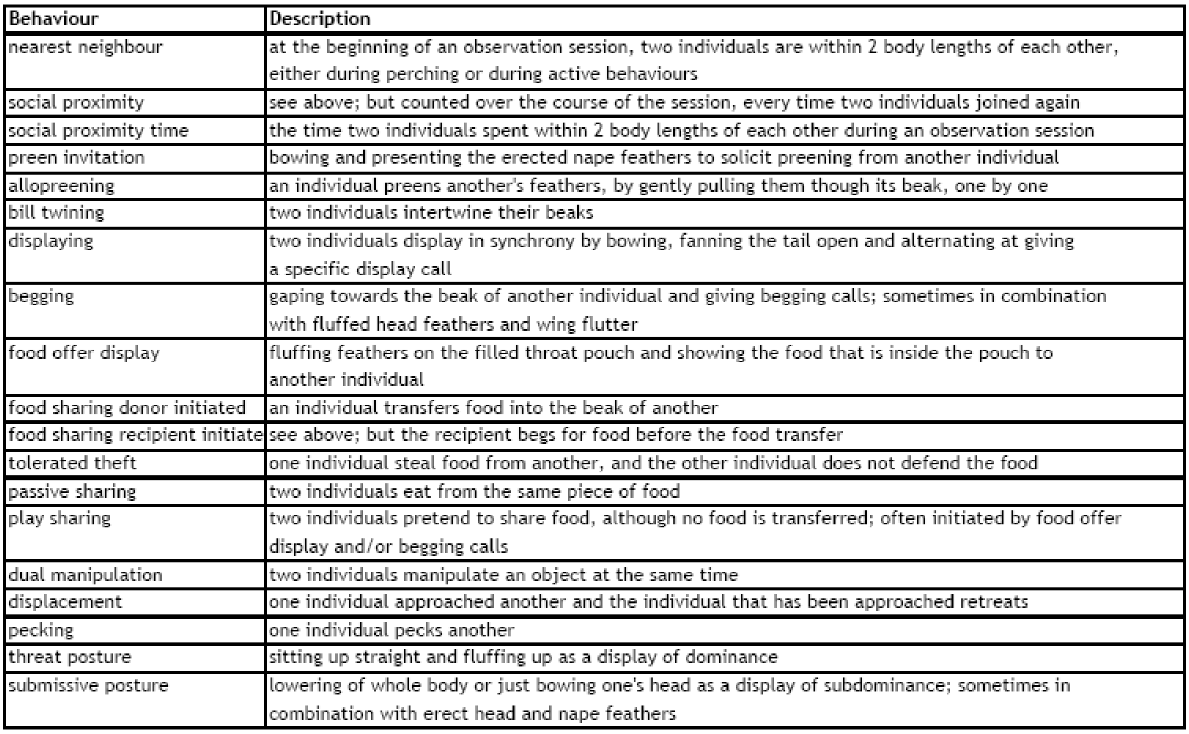
Table 4. Number of observations per month and bird group.



	J1	J2	R1	R2	R3	EJ1
Oct-06	n/a	17	n/a	15	15	n/a
Nov-06	n/a	19	n/a	17	19	n/a
Dec-06	n/a	11	n/a	10	10	n/a
Jan-07	n/a	5	n/a	16	17	n/a
Feb-07	n/a	x	n/a	11	11	n/a
Mar-07	n/a	x	n/a	14	13	n/a
Apr-07	n/a	x	n/a	16	16	n/a
May-07	n/a	8	27	12	10	n/a
Jun-07	4	8	15	5	5	n/a
Aug-07	4	7	5	7	7	5
Sep-07	7	7	8	8	8	8
Oct-07	8	10	9	11	10	9
Nov-07	10	9	10	12	12	11
Dec-07	3	3	3	3	4	2
Jan-08	4	3	6	4	4	3
Feb-08	7	6	7	9	10	6
Mar-08	7	8	7	9	9	3
Apr-08	4	4	4	4	4	n/a
May-08	1	n/a	1	n/a	n/a	n/a

Although jackdaws and rooks were housed together (Groups J1 & R1 and Groups J1 & R2), they were treated as separate groups, as they rarely interacted with each other. I therefore observed 6 individual groups. Behaviours recorded were based on an ethogram derived from my own observations of the three bird species and descriptions of behaviours in Coombs (1978), Goodwin (1986), Katzir (1981), Lorenz (1931), Roëll (1978) and von Bayern (2008). They included factors of social proximity, affiliative and agonistic behaviours and anecdotes (rare behaviours that were seen for the first time and were of interest). Definitions of the behaviours can be found in Table 5 (for examples of a few behaviours in each species see 'Appendix').

Table 5. Definitions of behaviours recorded during observation sessions. Apart from 'social proximity time', which was recorded as a time span (in seconds), all behaviours were counted as events (total numbers). For those, frequency and – where possible – direction was noted (for behaviours such as 'passive sharing' no direction could be determined).



Behaviour	Description
nearest neighbour	at the beginning of an observation session, two individuals are within 2 body lengths of each other, either during perching or during active behaviours
social proximity	see above; but counted over the course of the session, every time two individuals joined again
social proximity time	the time two individuals spent within 2 body lengths of each other during an observation session
preen invitation	bowing and presenting the erected nape feathers to solicit preening from another individual
allopreening	an individual preens another's feathers, by gently pulling them though its beak, one by one
bill twining	two individuals intertwine their beaks
displaying	two individuals display in synchrony by bowing, fanning the tail open and alternating at giving a specific display call
begging	gaping towards the beak of another individual and giving begging calls; sometimes in combination with fluffed head feathers and wing flutter
food offer display	fluffing feathers on the filled throat pouch and showing the food that is inside the pouch to another individual
food sharing donor initiated	an individual transfers food into the beak of another
food sharing recipient initiate	see above; but the recipient begs for food before the food transfer
tolerated theft	one individual steal food from another, and the other individual does not defend the food
passive sharing	two individuals eat from the same piece of food
play sharing	two individuals pretend to share food, although no food is transferred; often initiated by food offer display and/or begging calls
dual manipulation	two individuals manipulate an object at the same time
displacement	one individual approached another and the individual that has been approached retreats
pecking	one individual pecks another
threat posture	sitting up straight and fluffing up as a display of dominance
submissive posture	lowering of whole body or just bowing one's head as a display of subdominance; sometimes in combination with erect head and nape feathers

During each observation session, the whole group was observed using a version of continuous recording (all-occurrences recording), during which each occurrence of a behaviour was noted (Martin & Bateson 2007, p. 48). This allowed the calculation of frequencies, latencies and durations for both events (one-off behaviour, negligible duration) and states (time spans). For this study, I noted total numbers of all behaviours (events) and time spans for social proximity (state). Observed behaviours were recorded with a dictaphone. Time spans for social proximity were summarised for each session, and interactive behaviours (affiliative and agonistic) were arranged in data matrices per session; anecdotes were kept on separate sheets for each month. Data for each behaviour were then combined to create a sheet per behaviour per month for each of the six groups.

2.3.4 Data analysis

To calculate bonds, time spent in social proximity was combined across blocks of three months for each pair (Fig. 15) and divided by the number of observations. This allowed calculating the percentage of time the animals spent together per observation (for drawing sociograms).

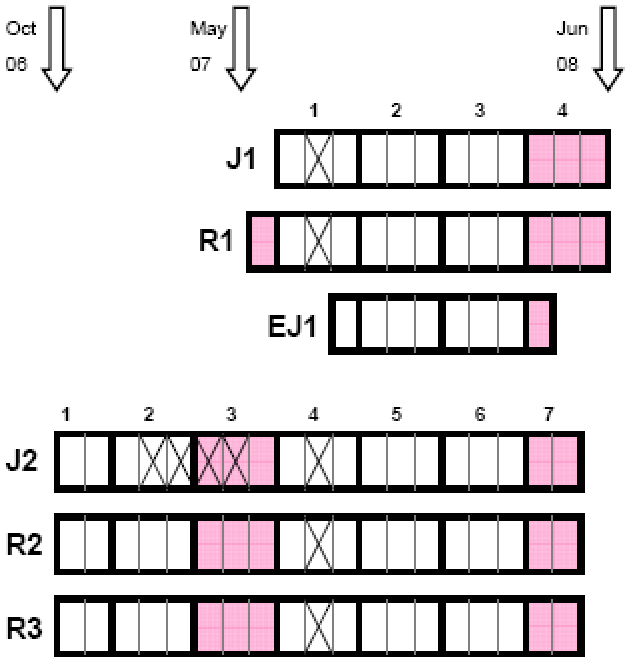


Figure 15. Blocks of observations for analysing social proximity and displacements for each of the six groups (4 blocks for fledglings Groups J1 and EJ1; 5 blocks for fledgling Group R1; 7 blocks for adult Groups J2, R2, R3). Arrows show the onset and end of the study, as well as the onset of the onset of the observations of the fledgling groups. Solid lines indicate blocks, dashed lines show months per block. Breeding seasons (March to May) are shaded pink. Crossed out months represent months where no data were taken.

The 4th block (March 2008 or March to May 2008) (fledgling Groups J1, R1, EJ1) or the 3rd (March to May 2007) and 7th block (March and April 2008) (adult Groups J2, R2, R3) covered most months of the breeding season. To look at the stability of social bonds, percentages of time spent together were analysed by comparing the four (fledgling groups) or seven blocks (adult groups) per group with a Friedman ANOVA. If a significant result was found, post-hoc Wilcoxon matched-pairs tests were performed to determine which blocks differed. I defined only pairs that spent more than 19% of the observation time together in the last block as 'bonded' and thus only included those pairs in the analysis (assessment of data sets illustrated that in all cases pairs that fell below this cut-off point were associated and only rarely, were outlying interactions observed above this cut-off point). Sociograms for each block were drawn using Microsoft PowerPoint 2002.

Displacement matrices for each observation session were combined to create matrices for blocks of three months according to Figure 15. In addition to analysing each of the blocks, overall data were analysed for the adult groups, assuming that in adult birds, the dominance hierarchy would have been stable for a few months or years prior to the observation phase.

The dominance hierarchy was calculated based on those combined displacement matrices using MatMan 1.0 (Noldus Technologies, Wageningen, The Netherlands). MatMan computes dominance relationships according to de Vries's I&IS method (1998; de Vries & Appleby 2000). Based on 10,000 random permutations of the displacement matrices, the matrices are then reordered so as to create a hierarchy that is most consistent with a linear hierarchy. This is done by minimising the number of inconsistencies (when a supposedly dominant animal is displaced by a lower-ranking individual) and the strength of those inconsistencies (de Vries 1998; see also de Vries et al. 2006). The only assumption made by this procedure is the existence of a linear or non-linear hierarchy; the linearity can be tested with MatMan as well, by calculating Landau's linearity index (*h*) (1 = linear dominance hierarchy, 0 = non-linear) based on Appleby's (1983) procedure. In order to rule out the possibility of accepting *P*-values that would be either to high or too low, de Vries' (1995) linearity index *h'* was used instead of *h* if there were unknown or tied relationships in the matrices. The directional consistency index (*dci*) revealed the consistency of the hierarchy (1 = complete unidirectionality, 0 = completely equal exchange).

The circular triads also indicate how linear a hierarchy is. The 'actual number of circular triads' that is found is compared with the 'expected number of circular triads', under the null-hypothesis of completely random relationships among all pairs of individuals. The smaller the 'actual number of circular triads', the stronger the linearity. Kendall's coefficient of linearity (*K*) was calculated according to Appleby (1983), taking into account the number of circular triads and the group size (*N*). This coefficient is only relevant for even values of *N*, as *K* and *h* are equal for odd values of *N*. Qui-square values and degrees of freedom calculated according to Appleby (1983) allowed consulting a chi-square table on levels of significance ('probability' in Tables 6-11). I rejected the null hypothesis of randomly distributed dominance relationships when significance levels were below 0.05. When unknown or tied relationships were found, an improved linearity test using the *h'* index was performed according to de Vries (1995). A procedure according to de Vries (1998) reorders the dominance hierarchy to fit a linear hierarchy, meaning that the individuals are reorganised in such a way that the new order is most consistent with a linear hierarchy. This was only applied to data if the original calculation of a linear hierarchy yielded significant results ('probability' in Tables 7-12). However, in order to explore and visualise the changes in the hierarchy, I have used that procedure on all data blocks, including significant and non-significant results. Graphs that include hierarchies stemming from previously non-significant calculations should thus be observed with caution and for purposes of visually investigating data only.

The total number of initial and final inconsistencies and the strength thereof are given in the Tables 7-12. Inconsistencies arose from instances where a higher ranking individual was displaced by a lower-ranking one. Initial inconsistencies were corrected by re-ordering (e.g. flipping) individuals. The remaining inconsistencies were stated as 'final inconsistencies'. The strength of such inconsistencies was the absolute difference between the ranks of the two individuals involved in an inconsistency. After minimising the number of inconsistencies, the strength of those inconsistencies was reduced by reordering individuals. In addition to analysing each of the blocks, overall data were analysed for the adult groups, assuming that in adult birds, the dominance hierarchy would have been stable for a few months or years prior to the observation phase.

2.4 Results

2.4.1 Social proximity

2.4.1.1 Fledgling groups

Fledgling jackdaw pairs of the Group J1 spent significantly different amounts of time together in the four observation blocks (Friedman ANOVA: X^2 = 14.04, N = 5, P = 0.003). Post-hoc analysis revealed significant differences between almost all of the blocks (Table 6).

Table 6. Z-scores for Wilcoxon matched pairs tests for Group J1 (n=5). Asterisks denote p < 0.05.

block	1	2	3	4
1				
2	0.345			
3	2.023*	2.023*		
4	2.023*	2.023*	2.023*	

No significant difference was found between the blocks of the three fledgling rook pairs of Group R1 (Friedman ANOVA: X^2 = 5.80, N = 3, P = 0.122). Data for Eurasian jay fledglings of Group EJ1 could not be analysed, because no two birds spent more than 19% of the observation time in the last block together. The development of bonds (i.e. the time partners spent together) is visualised in sociograms for each block (Fig. 16-18). Grey and black lines show the time two individuals spent within 2 body lengths of one another (percentage of observation time; see figure legend) in each of the observation blocks. Social bonds between conspecifics and between partners can be distinguished by the thickness of lines between two individuals: the thicker the line, the more time those two individuals spent together and the more likely it is that those two individual share a pair bond, rather than a bond between conspecifics. As can be seen in the sociograms (declining number of lines between individuals across blocks), individuals became more selective towards the end of the observation season.

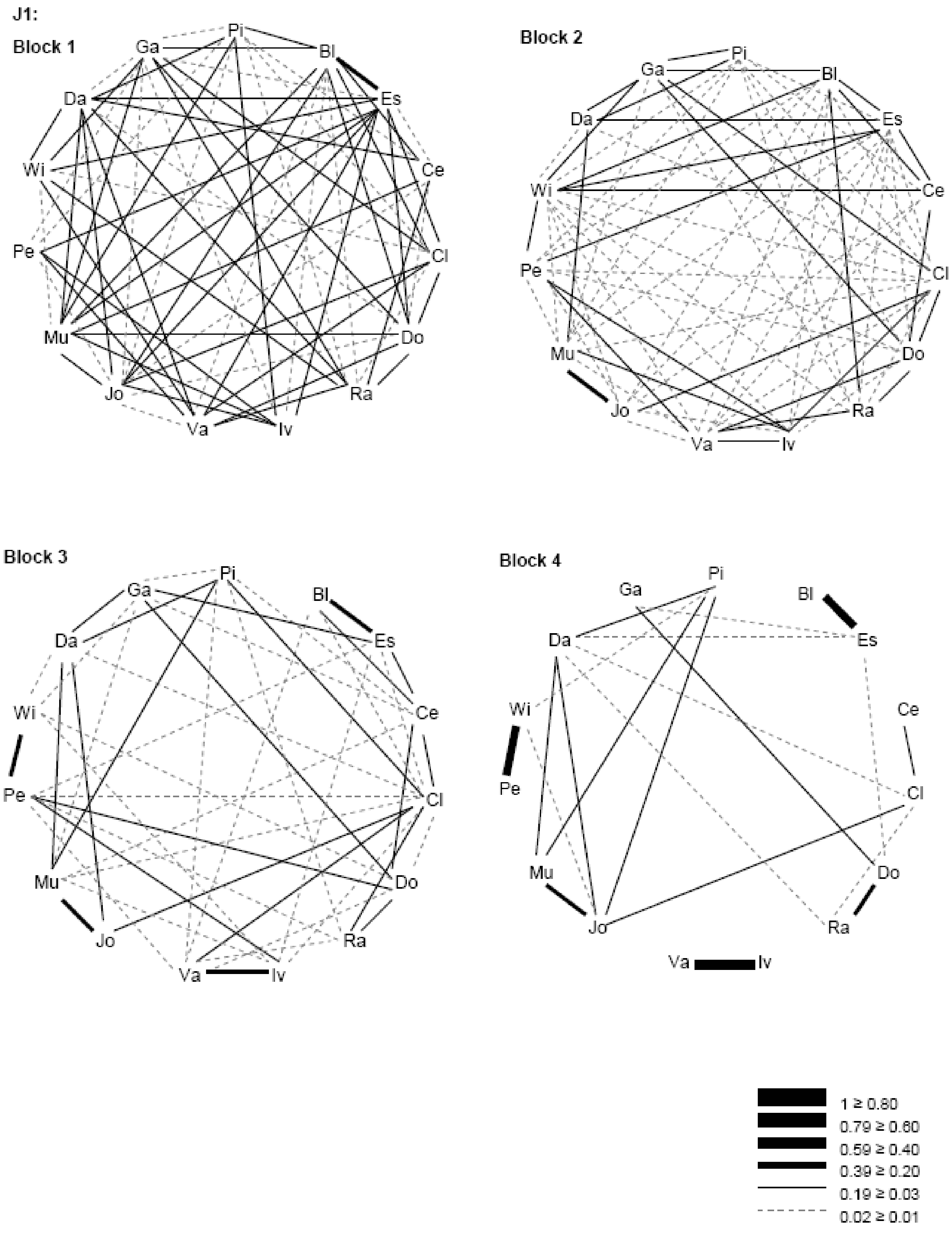


Figure 16. Sociograms for fledgling jackdaws of group J1. Abbreviations represent individuals; lines show the time those individuals spent together as a percentage of observation time (see legend).

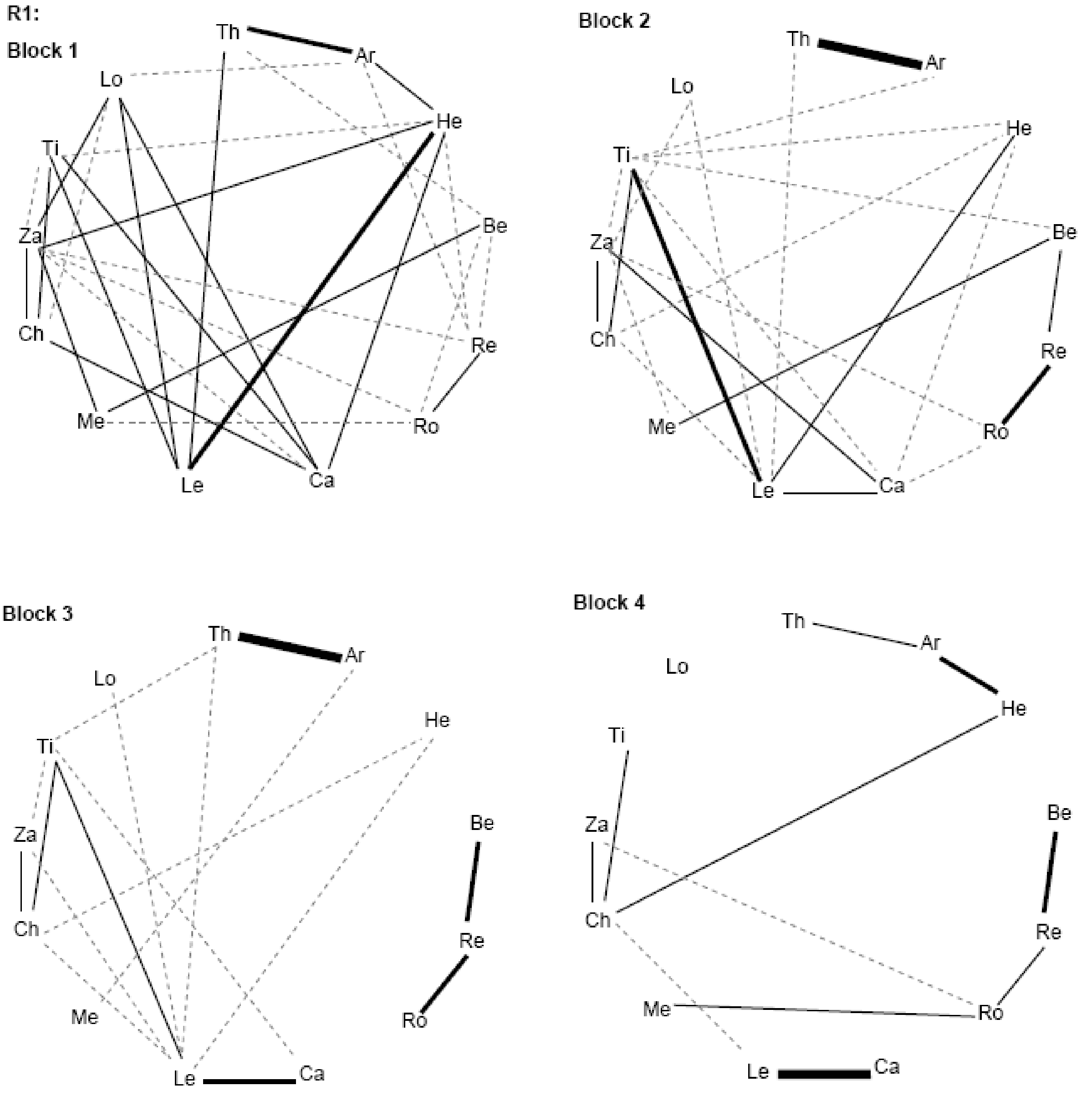


Figure 17. Sociograms for fledgling rooks of group R1.

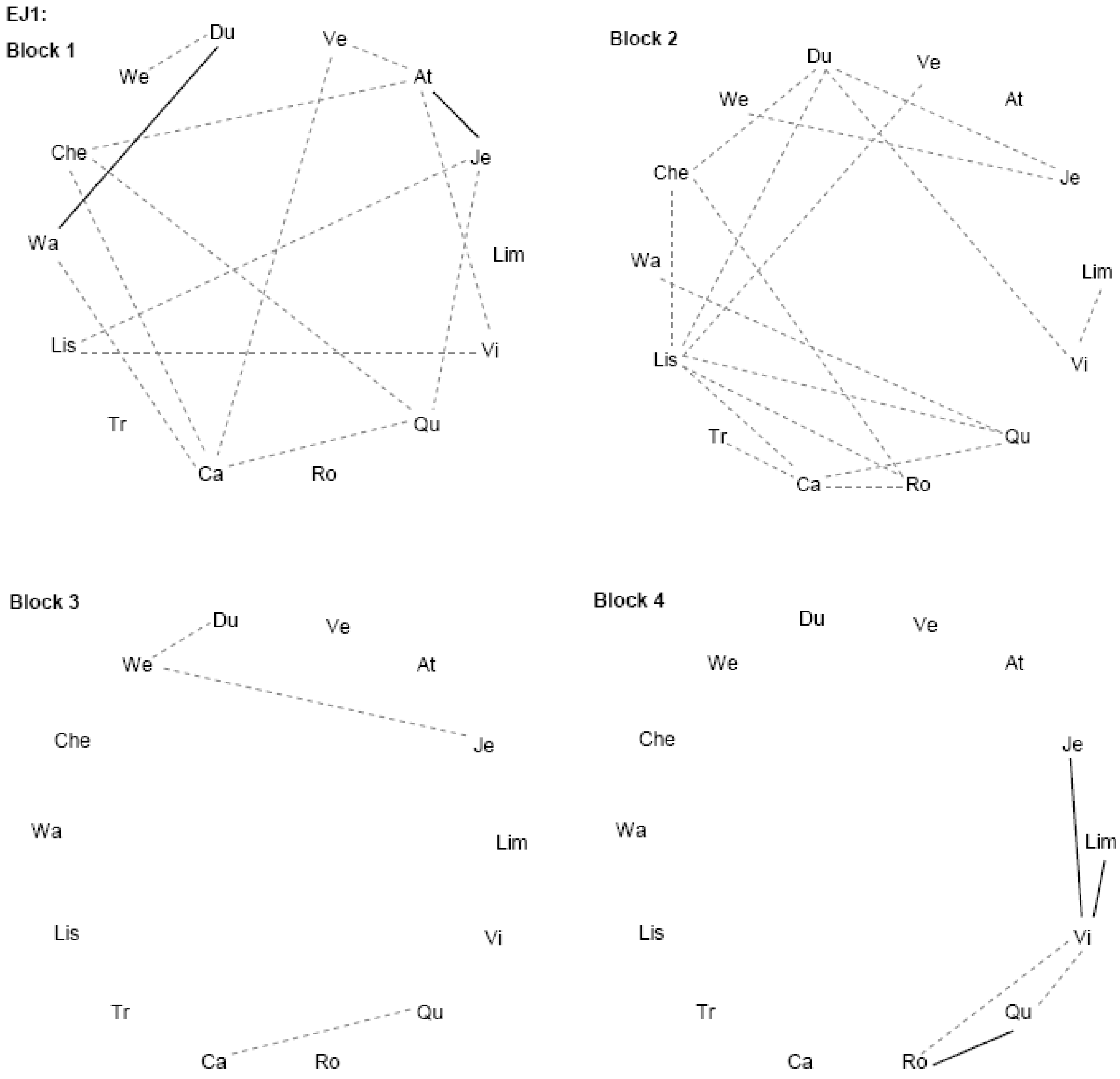
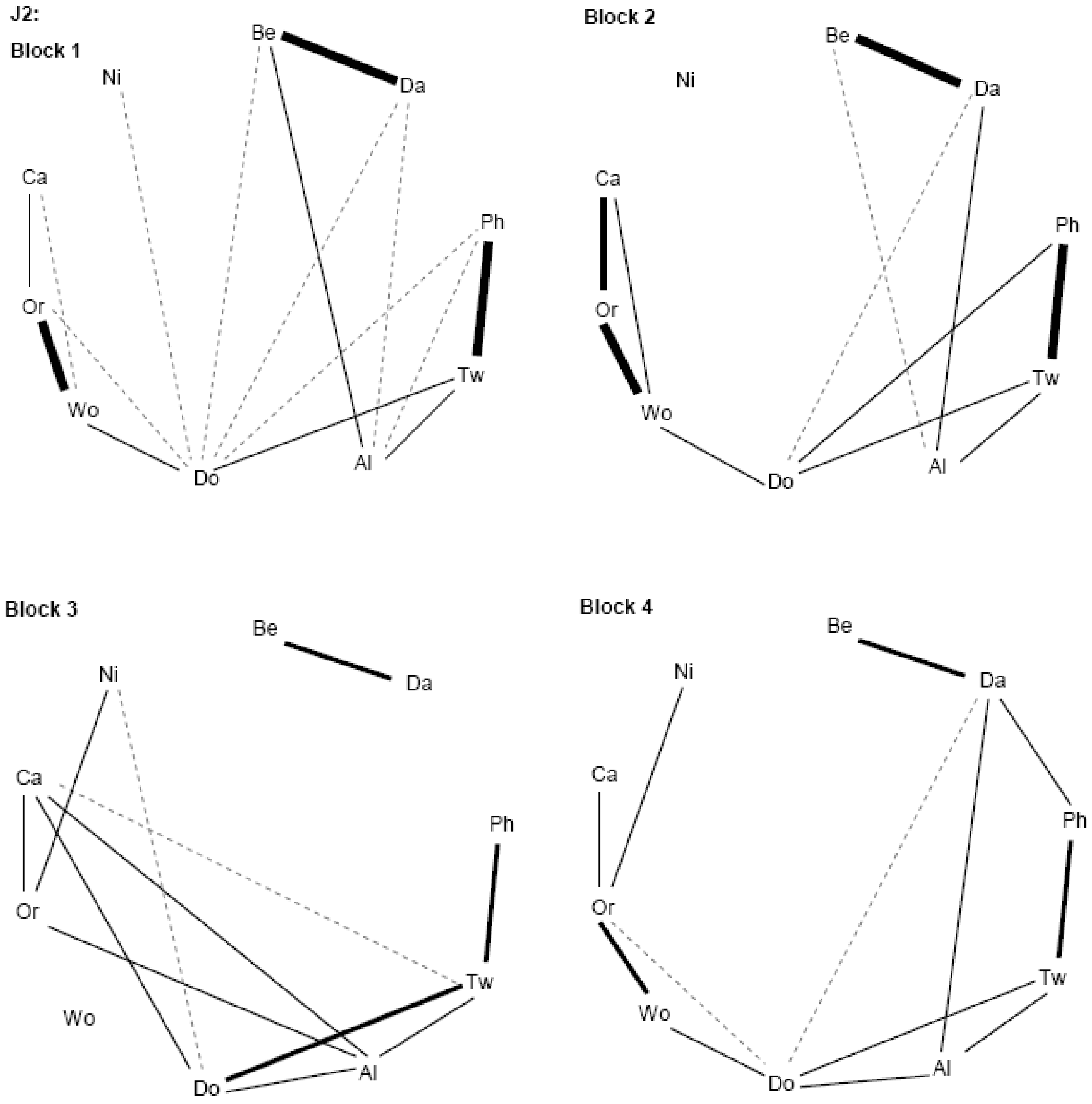


Figure 18. Sociograms for fledgling Eurasian jays of group EJ1.

Pair bond formation seemed to take place when jackdaws were approximately 8 to 10 months old (Block 3/4) and rooks were approximately 6 to 8 months old (Block 2/3). The three bonds that emerged in the last observation blocks in the fledgling jackdaws were Bl & Es, Iv & Va and Pe & Wi. Whereas Bl and Es are siblings, the other two bonds consisted of unrelated individuals (Table 2a). In the rooks one sibling bond emerged (Ca & Le), and one social bond between unrelated conspecifics (Ar & Th) (Table 2b).

2.4.1.2 Adult groups

Data for three adult jackdaw pairs of Group J2 were analysed, but no significant difference between the seven blocks was found (Friedman ANOVA: $X^2 = 11.00$, $N = 3$, $P = 0.088$). Pairs in the two adult rook groups also did not spend significantly different amounts of time together across blocks (Friedman ANOVAs: R2: $X^2 = 7.29$, $N = 4$, $P = 0.295$; R3: $X^2 = 10.57$, $N = 3$, $P = 0.103$). Changes in the bonds between conspecifics and between partners can be seen in the sociograms for each block in the three adult groups (Fig. 19-21). It seems they became more selective over the course of the study and in some blocks spent almost all their time with their partner.


J2:
Block 1
Be
Ni
Da
Ca
Ph
Or
Tw
Wo
Do
Al
Block 2
Be
Ni
Da
Ca
Ph
Or
Tw
Wo
Do
Al
Block 3
Be
Ni
Da
Ca
Ph
Or
Tw
Wo
Do
Al
Block 4
Be
Ni
Da
Ca
Ph
Or
Tw
Wo
Do
Al

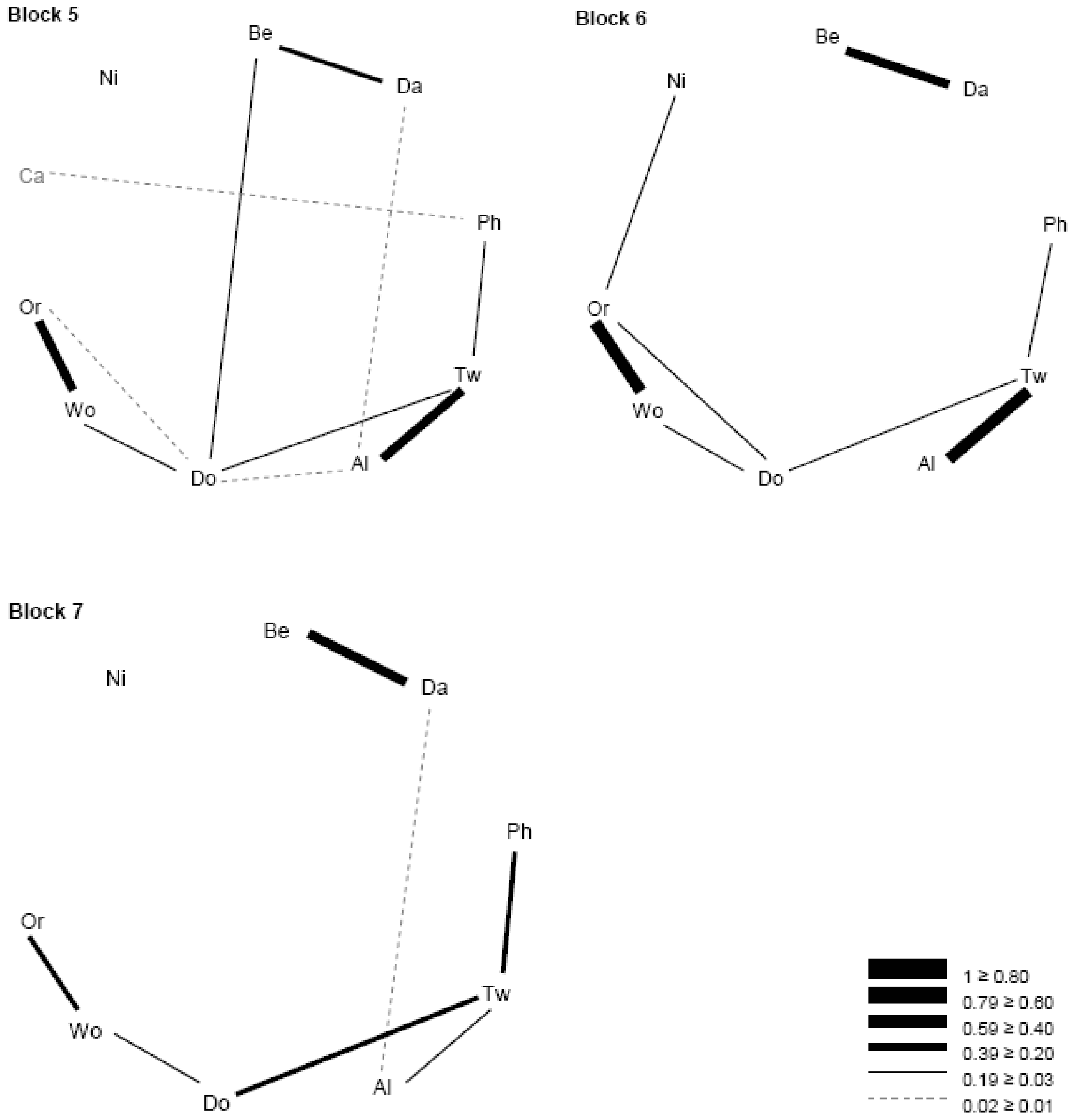
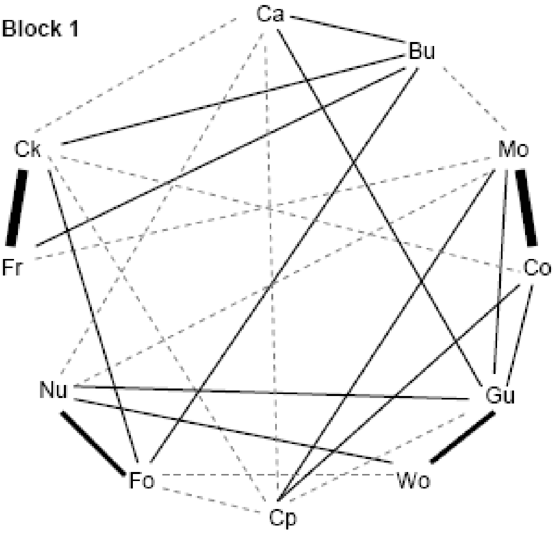


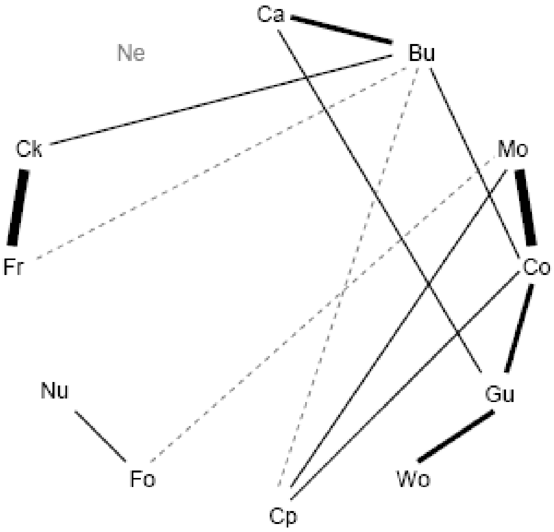
Figure 19. Sociograms for adult jackdaws of group J2. Jackdaw Ca died during the study (15.10.2007) and is therefore shaded grey in the block during which he died and then removed from the diagram in the following phases.

R2:

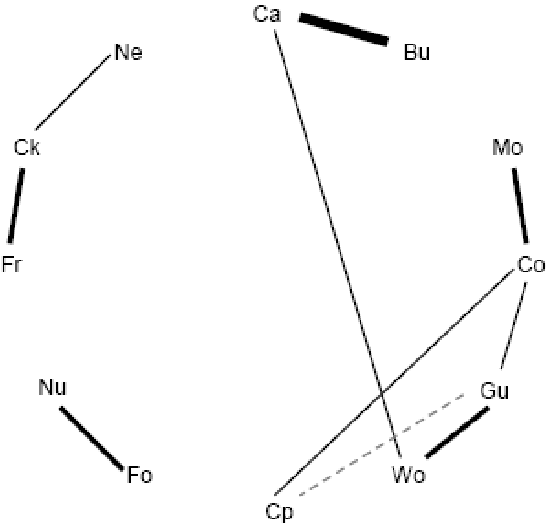
Block 1



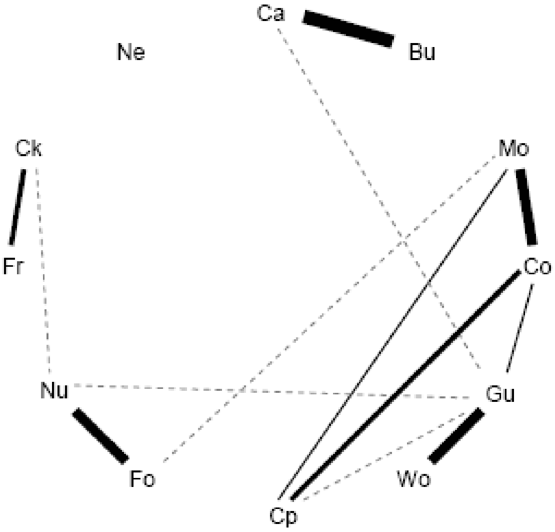
Block 2



Block 3



Block 4



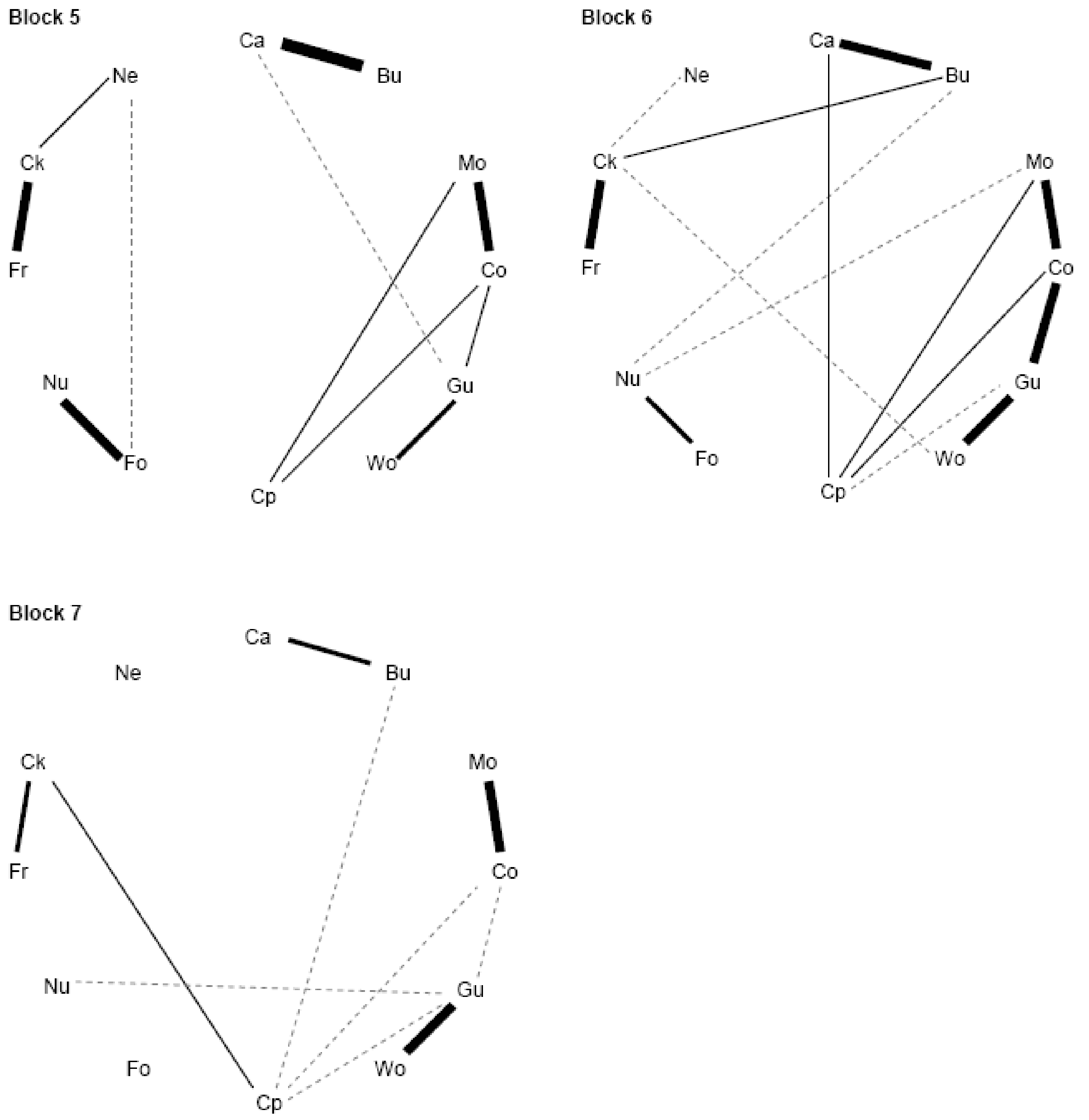
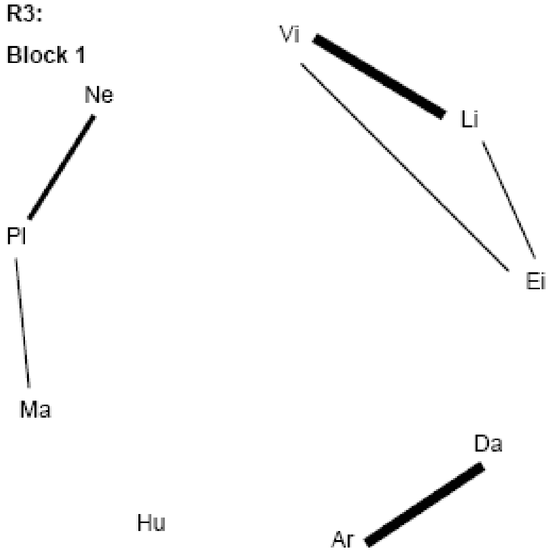


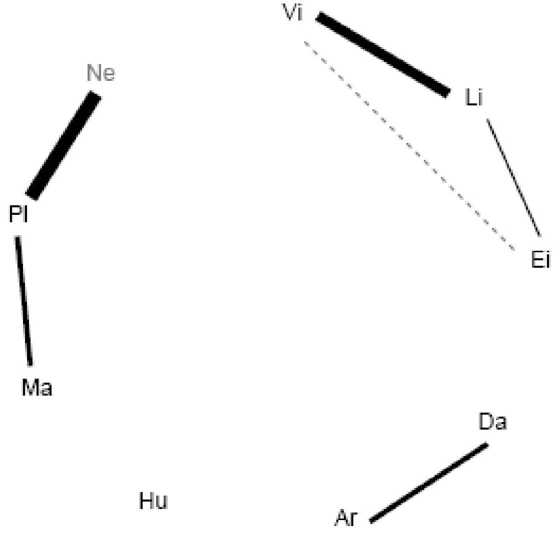
Figure 20. Sociograms for adult rooks of group R2. Rook Ne was moved from group R3 to group R2 during the study (15.1.2007) and therefore appears grey in the block that she was introduced into that group.

R3:

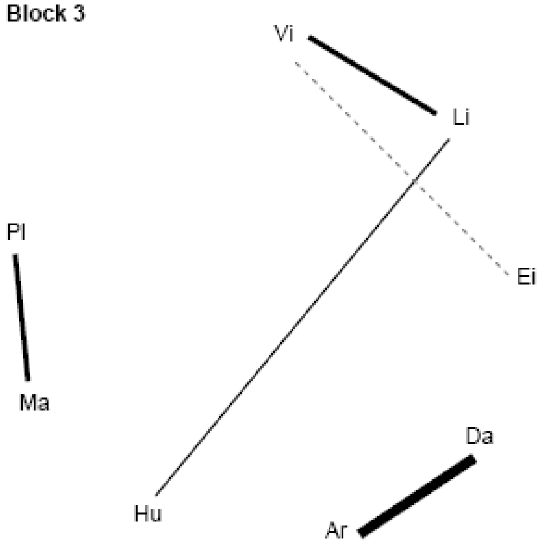
Block 1



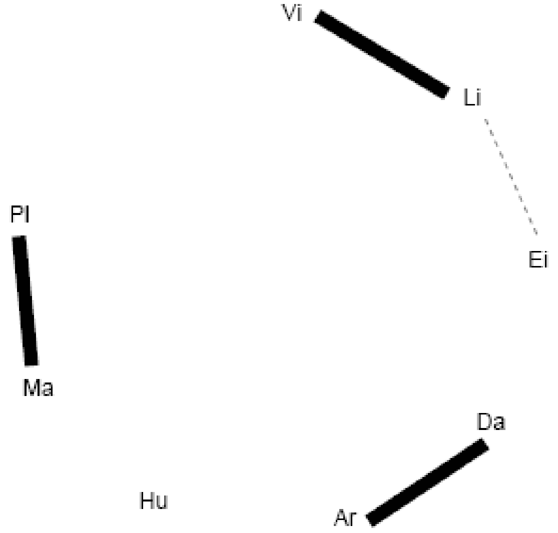
Block 2



Block 3



Block 4



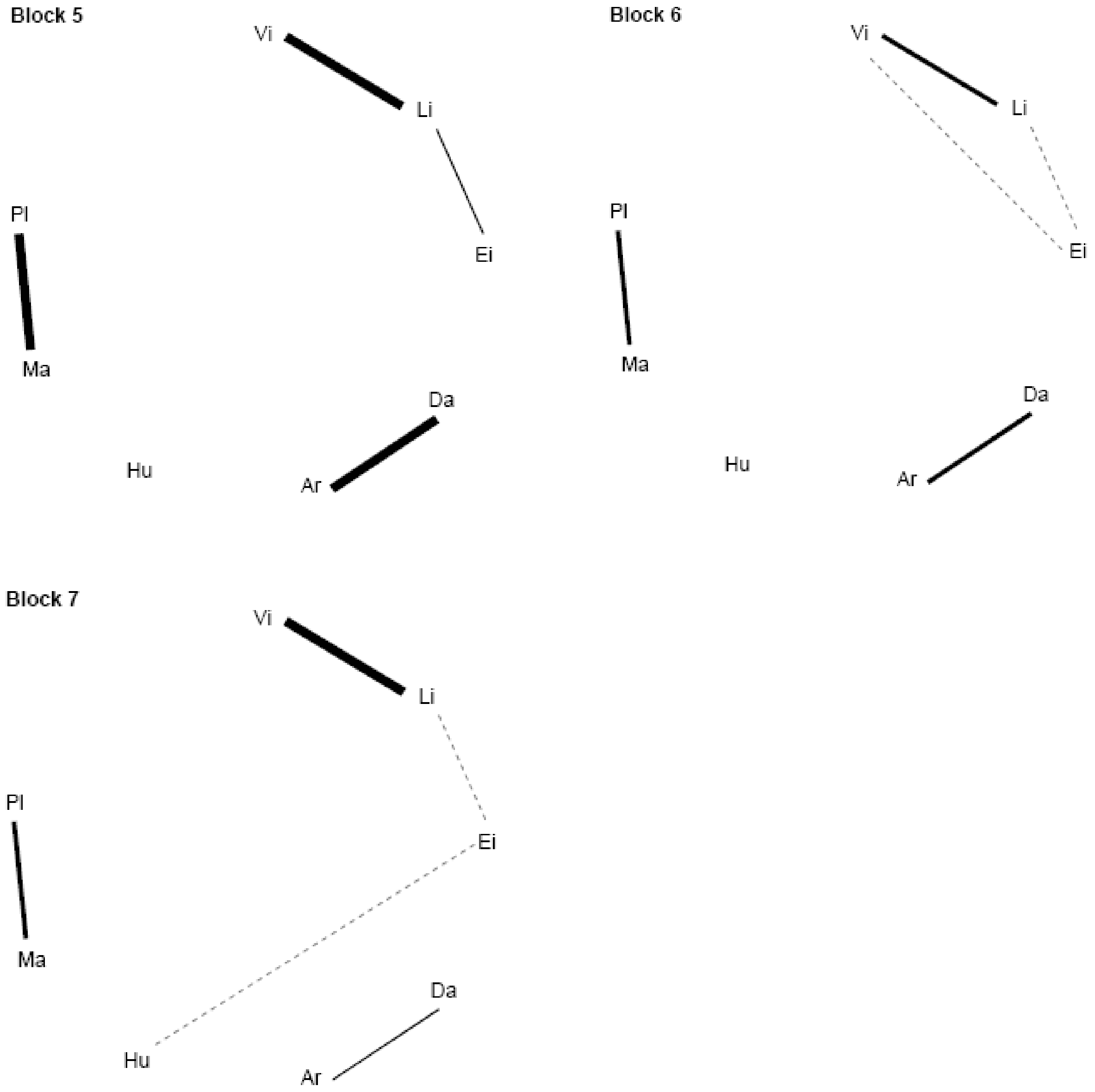


Figure 21. Sociograms for adult rooks of group R3. Rook Ne appears grey in the block during which she was moved to group R2 and was removed from diagrams of this group thereafter.

Social bonds were present from the start of observation in each of the three adult groups. With only one female in the adult jackdaw group (Table 2a), apart from one bond (Be & Da), all the bonds that were discovered were same-sex bonds (Al & Tw, Ca & Or, Or & Wo, Ph & Tw). In the younger adult rook group, three different-sex pair bonds (Ck & Fr, Co & Gu, Co & Mo) and three pair bonds between same-sex partners (Bu & Ca, Fo & Nu, Gu & Wo) existed. In the older adult rook group, there were only pair bonds between partners of different sex (Ar & Da, Li & Vi, Ne & Pl, Ma & Pl).

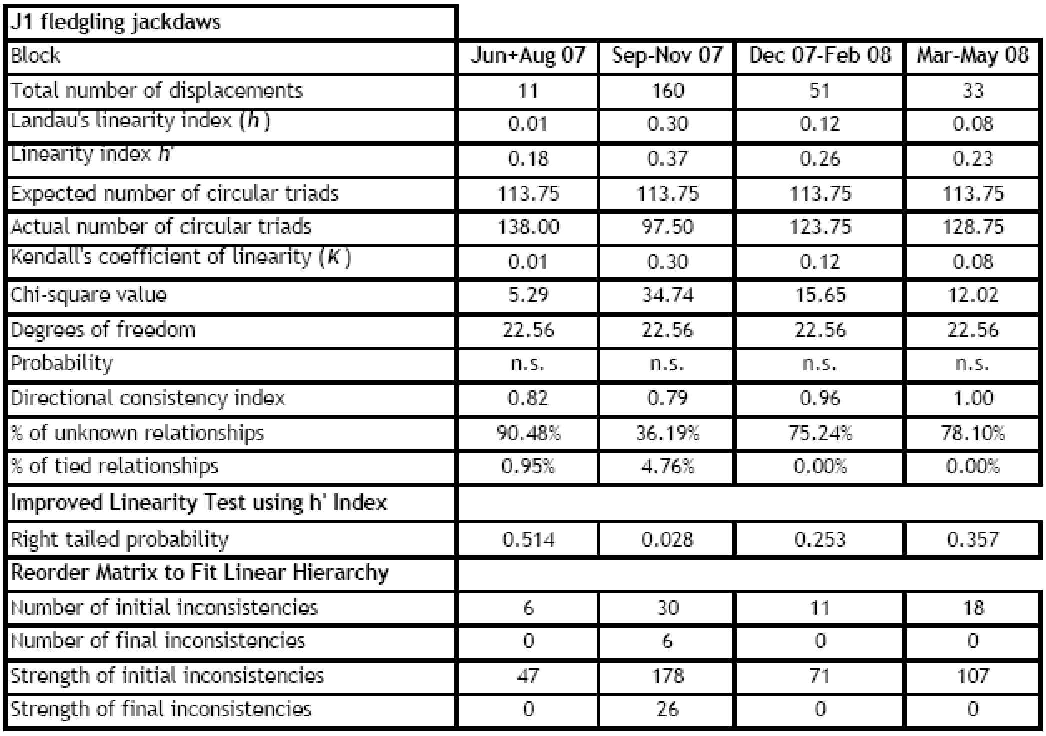
2.4.2 Displacements and dominance hierarchy

Results of linearity analyses and displacement matrices are presented in Tables 7-12 and Figures 22-27. Table 12 and Figure 27 show data for calculations across the whole observation period for the adult groups (J2, R2, R3).

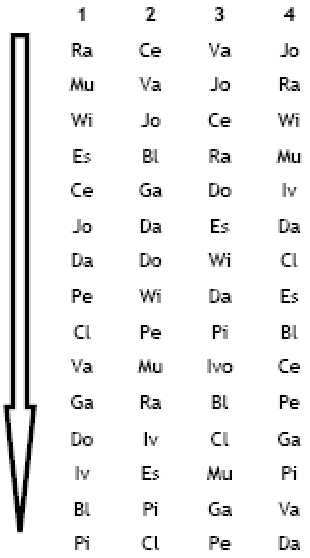
2.4.2.1 Fledgling groups

None of the three fledgling groups developed a linear hierarchy in any of the observation blocks (Tables 7-9). This might be due to the small total number of displacements per observation block (or changing hierarchies). However, due to their young age and their dominance hierarchies still developing, data could not be pooled and analysed across blocks.

Table 7. Results of the analysis of hierarchy linearity in the group of fledgling jackdaws J1.



J1 fledgling jackdaws				
Block	Jun+Aug 07	Sep-Nov 07	Dec 07-Feb 08	Mar-May 08
Total number of displacements	11	160	51	33
Landau's linearity index (*h*)	0.01	0.30	0.12	0.08
Linearity index *h'*	0.18	0.37	0.26	0.23
Expected number of circular triads	113.75	113.75	113.75	113.75
Actual number of circular triads	138.00	97.50	123.75	128.75
Kendall's coefficient of linearity (*K*)	0.01	0.30	0.12	0.08
Chi-square value	5.29	34.74	15.65	12.02
Degrees of freedom	22.56	22.56	22.56	22.56
Probability	n.s.	n.s.	n.s.	n.s.
Directional consistency index	0.82	0.79	0.96	1.00
% of unknown relationships	90.48%	36.19%	75.24%	78.10%
% of tied relationships	0.95%	4.76%	0.00%	0.00%
Improved Linearity Test using h' Index				
Right tailed probability	0.514	0.028	0.253	0.357
Reorder Matrix to Fit Linear Hierarchy				
Number of initial inconsistencies	6	30	11	18
Number of final inconsistencies	0	6	0	0
Strength of initial inconsistencies	47	178	71	107
Strength of final inconsistencies	0	26	0	0

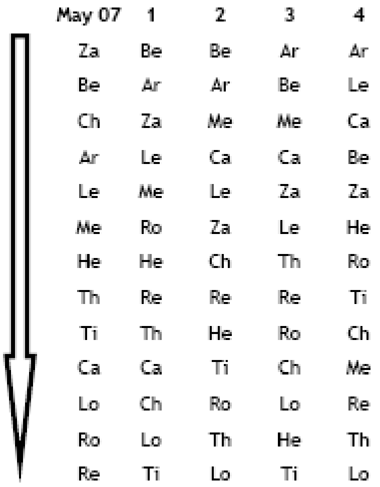


1	2	3	4
Ra	Ce	Va	Jo
Mu	Va	Jo	Ra
Wi	Jo	Ce	Wi
Es	Bl	Ra	Mu
Ce	Ga	Do	Iv
Jo	Da	Es	Da
Da	Do	Wi	Cl
Pe	Wi	Da	Es
Cl	Pe	Pi	Bl
Va	Mu	Ivo	Ce
Ga	Ra	Bl	Pe
Do	Iv	Cl	Ga
Iv	Es	Mu	Pi
Bl	Pi	Ga	Va
Pi	Cl	Pe	Da

Figure 22. The dominance hierarchy as calculated with MatMan 1.0 for the fledgling jackdaws of Group J1 for the four observation blocks. The highest ranking individual is at the top of each column; numbers indicate observation blocks (see Figure 15).

Table 8. Results of the analysis of hierarchy linearity in the group of fledgling rooks R1.

R1 fledgling rooks					
Block	May-07	Jun+Aug 07	Sep-Nov 07	Dec 07-Feb 08	Mar-May 08
Total number of displacements	24	60	92	47	20
Landau's linearity index (*h*)	0.06	0.28	0.29	0.20	0.07
Linearity index *h'*	0.23	0.38	0.37	0.34	0.23
Expected number of circular triads	71.50	71.50	71.50	71.50	71.50
Actual number of circular triads	85.50	65.50	64.75	72.50	84.75
Kendall's coefficient of linearity (*K*)	0.06	0.28	0.29	0.20	0.07
Chi-square value	9.19	26.96	27.63	20.74	9.85
Degrees of freedom	21.19	21.19	21.19	21.19	21.19
Probability	n.s.	n.s.	n.s.	n.s.	n.s.
Directional consistency index	0.83	0.90	0.96	0.87	1.00
% of unknown relationships	76.92%	48.72%	38.46%	61.54%	75.64%
% of tied relationships	1.28%	2.56%	1.28%	2.56%	0.00%
Improved Linearity Test using h' Index					
Right tailed probability	0.465	0.092	0.089	0.155	0.464
Reorder Matrix to Fit Linear Hierarchy					
Number of initial inconsistencies	7	22	28	19	9
Number of final inconsistencies	1	0	4	0	1
Strength of initial inconsistencies	37	120	133	90	38
Strength of final inconsistencies	2	0	17	0	2

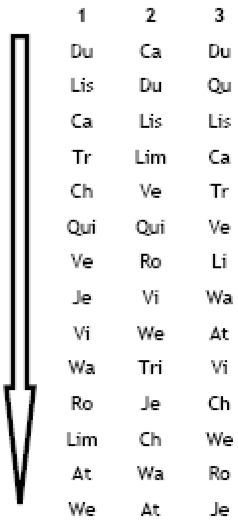


May 07	1	2	3	4
Za	Be	Be	Ar	Ar
Be	Ar	Ar	Be	Le
Ch	Za	Me	Me	Ca
Ar	Le	Ca	Ca	Be
Le	Me	Le	Za	Za
Me	Ro	Za	Le	He
He	He	Ch	Th	Ro
Th	Re	Re	Re	Ti
Ti	Th	He	Ro	Ch
Ca	Ca	Ti	Ch	Me
Lo	Ch	Ro	Lo	Re
Ro	Lo	Th	He	Th
Re	Ti	Lo	Ti	Lo

Figure 23. The dominance hierarchy for the fledgling rooks of Group R1 for the 5 observation blocks.

Table 9. Results of the analysis of hierarchy linearity in the group of fledgling Eurasian jays EJ1. There were no displacements in block 4 (however, for that block proximity data were analysed, see Figure 18).

EJ1 fledgling Eurasian jays			
Block	Aug-07	Sep-Nov 07	Dec 07-Feb 08
Total number of displacements	41	224	21
Landau's linearity index (*h*)	0.07	0.31	0.06
Linearity index *h'*	0.21	0.37	0.23
Expected number of circular triads	91.00	91.00	91.00
Actual number of circular triads	106.00	78.25	106.50
Kendall's coefficient of linearity (*K*)	0.05	0.30	0.05
Chi-square value	10.24	32.44	9.84
Degrees of freedom	21.84	21.84	21.84
Probability	n.s.	n.s.	n.s.
Directional consistency index	0.90	0.77	0.90
% of unknown relationships	69.23%	28.57%	83.52%
% of tied relationships	0.00%	5.49%	0.00%
Improved Linearity Test using h' Index			
Right tailed probability	0.493	0.044	0.404
Reorder Matrix to Fit Linear Hierarchy			
Number of initial inconsistencies	11	29	6
Number of final inconsistencies	2	7	0
Strength of initial inconsistencies	59	155	29
Strength of final inconsistencies	9	35	0



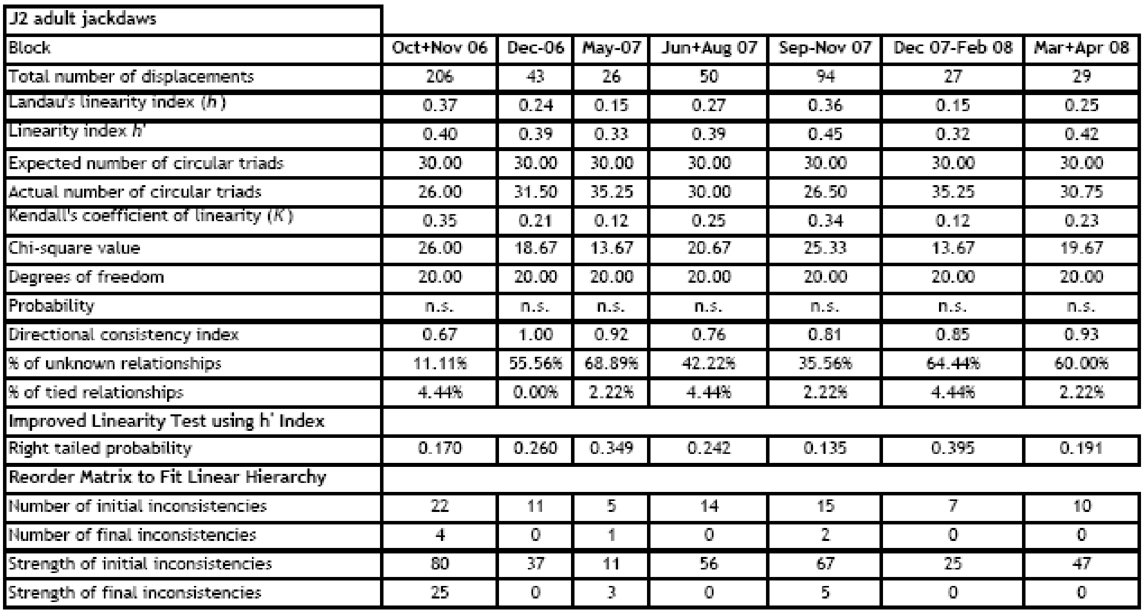
1	2	3
Du	Ca	Du
Lis	Du	Qu
Ca	Lis	Lis
Tr	Lim	Ca
Ch	Ve	Tr
Qui	Qui	Ve
Ve	Ro	Li
Je	Vi	Wa
Vi	We	At
Wa	Tri	Vi
Ro	Je	Ch
Lim	Ch	We
At	Wa	Ro
We	At	Je

Figure 24. The dominance hierarchy for the fledgling Eurasian jays of Group EJ1 for the 3 observation blocks.

2.4.2.2 Adult groups

Apart from in 2 blocks in group R2 and 1 block in R3, hierarchies were not linear in the adult groups (Tables 10-12). Similar to the fledgling groups, this might be an effect of small sample sizes (or changing hierarchies). Therefore, data were also analysed across all observation blocks (Table 13, Figure 28). This procedure was valid for adult birds only, as I assumed the dominance hierarchy would have been stable for a few months or years prior to the observation phase.

Table 10. Results of the analysis of hierarchy linearity in the group of adult jackdaws J2.



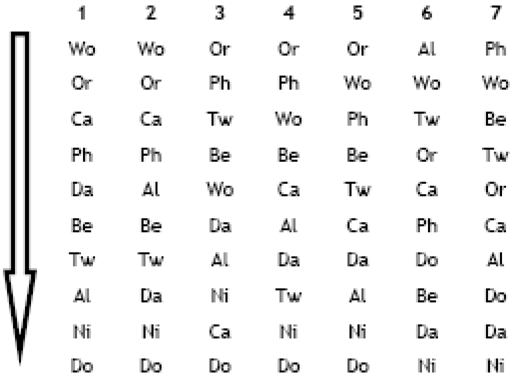
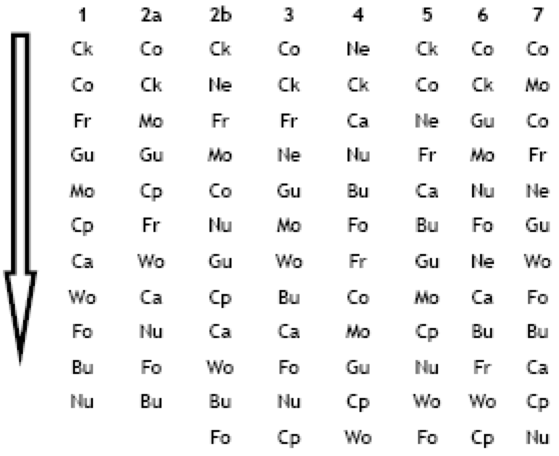
J2 adult jackdaws							
Block	Oct+Nov 06	Dec-06	May-07	Jun+Aug 07	Sep-Nov 07	Dec 07-Feb 08	Mar+Apr 08
Total number of displacements	206	43	26	50	94	27	29
Landau's linearity index (*h*)	0.37	0.24	0.15	0.27	0.36	0.15	0.25
Linearity index *h*'	0.40	0.39	0.33	0.39	0.45	0.32	0.42
Expected number of circular triads	30.00	30.00	30.00	30.00	30.00	30.00	30.00
Actual number of circular triads	26.00	31.50	35.25	30.00	26.50	35.25	30.75
Kendall's coefficient of linearity (*K*)	0.35	0.21	0.12	0.25	0.34	0.12	0.23
Chi-square value	26.00	18.67	13.67	20.67	25.33	13.67	19.67
Degrees of freedom	20.00	20.00	20.00	20.00	20.00	20.00	20.00
Probability	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Directional consistency index	0.67	1.00	0.92	0.76	0.81	0.85	0.93
% of unknown relationships	11.11%	55.56%	68.89%	42.22%	35.56%	64.44%	60.00%
% of tied relationships	4.44%	0.00%	2.22%	4.44%	2.22%	4.44%	2.22%
Improved Linearity Test using h' Index							
Right tailed probability	0.170	0.260	0.349	0.242	0.135	0.395	0.191
Reorder Matrix to Fit Linear Hierarchy							
Number of initial inconsistencies	22	11	5	14	15	7	10
Number of final inconsistencies	4	0	1	0	2	0	0
Strength of initial inconsistencies	80	37	11	56	67	25	47
Strength of final inconsistencies	25	0	3	0	5	0	0

1	2	3	4	5	6	7
Wo	Wo	Or	Or	Or	Al	Ph
Or	Or	Ph	Ph	Wo	Wo	Wo
Ca	Ca	Tw	Wo	Ph	Tw	Be
Ph	Ph	Be	Be	Be	Or	Tw
Da	Al	Wo	Ca	Tw	Ca	Or
Be	Be	Da	Al	Ca	Ph	Ca
Tw	Tw	Al	Da	Da	Do	Al
Al	Da	Ni	Tw	Al	Be	Do
Ni	Ni	Ca	Ni	Ni	Da	Da
Do	Do	Do	Do	Do	Ni	Ni

Figure 25. The dominance hierarchy as calculated with MatMan 1.0 for the adult jackdaws of Group J2 for the 7 observation blocks.

Table 11. Results of the analysis of hierarchy linearity in the younger group of adult rooks R2. Rook Ne was moved from Group R3 to Group R2 in January 2007, which is why block 2 (Dec 06 – Feb 07) was split up into two blocks (Dec 06 + Jan I 07 / Jan II + Feb 07) and data were analysed separately for before and after Ne was introduced into Group R2.

R2 adult rooks								
Block	Oct+Nov 06	Dec 06+Jan I 07	Jan II+Feb 07	Mar-May 07	Jun+Aug 07	Sep-Nov 07	Dec 07-Feb 08	Mar+Apr 08
Total number of displacements	279	90	112	238	51	123	48	94
Landau's linearity index (*h*)	0.67	0.30	0.24	0.55	0.19	0.29	0.20	0.34
Linearity index *h'*	0.68	0.39	0.32	0.60	0.34	0.37	0.33	0.43
Expected number of circular triads	41.25	41.25	55.00	55.00	55.00	55.00	55.00	55.00
Actual number of circular triads	18.00	38.25	54.25	32.25	57.75	50.75	57.50	47.50
Kendall's coefficient of linearity (*K*)	0.67	0.30	0.23	0.54	0.18	0.28	0.18	0.32
Chi-square value	47.35	24.20	21.88	43.88	18.38	25.38	18.63	28.63
Degrees of freedom	20.20	20.20	20.20	20.20	20.20	20.20	20.20	20.20
Probability	< 0.001	n.s.	n.s.	0.01	n.s.	n.s.	n.s.	n.s.
Directional consistency index	0.71	0.84	0.77	0.83	0.80	0.80	0.88	0.89
% of unknown relationships	0.04	0.33	0.35	0.21	0.62	0.33	0.59	0.42
% of tied relationships	0.05	0.02	0.09	0.03	0.02	0.05	0.03	0.00
Improved Linearity Test using h' Index								
Right tailed probability	< 0.001	0.154	0.233	0.002	0.228	0.160	0.205	0.058
Reorder Matrix to Fit Linear Hierarchy								
Number of initial inconsistencies	23	10	17	21	14	16	13	17
Number of final inconsistencies	4	3	3	2	0	2	1	3
Strength of initial inconsistencies	84	69	67	86	62	80	62	69
Strength of final inconsistencies	17	16	13	17	0	8	2	9



1	2a	2b	3	4	5	6	7
Ck	Co	Ck	Co	Ne	Ck	Co	Co
Co	Ck	Ne	Ck	Ck	Co	Ck	Mo
Fr	Mo	Fr	Fr	Ca	Ne	Gu	Co
Gu	Gu	Mo	Ne	Nu	Fr	Mo	Fr
Mo	Cp	Co	Gu	Bu	Ca	Nu	Ne
Cp	Fr	Nu	Mo	Fo	Bu	Fo	Gu
Ca	Wo	Gu	Wo	Fr	Gu	Ne	Wo
Wo	Ca	Cp	Bu	Co	Mo	Ca	Fo
Fo	Nu	Ca	Ca	Mo	Cp	Bu	Bu
Bu	Fo	Wo	Fo	Gu	Nu	Fr	Ca
Nu	Bu	Bu	Nu	Cp	Wo	Wo	Cp
		Fo	Cp	Wo	Fo	Cp	Nu

Figure 26. The dominance hierarchy for the adult rooks of Group R2 for the 7 observation blocks. Data for before and after introducing Ne are presented in blocks 2a and 2b.

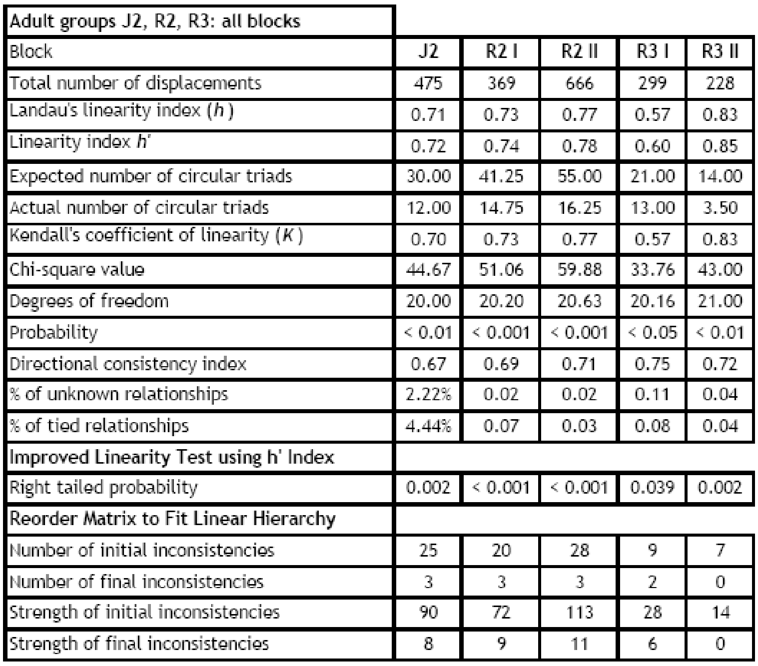
Table 12. Results of the analysis of hierarchy linearity in the older Group of adult rooks R3. Block 2 was split up into two blocks which were analysed separately, due to moving rook Ne from Group R3 to Group R2 in January 2007.

R3 adult rooks								
Block	Oct+Nov 06	Dec+Jan I 07	Jan II 07+Feb 07	Mar-May 07	Jun+Aug 07	Sep-Nov 07	Dec 07-Feb 08	Mar+Apr 08
Total number of displacements	199	100	51	67	29	36	19	17
Landau's linearity index (*h*)	0.56	0.40	0.55	0.50	0.33	0.35	0.19	0.15
Linearity index *h'*	0.61	0.49	0.67	0.63	0.51	0.46	0.36	0.38
Expected number of circular triads	21.00	21.00	14.00	14.00	14.00	14.00	14.00	14.00
Actual number of circular triads	13.25	18.00	9.50	10.50	14.00	13.75	17.00	17.75
Kendall's coefficient of linearity (*K*)	0.56	0.40	0.53	0.48	0.30	0.31	0.15	0.11
Chi-square value	33.36	25.76	31.00	29.00	22.00	22.50	16.00	14.50
Degrees of freedom	20.16	20.16	21.00	20.16	20.16	20.16	20.16	0.65
Probability	< 0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Directional consistency index	0.80	0.74	0.92	0.79	1.00	0.78	0.79	14.5
% of unknown relationships	0.17	0.31	0.36	0.39	0.54	0.36	0.50	0.68
% of tied relationships	0.03	0.03	0.00	0.11	0.00	0.04	0.04	0.04
Improved Linearity Test using h' Index								
Right tailed probability	0.037	0.118	0.085	0.074	0.228	0.243	0.457	0.411
Reorder Matrix to Fit Linear Hierarchy								
Number of initial inconsistencies	8	9	5	7	3	5	4	2
Number of final inconsistencies	2	2	0	0	0	1	1	8
Strength of initial inconsistencies	24	28	10	13	6	12	8	5
Strength of final inconsistencies	6	8	0	0	0	4	2	0

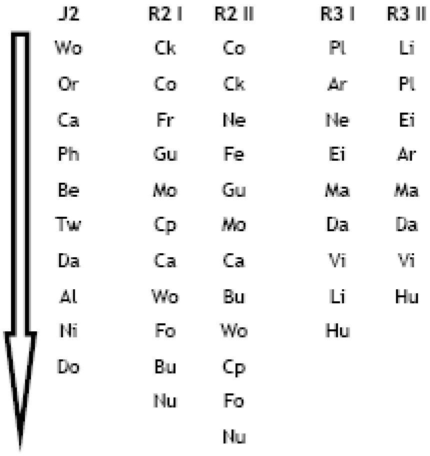
1	2a	2b	3	4	5	6	7
Pl	Ar	Li	Li	Pl	Pl	Li	Li
Ar	Ne	Ei	Pi	Li	Li	Pl	Pl
Ne	Li	Ar	Da	Ma	Ei	Ei	Ma
Ei	Pl	Pl	Ar	Ei	Da	Ma	Ei
Ma	Ma	Ma	Vi	Vi	Ar	Da	Da
Da	Ei	Vi	Ei	Ar	Vi	Ar	Vi
Vi	Da	Hu	Ma	Da	Ma	Vi	Ar
Li	Vi	Da	Hu	Hu	Hu	Hu	Hu
Hu	Hu						

Figure 27. The dominance hierarchy for the adult rooks of Group R3 for the 7 observation blocks. Data for before and after moving Ne to Group R2 are presented in blocks 2a and 2b.

Table 13. Results of the analysis of hierarchy linearity across all blocks in the 3 adult groups (J2, R2, R3). Data for Group R2 and R3 were split up into blocks I and II: before and after moving rook Ne in January 2007.



Adult groups J2, R2, R3: all blocks					
Block	J2	R2 I	R2 II	R3 I	R3 II
Total number of displacements	475	369	666	299	228
Landau's linearity index (*h*)	0.71	0.73	0.77	0.57	0.83
Linearity index *h*'	0.72	0.74	0.78	0.60	0.85
Expected number of circular triads	30.00	41.25	55.00	21.00	14.00
Actual number of circular triads	12.00	14.75	16.25	13.00	3.50
Kendall's coefficient of linearity (*K*)	0.70	0.73	0.77	0.57	0.83
Chi-square value	44.67	51.06	59.88	33.76	43.00
Degrees of freedom	20.00	20.20	20.63	20.16	21.00
Probability	< 0.01	< 0.001	< 0.001	< 0.05	< 0.01
Directional consistency index	0.67	0.69	0.71	0.75	0.72
% of unknown relationships	2.22%	0.02	0.02	0.11	0.04
% of tied relationships	4.44%	0.07	0.03	0.08	0.04
Improved Linearity Test using h' Index					
Right tailed probability	0.002	< 0.001	< 0.001	0.039	0.002
Reorder Matrix to Fit Linear Hierarchy					
Number of initial inconsistencies	25	20	28	9	7
Number of final inconsistencies	3	3	3	2	0
Strength of initial inconsistencies	90	72	113	28	14
Strength of final inconsistencies	8	9	11	6	0



J2	R2 I	R2 II	R3 I	R3 II
Wo	Ck	Co	Pl	Li
Or	Co	Ck	Ar	Pl
Ca	Fr	Ne	Ne	Ei
Ph	Gu	Fe	Ei	Ar
Be	Mo	Gu	Ma	Ma
Tw	Cp	Mo	Da	Da
Da	Ca	Ca	Vi	Vi
Al	Wo	Bu	Li	Hu
Ni	Fo	Wo	Hu	
Do	Bu	Cp		
	Nu	Fo		
		Nu		

Figure 28. The dominance hierarchy for adult Groups J2, R2 and R3 across all blocks. Two separate hierarchies are shown for blocks I and II in the two adult rook groups (R2 and R3).

When data from all observation blocks were pooled for each of the three adult groups, the dominance hierarchies in each group appeared linear. Moving one adult rook from one group to another did not have an influence on the linearity of the two groups. Interestingly, Ne was able to hold a relatively high rank after being introduced into the younger adult rook group.

2.5 Discussion

This study revealed developing social bonds in rooks and jackdaws, but not in Eurasian jays, and non-linear dominance hierarchies within each of the six groups. However, pooling data for each of the three adult groups, the dominance hierarchies in those groups appeared linear.

2.5.1 Social proximity and social bonds

Social bonds of varying strength were found between conspecifics of all six bird groups. In the three fledgling groups the patterns visible in the sociograms illustrated that individuals became more and more selective over the course of the study as to whom to spend time with. Moreover, a lot of changes and re-organisation within the group became obvious, as demonstrated by the differences in the time pairs spent together between all four observation blocks in the fledgling jackdaws. In both jackdaws and rooks, the end of the observational study seems to have marked the beginning of pair bond formation. Over the course of the study, individuals spent varying amounts of time in close proximity to numerous conspecifics; in the final blocks dyads that spent more time together than others emerged. Thus, pair bonds were developed when jackdaws were approximately 8 to 10 months and rooks were 6 to 8 months old. The last observation block was also the onset of the first breeding season for the fledgling birds. However, they did not breed in their first year. In contrast, the Eurasian jays, despite their increasing selectivity, did not form pair bonds over the course of the study.

With the adult groups, only marginal changes in the social bonds between individuals were observed, and the sociograms clearly visualised which social bonds were pair bonds (because of the disproportionately large amount of time those individuals spent together) and which were bonds between conspecifics.

Given the different social structures of the three species, the findings are not surprising. Both rooks and jackdaws are highly social and breed in huge colonies (Clayton & Emery 2007). The territorial Eurasian jays do not need social bonds, as their simple social structure consists only of a breeding pair in a home range that is defended. Outside of the breeding season, the Eurasian jays spend most of their time on their own. In social species, bonds between partners create the basic unit of a group: the pair. Formation and maintenance of those bonds, bonds between other conspecifics and bonds between partners of a pair and other conspecifics modulate social relationships and facilitate social organisation within a species (Schweitzer et al 2010). This ensures group cohesion (Curley & Keverne 2005, Emery et al. 2007). Group cohesion brings with it all the benefits of living in a big social group, such as shared vigilance for predators during foraging (see *Chapter 1*).

Various different types of bonds have been described in the literature, such as social, sexual and maternal bonds. All of those types are defined as preferential affiliative interactions between two individuals. (In this context, ‘affiliative’ means the individual with the most interactions amongst those available; i.e. a plurality, not necessarily a majority.) Mother-infant attachment, an affectional relationship between mother and offspring that endures over time (Gubernick 1981), did not play a role in the current study. The two types of bonds that were discovered in the observed bird groups were social bonds and sexual bonds. Sexual bonds between conspecifics can be maintained for one breeding season only or in a permanent way (Schweitzer et al 2010). Looking at my data, the sexual bonds in the adult groups were relatively easy to make out, as in the adult groups some pairs almost exclusively spent time with each other. In the fledgling groups, sexual pairs seemed to start forming by the end of the observation period, notable by the increase of time spent with their then ‘partner’. Two of the bonds observed in the fledgling jackdaws and one of the bonds in the fledgling rooks were between unrelated conspecifics, pointing towards sexual bonding.

A few studies report evidence in birds of parent-offspring bonds, sibling bonds and sexual bonds in birds (Cézilly et al. 2000, Lefevre et al. 1998, Nakagawa & Waas 2004, Waldman & Bateson 1989). However, relatively little is known about social bonds between conspecifics that do not develop into sexual bonds, either in birds or in mammals (Ligout & Porter 2003). However, some studies indicate the importance of social proximity (Jones & Mills 1999, Schweitzer et al. 2010, Väisänen & Jensen 2003). In the current study, social bonds were discovered between same-sex pairs in one of the adult rook groups and in the adult jackdaw group. No mating attempts were observed between same-sex partners (neither did I observe mating attempts between different-sex pairs); however, in terms of time spans spent together those pairs did not seem to differ from pairs of different sex (due to lack of data, this could not be analysed). Homosexuality is a well-known and well-studied phenomenon in animal behaviour research (Bagemihl 1998, Poiani 2010). However, given the benefits derived by being in a pair, such as the potential increase of dominance over others, it is difficult to define such same-sex pairings as homosexual per se. Similar same-sex pair bonds were found in earlier studies of jackdaws (Katzir 1981, Roëll 1978, von Bayern 2008, Wechsler 1989).

Future studies should investigate in more detail the differences between same-sex and different-sex partners to determine what characterises same-sex pair bonds and what distinguishes them from different-sex pair bonds. Fine-grained analyses of initial encounters between two individuals that later become a pair would shed light on the issue of the cognitive mechanism by which pair bonds are formed and the nature of the initial interactions that form the attraction between partners, whether mutual or one-sided (but see Emery et al. 2007). Moreover, the role of the neuropeptides oxytocin and vasopressin in pair bond formation in birds should be explored further, as it has been in mammals (Curley & Keverne 2005). Field studies with banded individuals would reveal potential differences between captive and wild animals in the establishment of bonds and would also contribute to understanding the influence of captivity on the formation of same-sex pairs.

2.5.2 Displacements and dominance hierarchy

Initially, dominance hierarchies within the six groups of birds studied were non-linear, with less linearity in fledgling than in adult groups and in fledgling Eurasian jays than in fledgling rooks or jackdaws. However, there was a substantial impact of sample size on the calculation of a dominance hierarchy (too few interactions): when data were pooled for the adult groups, linearity was revealed.

In the fledgling groups, linearity fluctuated across blocks, and individuals frequently changed places in the hierarchy. However, in rooks and Eurasian jays it seemed that the same individuals stayed in the upper and lower third of the hierarchies across blocks. In the adult groups, the hierarchies seemed slightly more stable, both in terms of linearity index and relative position of individuals in the hierarchies. In the adult jackdaws, one of two individuals was at the bottom of each one of the hierarchies for the seven observation blocks. The same was true for the older adult rook group. Similarly, the same individuals alternated on the top end of the hierarchies in each one of the three adult groups. However, only when the data were pooled did the hierarchy for the groups become stable, indicating the importance of a high number of observations when gathering data for the calculation of a dominance hierarchy.

In future studies, more observational data should be taken for each adult group that is investigated and where a linear hierarchy is predicted. Specifically, a higher number of displacements should be observed, which would allow the potential emergence of linear hierarchy in the analysis. This also applies to the observation of fledgling groups: higher numbers of displacements documented per observation block would allow for a more detailed characterisation of developing dominance hierarchies. Equal numbers of males and females in the observed group (and determining the sex of fledgling birds) would allow an analysis in terms of a potential gender effect. In corvids, such a gender effect on dominance relationships was found in an earlier study on jackdaws (Röell 1978) and in carrion crows (Richner 1989), jungle crows (Izawa & Watanabe 2008), ravens (Marzluff & Heinrich 1991) and scrub-jays (Woolfenden & Fitzpatrick 1977).

Intrinsic or extrinsic mechanisms could underlie the establishment and/or maintenance of a dominance relationship between two individuals (Izawa & Watanabe 2008). Landau (1951a) described the intrinsic mechanism as perceiving one's opponent's 'dominance ability' via individual characteristics, such as body size, sex or age. Those characteristics may act as a signal and determine the relative dominance rank of two individuals in an encounter. Although some question whether an intrinsic mechanism can account for the establishment of dominance hierarchies (Maynard & Smith 1974; discussed in Izawa and Watanabe 2008), other studies support the role of an intrinsic mechanism (Richner 1989, Piper 1979).

Alternatively, an extrinsic mechanism could account for the establishment and maintenance of dominance hierarchies (Landau 1951b): Through agonistic interactions and memory of the outcome of those, relative dominance relationships are formed. Whereas an intrinsic mechanism allows individuals to assess the situation before or during an encounter and act accordingly, an extrinsic mechanism enables individuals to establish their relationship only afterwards, based on remembering the outcome of their past encounters. After a first encounter, which would determine the relationship, two individuals could then in consecutive encounters base their behaviour on the memory of that first encounter, decrease their aggression levels over the course of future encounters and thus save energy that would otherwise have to be invested in conflict (e.g. crayfish, *Astacus astacus*: Goessmann et al. 2000; chickens, *Gallus gallus*: Guhl 1968).

Two different extrinsic mechanisms for establishing dominance hierarchies have been determined: a mechanism based on individual recognition (Izawa & Watanabe 2008) and the 'confidence effect' (winner/loser effect) (Dugatkin 1997). Individual recognition would allow an individual to remember not only the interaction and its outcome, but also who it was interacting with. In consecutive encounters, individuals would then become discriminatively aggressive or submissive, dependent upon whom they were interacting with (Izawa & Watanabe 2008). This has been documented in various species, such as hermit crabs, *Pagurus* *longicarpus* (Gherardi & Atema 2005), lizards, *Podarcis hispanica* (López & Martín 2001) and lobsters, *Homarus americanus* (Karavanich & Atema 1998). Two studies on corvids have suggested the involvement of individual recognition in dominance hierarchy formation: a study on jungle crows (*Corvus macrorhynchos*; Izawa & Watanabe 2008) and a study on pinyon jays (*Gymnorhinus cyanocephalus*; Paz-y-Miño et al. 2004).

The confidence effect is a more general effect that influences the behaviour of an individual, independent of the identity of an opponent. Thus, the more often an individual loses a fight, the more submissive it becomes in following conflicts. In encounters with others the submissive behaviour would be noted by the opponent, who would then act more dominantly in comparison. Similarly, the winner of a conflict would become more aggressive when meeting other individuals after that conflict (Barnard & Burk 1979). The confidence effect has been thought to facilitate the establishment of a linear dominance hierarchy (Chase et al. 1994, Drummond & Osorno 1992, Dugatkin 1997, Dugatkin & Early 2004).

To investigate the underlying mechanism – intrinsic or extrinsic - by which dominance hierarchies emerge, more detailed data on the intensity of aggression in consecutive encounters could be taken during observations, or experiments with staged encounters could be conducted. High levels of aggression in both individuals of the pair during the first encounter which subsequently decrease over further encounters would indicate an extrinsic mechanism; similar aggression levels between individuals over the course of a few encounters would indicate an intrinsic mechanism as the underlying factor, based on the outward ‘appearance’ of the opponents (influenced by e.g. sex, age, physical condition). If an extrinsic mechanism is determined, one could distinguish between the confidence effect and individual recognition by observing the behaviour of the winner and loser of a conflict in subsequent encounters during observation sessions or in experiments with staged encounters. Individuals becoming discriminatively aggressive towards certain other individuals would be a sign of individual recognition ability and its usage in encounters with others. Studies on hierarchies in bird groups in the wild would have implications for understanding the relevance of captive studies to studying the social structure of group-living animals.

2.6 Conclusions

Social bonds and dominance hierarchies existed from the onset of the study in adult rooks and jackdaws. Moreover, fledgling rooks and jackdaws developed bonds and hierarchies over the course of the observation period. Eurasian jays did not form bonds or establish a hierarchy.

Findings are in line with the species' levels of sociality in the wild. Whereas Eurasian jays are territorial and only spend time with members of the opposite sex during the breeding season, rooks and jackdaws are highly social and stay in life-long pairs (Coombs 1978, Cramp & Perrins 1994, Emery et al. 2007, Goodwin 1986, Lorenz 1970, Roëll 1978). As within a social group, the same individuals interact with each other almost on a daily basis, established relationships are beneficial to rooks and jackdaws. Social bonds between conspecifics facilitate group cohesion, and an established dominance hierarchy saves energy, because a re-establishment of relative relationships each time two individuals meet becomes unnecessary. The territorial Eurasian jays rarely interact in the wild and are thus not in need of establishing social bonds or a hierarchy.

Chapter 3. Testing social learning in jackdaws with a two-action task

3.1 Abstract

Studies in the field of social learning have focused on primates and certain bird species, such as Japanese quails (*Coturnix japonica*) and pigeons (*Columba livia*). However, there is relatively little known about the social learning of corvids, despite a wealth of research into their cognitive abilities. Here I present a study conducted on jackdaws that were able to acquire information about how to access a food resource by watching a conspecific. I discuss the social learning mechanism involved through taking into account the feeding ecology of jackdaws, but also discuss the results in light of a the new social learning framework, combining the work of behavioural ecologists and comparative psychologists (see *Chapter 1*).

3.2 Introduction

Social learning is an alternative to individual trial-and-error learning (or ‘asocial learning’, Heyes 1994). As outlined in *Chapter 1*, biologists have hypothesised that individual trial-and-error learning is more costly than social learning, because it takes more time, which then leads to forgoing other behaviours. However, trial-and-error learning also provides more exact information than social learning, as more detailed information is usually acquired during a longer time span (Boyd & Richerson 1988). Social learning could also fill the niche between genetically predisposed behaviour, such as nest building behaviour (Hansell 2000), which is mostly hardwired and reliable, although inflexible, and individual learning, which seems to be costly, but flexible and therefore useful to overcome changes in the environments (Boyd & Richerson 1988, Zentall 2006). Social learning seems to combine the advantages of both flexibility and lower cost and it enables individuals to avoid the (potentially fatal) negative consequences of individual learning, for example learning about poisonous foods or predators.

Social learning is commonly found in three different contexts: (1) a relatively passive phase, during which an animal watches a conspecific performing an action; (2) a more interactive one, when teaching is involved and an 'experienced' animal goes out of its way to facilitate learning by naïve conspecifics (usually found between parents and their offspring; for definitions see Caro & Hauser 1992; for an example in meerkats, *Suricata suricatta*, see Thornton & McAuliffe 2007); and (3) in other contexts that are usually not termed 'social learning', such as a fish swimming along in a shoal (i.e. social learning via contact) or eavesdropping (picking up information by 'reading' someone else's cues, e.g. deducing the size of a predator by looking at the scratch marks on a tree or listening in on another's song; Peake 2005).

When social learning is reported in a species for the first time, such as the observation of socially-learned termite fishing in chimpanzees (Goodall 1963) or examples of teaching, it often stems from field observations. However detailed research into the underlying mechanisms and other factors that might influence social learning performance is more commonly investigated by laboratory studies. As outlined in *Chapter 1*, various mechanisms of social learning have been identified and defined, ranging from high-fidelity processes of copying, such as imitation and emulation, to lower fidelity processes, such as mechanisms of social influence and local/stimulus enhancement.

In order to determine the specific social learning mechanism underlying behaviour in certain contexts, experimenters are required to use methods that rule out alternative mechanisms. For example, when testing for the presence of cognitively less demanding social learning mechanisms (such as stimulus or local enhancement) it is sufficient to present a demonstrator with an object and determine whether an observer subsequently prefers that object instead of other objects provided (e.g. ravens prefer to manipulate objects that they have seen their siblings interact with when compared to other objects not manipulated by their siblings; Schwab et al. 2008). When testing for cognitively more demanding mechanisms (such as imitation or emulation) more sophisticated methods are required. In a quest to rule out alternative mechanisms such as local and stimulus enhancement, researchers have developed the 'do-as-I-do' paradigm (e.g. dogs, Huber et al. 2009) and the bi-directional control (e.g. rats, Heyes 1994) to test for imitation. In the 'do-as-I-do' procedure, dogs are trained on the 'do-as-I-do' command that prompts them to mimic actions they had just seen. After learning that command, the dogs are shown a new action and then asked to 'do-as-I-do'. Exact mimicry of the human's actions would be a clear indication of imitation as the underlying process.

The bi-directional control was a handle that could be pushed in one of two directions (left and right). The demonstrator rat would push it in one direction and then get a reward; the observer rat would be opposite the demonstrator rat, watching, and would then afterwards be tested in the same set up. Designed to test for imitation, the method has been criticised in favour of other possible alternative explanations such as odour cues on the side of the handle that the demonstrator rat had touched and the potential employment of object movement re-enactment (OMR), a social learning mechanism closely related to emulation. However, the most effective and commonly used technique is the two-action procedure (e.g. budgerigars, *Melopsittacus undulates*: Dawson & Foss 1965; common marmosets, *Callithrix jacchus*: Voelkl & Huber 2000). For this technique, two demonstrators are trained on performing two different actions that lead to the same outcome. Because both actions are performed at the exact same point of the apparatus, the task allows ruling out a 'simple' form of social learning: local/stimulus enhancement. The fact that both actions lead to the same outcome, i.e. reward, means that motivational levels in both observer groups should therefore be similar. If preferential performance of one action (e.g. pecking) is found in one observer group and preferential performance of the other (e.g. stepping) in the other group, this would indicate imitation as the underlying mechanism (Akins & Zentall 1996, Dawson & Foss 1965).

Whereas much work on social learning has been done with apes, social learning research in birds is still developing (for a recent review see Federspiel et al. 2009). Some birds appear to copy the mate choice of others (White 2004) and songbirds, parrots and hummingbirds learn their vocalisations from others and even mimic a variety of sounds (Kelley et al. 2008), however little is known about social learning of actions (see Zentall 2004). Here, I present a social learning study with jackdaws (*Corvus monedula*), a gregarious species of corvid that are attentive to the behaviour of others in various contexts (Röell 1978, Schwab et al. 2008a, von Bayern & Emery, 2009). When feeding in flocks on seeds and insects on the ground, single birds that are searching for a food source join these larger groups (Wechsler 1988a; see *Chapter 1*, *Fig. 7*). Social learning may thus play an important role in a jackdaw's life, especially during foraging. Three previous studies found an influence of social information on jackdaws' foraging decisions, but the studies were either not well controlled (Röell 1978, Wechsler 1988b) or limited in their design (Schwab et al. 2008a), so mechanisms other than stimulus enhancement would not have been able to be detected.

In the current study, jackdaws were tested for their ability to learn to open a food box either through individual learning or watching a demonstrator perform an action that resulted in gaining a food reward. The findings of this study are discussed in light of the proposed new framework for social learning research (*Chapter 1*; Federspiel et al. 2009).

3.3 Methods

3.3.1 Subjects & housing

The subjects were 9 hand-raised adult jackdaws of Group J2 (all birds of the group but Alex), 4 years old at the time of the study, except for one individual, Nico, who was 5 years old (see *Chapter* 2, Table 2).

3.3.2 Apparatus & experimental set up

All tests were conducted in the indoor test compartments. There were 3 platforms in each compartment: a central one and one on either side (Fig. 29). The two compartments that were used for all phases were divided by a wooden wall with a small window measuring 23 cm x 32 cm cut out of its centre, which allowed observers to watch the actions of the demonstrator in an adjacent compartment (see ‘Procedure’). Furthermore, the window helped to determine how many demonstrations the observers had seen, since he needed to sit close enough to see through the window. When the demonstrator was opening the apparatus at the same time, the observer was sitting in a spot from which he could see through the window, with his head oriented towards the window, I counted it as an observed demonstration. The apparatus was placed on the central platform in a way that the feeder opening (see below) faced the entrance of the compartment leading to the adjoining outside run.

The wooden test apparatus was 33 cm high, 18 cm wide and 16 cm deep (Fig.29). It had a 11 cm x 11 cm x 1.5 cm treadle mounted horizontally 5cm from the floor and a 6 cm x 4 cm x 4.5 cm feeder opening in the centre of the box, at jackdaw eye-level. This opening was baited with mealworms (a preferred food) in view of the subjects before the start of the demonstrator training trials and the observer test trials. It was closed by a sliding door which could be opened with a remote control (‘Digital Proportional Radio Control System Zebra 2 AM’), controlling a motor connected to the sliding door on the inside of the apparatus.

Immediately after pecking in the demonstrator training trials and after any response on the treadle during the observer and non-observer testing trials, the experimenter opened the sliding door and the jackdaws could feed from the opening. All trials were recorded onto digital videotape using an Atom Dome camera (Model AHC, CSP Technology Ltd, Scunthorpe, UK), which had been mounted at the back of each test compartment. The birds' behaviour was also monitored by the experimenter via a connected screen, located in an adjacent building.

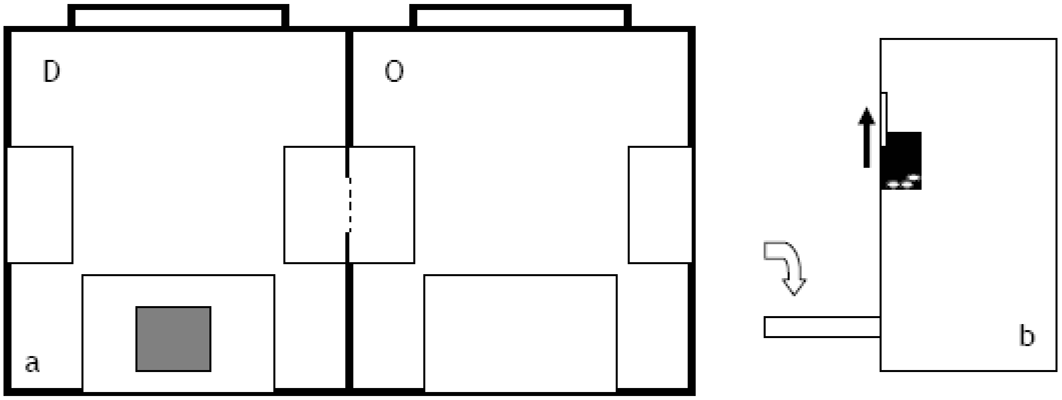


Figure 29. A diagram of (a) the experimental setup from above and (b) the test apparatus. (a) D denotes the Demonstrator compartment and O denotes the Observer compartment. The thick lines indicate testing compartments and hatches leading to the runs (top of drawing), thin lines show platforms, and dashed lines stand for wire mesh. The test apparatus is depicted by a grey square. (b) The white arrow indicates the action demonstrated by the demonstrator: pecking at the treadle; the black arrow shows the opening direction of the sliding door, circles represent mealworms in the feeder opening.

3.3.3 Procedure

The study was conducted from December 2006 to December 2007 (demonstrator training: March-June 2007; habituation of observers and non-observers: December 2006-June 2007; observation and non-observation trials: July-October 2007; testing: October-December 2007). One individual was assigned the role of demonstrator on the basis of being the most tolerated individual within the group. The remaining 8 birds were randomly assigned to either observer group or non-observer (control) group. There were two training phases (demonstrator training, observer & non-observer training) and a testing phase.

3.3.3.1 Demonstrator training

Initially, this experiment was designed to determine the social learning mechanism jackdaws would employ. Thus, two demonstrators were trained on two different actions – stepping and pecking – to be executed at exactly the same spot on the apparatus. However, during the training period, the demonstrator trained on stepping stopped performing the desired action. I then stopped working with this demonstrator and in an attempt to not further decrease the sample size, I continued the experiment with just one demonstrator.

The demonstrator was selected on the basis of daily observations (over the course of 1 month prior to the experiment). Birds sitting in close proximity during a time span of 20 minutes were labelled as ‘attracted’. The bird with the largest number of attracted partners was chosen as the demonstrator. The demonstrator was separated from the group and provided with the test apparatus in the demonstrator compartment. The demonstrator was then trained to peck the treadle by stepwise approximation, starting off with a piece of yolk on the treadle that was gradually made smaller over the course of training trials. Upon pecking the treadle, the sliding door of the apparatus was opened, and the bird was able to feed from the feeder opening. Training was completed when the demonstrator responded by pecking and feeding from the feeder opening 10 out of 10 times on 3 consecutive days.

3.3.3.2 Observer & non-observer training

The training consisted of habituation and observation trials (for observers) or ‘non-observation’ trials (for non-observers). Both observers and non-observers were habituated individually to a non-functional version of the test apparatus (without treadle and sliding door) baited with mealworms in the observer compartment in order to rule out neophobia as an explanation for different behaviour between observers and non-observers. Afterwards, subjects were habituated to the presence of the demonstrator in the adjacent compartment (observers) or the compartment next to the adjacent one (non-observers; for the set up see Fig. 29). Habituation was continued until the birds had reached a criterion of feeding from the apparatus in 8 out of 10 trials on 3 consecutive days.

Once habituated to the apparatus, the observers individually received demonstrations in the observation trials for a block of up to 20 trials per day until they had watched 10 demonstrations or until they or the demonstrator left the set up, i.e. the platforms, for 10 min. At the beginning of the observation trials, the demonstrator entered the demonstrator compartment and the observer entered the observer compartment for 1 min without the apparatus to habituate to the new situation. Subsequently, the apparatus was placed in the demonstrator's compartment, and the experimenter watched observer and demonstrator on the screen and operated the remote control that opened the feeder accordingly.

Instead of watching demonstrations, the non-observers had the opportunity to observe the test apparatus through the window for approximately the same amount of time that the observers watched the demonstrations. To avoid shorter looking times in comparison to the observers due to the lack of a social stimulus, and to ensure that the apparatus in both the observer and non-observer conditions was associated with a social stimulus, the demonstrator was placed into the compartment adjacent to the compartment containing the apparatus (Fig. 30). Consequently, similar to the observers, when the non-observers looked through the window, they could see both the apparatus and the demonstrator, but in two different compartments.

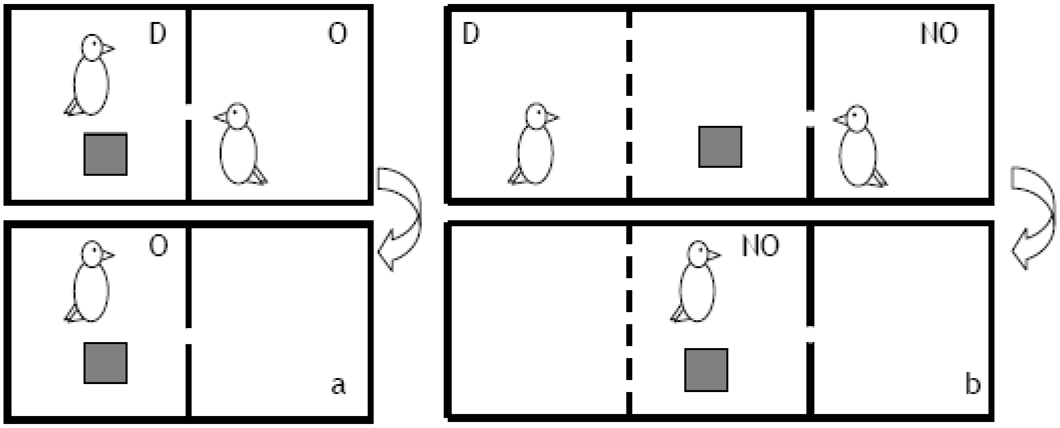


Figure 30. (a) The procedure for observers (O; left) and (b) non-observers (NO; right) with the demonstrator (D). Block arrows show the two parts of the procedure: observational/'non-observation' trials (above) and testing (below). Solid lines indicate compartments; broken lines show the compartment wall with the window, dashed lines represent wire mesh. The apparatus is indicated by the grey square.

3.3.3.3 Testing

After the tenth observed demonstration, the observers were individually tested with the functional test apparatus for 5 test trials. Immediately after the final demonstration, the demonstrator was released into the aviary, and the test subject was moved into the demonstrator compartment. To avoid the influence of social facilitation, i.e. contagious behaviour, where the 'performance of a more or less instinctive pattern of behaviour by one will tend to act as a releaser for the same behaviour in another' (Thorpe 1963, p. 133), the subject was then given an interval of 1 min before the test apparatus was put into the compartment. The experimenter subsequently left the inside area of the aviary, watched the subject on the screen and operated the sliding door of the apparatus with the remote control.

If the bird was on one of the 3 platforms, but did not approach the apparatus for 5 min, the box was removed, and the next trial was given approx. 1 min later. If the bird left the set up for more than 5 min, the session was terminated and the test session was continued the next day. The non-observers were also tested 5 times. All trials were videotaped for later analysis (Canon Digital Camcorder, Model MD101 Pal). During the observation trials, using a video splitter (‘Videoswitch VQ-403C Real-Time Screen Splitter’), observers and demonstrators were filmed at the same time.

3.3.3.4 Analysis

Videotapes were coded with The Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands) and analyzed using STATISTICA 7 (StatSoft Inc., 1984-2004) and by hand, according to Siegel (1956), to control for effects of a small sample size (Mundry & Fischer 1998). I scored events of opening the apparatus, either by pecking or stepping onto the treadle, manipulating the door or other parts of the apparatus (i.e. touching these parts with the beak) and comfort behaviour (i.e. shaking and fluffing), which is an indicator of low stress levels, for both observers and non-observers during the test trials. Furthermore, I calculated latencies to first touch and/or first open the apparatus and to approach the apparatus.

I used Mann-Whitney U tests on the mean value across the individuals’ 5 test trials to compare the observers’ and the non-observers’ performance. I hypothesised that higher success rates in the observers than the non-observers would provide evidence for social learning; close matching of the response topographies of the demonstrator and the observers would point towards imitation as an underlying mechanism. Similar responses of the demonstrator and the non-observers would indicate a greater likelihood of a natural occurrence of the observed behaviour (i.e. opening technique), even without having seen the behaviour just before performing it. Differences in the latency to approach the apparatus between observers and non-observers, with observers being predicted as quicker than non-observers, and possibly also higher rates of comfort behaviour in the observers than in the non-observers, might indicate the presence of neophobia in the non-observers. I used a Spearman rank correlation to examine possible effects of test trial number on number of openings of the apparatus in each of the tested individuals (observers and non-observers). All tests were two-tailed, and alpha was set at 0.05. Trends were reported for 0.10 > α > 0.05.

3.4 Results

Overall, the observers opened the apparatus more frequently than the non-observers (Mann-Whitney U test: $U = 0.00$, $N_1 = 4$, $N_2 = 4$, $P = 0.014$; Fig. 31 & Table 14).

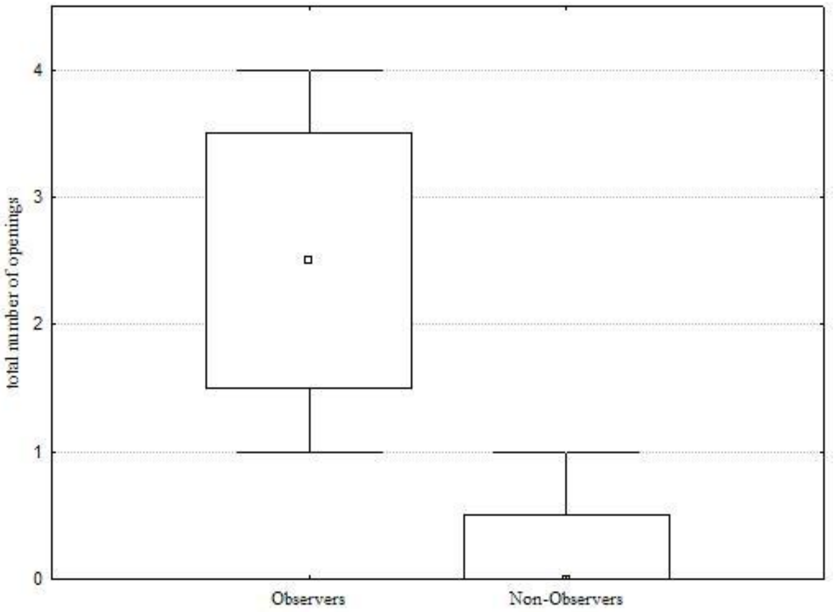


Figure 31. Box and whisker plots for the total number of openings performed by the observers (left) and non-observers (right). Boxes show the interquartile range; the square in the centre of the boxes stands for the median value. Whiskers indicate the largest and smallest value.

The non-observers never opened the box, except for Daffy who employed stepping once (Table 14). All of the observers opened the apparatus in their first test trial, whereas Daffy only did so in her third test trial.

Table 14. Total number of events for both observers and non-observers. Touching the box or the sliding door in any way with their beak was classified as 'manipulating'. Comfort behaviour describes shaking and fluffing.

		Overall openings	Peck openings	Step openings	Manipulating box & door	Comfort behaviour
Observers	Phoenix	2	0	2	2	7
	Bert	3	2	1	41	7
	Donald	1	1	0	0	2
	Calimero	4	1	3	34	0
Non-observers	Orville	0	0	0	0	4
	Daffy	1	0	1	1	0
	Woody	0	0	0	0	2
	Nico	0	0	0	0	2

For two of the observers, the topography of the first response was the same as the observed one, i.e. pecking at the treadle; the other two birds opened the apparatus first using a different method, namely stepping onto the treadle (Table 15).

Table 15. The sequence of opening events for the four observers over the 5 test trials.

	Phoenix		Bert		Donald		Calimero		
Trial	peck	step	peck	step	peck	step	peck	step	SUM
1	0	1	1	0	1	0	0	1	4
2	0	0	0	0	0	0	0	0	0
3	0	0	1	0	0	0	1	0	2
4	0	1	0	0	0	0	0	1	2
5	0	0	0	1	0	0	0	1	2
SUM	0	2	2	1	1	0	1	3	10

It seemed that overall, the observers also manipulated the test apparatus more frequently than the non-observers (Table 14), with two of the observers touching the box with their beak 34 and 41 times, respectively. However, possibly due to the small sample size, analysis only revealed a trend towards a significant difference between observers and non-observers (U = 14.00, N_1 = 4, N_2 = 4, P = 0.057). No significant difference was found between the average time observers and non-observers spent at the box (U = 4.00, N_1 = 4, N_2 = 4, P > 0.05), at the central platform ($U = 5.00$, $N_1 = 4$, $N_2 = 4$, $P > 0.05$) or at the set up overall across the five test trials ($U = 6.00$, $N_1 = 4$, $N_2 = 4$, $P > 0.05$) (Table 16).

Table 16. Median, confidence intervals and range for the average amount of time (sec) the observers and non-observers spent at the box, the platform and the set up.

		Median	Confidence -95%	Confidence +95%	Range
Observers	box	19.66	-20.21	71.89	61.96
	platform	94.62	-25.15	204.92	166.23
	set up	234.09	52.57	359.28	220.33
Non-observers	box	2.43	-2.46	9.54	8.31
	platform	39.57	2.94	83.84	61.15
	set up	165.28	38.1	290.83	181.4

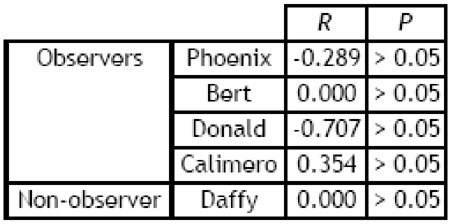
The observers' and the non-observers' latencies to first approach the apparatus did not differ significantly ($U = 4.00$, $N_1 = 4$, $N_2 = 4$, $P > 0.05$), nor did the latencies to touch ($U = 8.00$, $N_1 = 4$, $N_2 = 4$, $P > 0.05$) or open it ($U = 2.00$, $N_1 = 4$, $N_2 = 4$, $P > 0.05$) (Table 17).

Table 17. Median, confidence intervals and range for the average latency (sec) to approach the box, to first touch it and to first open it by pecking or stepping in the observers and non-observers.

		Median	Confidence -95%	Confidence +95%	Range
Observers	at box	99.3	17.52	157.54	95.51
	touch	100.9	31.41	160.29	90.88
	peck/step	93.64	-35.21	225.6	156.78
Non-observers	at box	161.01	-6.89	304.73	235.39
	touch	77	-57.85	311.55	246.58
	peck/step	300	81.09	414.23	209.36

Comparing the shaking and fluffing behaviour of observers and non-observers revealed no significant difference in the comfort behaviour between the two groups ($U = 5.50$, $N_1 = 4$, $N_2 = 4$, $P > 0.05$; observers: median = 4.50, conf. -95% = -1.66, conf. +95% = 9.66, range = 7.00; non-observers: median = 2.00, conf. -95% = -0.60, conf. +95% = 4.60, range = 4.00). No effect of test trial number (N = 5) on the number of openings was found, either for observers or the one non-observer that opened the apparatus (Spearman rank correlations, Table 18).

Table 18. Results for Spearman rank correlations of trial number (1-5) and total number of openings for observers and the non-observer that performed an opening.



		R	*P*
Observers	Phoenix	-0.289	> 0.05
	Bert	0.000	> 0.05
	Donald	-0.707	> 0.05
	Calimero	0.354	> 0.05
Non-observer	Daffy	0.000	> 0.05

3.5 Discussion

The present findings provide some evidence for social learning in jackdaws as observers opened the apparatus more often than non-observers. Due to the similar latencies to approach the apparatus and the similar rates of comfort behaviour of the two groups, a neophobic effect may be ruled out for explaining the difference between the observers and non-observers. Another indication for social learning is the relatively long time it took to train the demonstrator and the comparatively quick response of the observers to the demonstrations. Some species, such as jackdaws, are known to take a long time to overcome their initial fear of novel objects or situations (see Katzir 1981). Neophobia could thus account for the relatively long training phase during which the birds were habituated to the non-functional apparatus, and to feeding from it, as well as the presence of another bird.

Although the sample size of this study was relatively small, one may conclude that jackdaws have the potential to learn from one another. What remains unclear is the mechanism underlying this social learning process. The observers did not consistently copy the exact action that was demonstrated, thus one can rule out imitation as an explanation for the results. To determine the mechanism with certainty, the next step should be to replicate the experiment as a two-action task with two demonstrators (Akins & Zentall 1996). Emulation and local/stimulus enhancement could also explain the difference between observers and non-observers. Although I cannot rule out emulation completely, I will focus my attention on the most parsimonious explanation and thus on how stimulus or local enhancement could account for our results. Whereas in local enhancement the attention of an observer is drawn to a point in the environment by the activity of a demonstrator (Roberts 1941; Thorpe 1963), in stimulus enhancement, the attention of the observer is drawn to a particular object with which the demonstrator is interacting (Spence 1937). In most experiments, the test apparatus is fixed to a certain location, which makes the two very similar mechanisms impossible to distinguish. When two different manipulanda are involved, one being used by the demonstrator, the other being the observer's target object for copying the demonstrator's action, the observers have to be able to generalise the stimulus between both manipulanda (Zentall & Levine 1972). The social learning mechanism employed in that context therefore seems to be stimulus enhancement, which consists of two components: drawing the attention of the observer to the object in question (i.e. the specific manipulandum) and stimulus generalisation between the two levers (Zentall 1996, 2006). In contrast to that, local enhancement is based on just one component: the location at which the demonstrator is behaving. Thus, it seems stimulus enhancement subsumes local enhancement (Galef 1988). As I used two different apparatuses in our experiment – one for habituation and one for demonstrations and testing – and the birds seemed to be able to generalise between the two, it seems likely that the jackdaws employed stimulus enhancement.

Enhancement is a widespread social learning mechanism in birds and mammals that is more flexible and readily transfers to new contexts, unlike for example imitation. Although considered cognitively highly demanding, employing imitation may have its downsides. It has been described as 'blind' (because pigeons were insensitive to the outcome of the actions they were copying; McGregor et al. 2006) or 'automatic' (because budgerigars learned faster to peck when they observed pecking than to step when they observed pecking, or the other way around, which indicates a tendency to automatically imitate the observed action; Mui et al. 2008) and seems to be very inflexible when compared to emulation or enhancement.

Utilising a 'flexible' social learning mechanism may be especially beneficial for animals that live in constantly changing environments, or species that include various ecologically different environments in their natural habitat. Another example for a more 'flexible' social learning mechanism is emulation, which is employed in keas (*Nestor notabilis*; see *Chapter 1*). Similar to enhancement, emulation seems to be much more flexible than imitation: only goals and outcomes are learned, not the whole action sequence. The knowledge could therefore be transferred and applied to similar objects. Because these two mechanisms – enhancement and emulation - seem to be so similar in their flexibility, emulation was called the 'cognitivist's answer to enhancement' (Tomasello 1996). The difference between these two mechanisms is the cognitive demand: whereas in emulation, the animal has to remember an action it has seen or even understand the intention of the demonstrator (i.e. 'copying the *goal'*, Whiten et al. 2004), in local enhancement, the animal does not learn anything about the action of the demonstrator, but is only attracted to a location or a stimulus in the environment, where it then learns the solution to a problem by trial-and-error learning.

Whereas one may therefore conclude that 'intelligent' animals should always employ the most complex mechanism they are capable of, I will argue in the following that 1. the environmental influences on an animal may play a much more important role than is sometimes anticipated and that 2. if capable of employing various mechanisms, when choosing a mechanism (not necessarily a conscious process) individuals experience a trade off between gaining as much information as possible and at the same time saving energy and employing the cognitively least demanding mechanism suitable in a given context.

Keas feed on various types of food, including plants, animals, nectar and larvae beneath stones (Diamond and Bond 1999). Thus, they face the need for a social learning mechanism like emulation that enables them to learn something about how to get to the palatable part of hard-to-access foods. In contrast, jackdaws' diet does not contain hard-to-access foods, indicating that all they might have to learn from watching a conspecific is the location of food, but not how to process it. They usually feed on the ground, and single birds join feeding flocks when searching for a food resource (Wechsler 1988a). Enhancement therefore seems to be the adequate mechanism for their requirements. Earlier studies seem to confirm this (Röell 1978, Wechsler 1988b). A recent study found that jackdaws employ stimulus enhancement and preferentially so from non-affiliated individuals. They showed no social learning in a non-food context (handling objects), but did so in a context involving food: out of two film boxes, observers preferred feeding from a film box that the demonstrator had fed from in the demonstration trials. Due to the limited design, the study only made it possible to examine that one mechanism and did not rule out the possibility that the jackdaws might have employed a different mechanism (Schwab et al. 2008a). In other corvid species, enhancement plays a role in finding food (magpie-jays, *Calocitta formosa*: Langen 1996; ravens, *Corvus corax*: Fritz & Kotrschal 1999; rooks: Waite 1981) or exploration in general (ravens: Schwab et al. 2008b).

Future studies will examine the social learning mechanism employed by jackdaws by using more control procedures, a larger sample size and two demonstrators. When designing experiments and interpreting results, one should thus bear in mind the costs and benefits of employing any given mechanism and the need of an animal to do so. Using the most suitable mechanism, i.e. the 'cognitively cheapest', that still fulfils the needs in a given context and thus saves time and energy may be an even 'smarter' way of gaining knowledge about solving a task than always using the most complex mechanism. What remains unclear at this stage is why certain species, such as Japanese quail or pigeons, seem to employ mechanisms way above their 'ecological needs' (i.e. imitation; Japanese quail: Akins & Zentall 1996, Akins et al. 2002; pigeons: Klein & Zentall 2003, Zentall et al. 2003). Conducting a similar study in a group setting could shed more light on the influence of social relationships, tolerance towards conspecifics, sex and dominance rank. Overall, I would like to conclude that when studying social learning in birds, instead of approaching the subject from a purely psychological perspective, experiments should be embedded within a framework combining psychology and ecology (Federspiel et al 2009). This approach should go some way to reconciling the many disparate disciplines studying social learning and fill in the gaps of our knowledge about how, why, what and when animals learn from others.

Chapter 4. Social learning in jackdaws: a group experiment

4.1 Abstract

For group-living animals, social information is omnipresent and available to everyone who is able to perceive and process it. In previous studies, including the previous chapter, jackdaws have been shown to use social information to learn about novel foraging strategies. Following up from the study presented in *Chapter* 3, I investigated social learning in three groups of jackdaws, two of which had observed a conspecific demonstrator opening a food box using one of two techniques. The observers were tested with the same box in a group setting, and their performance was compared to a control group that had not observed any demonstrations. I found that observers spent more time at the apparatus and manipulated it more often than the non-observers, which indicates that the observers had learned socially. The two observer groups differed in task performance: although both groups approached the apparatus, only one of them learned how to open the apparatus. I conclude that an initial enhancement effect accounted for the difference between observers and non-observers, and that social learning was then followed by individual learning in one of the groups, which led to the difference between the two observer groups.

4.2 Introduction

In an environment where animals interact with each other on a daily basis, social information is omnipresent and available to everyone who is able to perceive and process it (‘inadvertent social information’, Danchin et al. 2004). As outlined in *Chapter* 1, two main hypotheses for the development of social learning skills in social species have been proposed: social learning as an adaptive specialisation (Klopfer 1959) or social learning as a more general process (Lefebvre & Palameta 1988). Regardless of the origin of enhanced learning skills, it seems likely that social animals would be able to utilise the readily available social information in a group (i.e. 'information scrounging', Giraldeau et al. 2002; see *Chapter 1*), and those who are successful at using such information from others will experience some advantage over other group members (Russon 1997, Whiten & van Schaik 2007). In particular, in the foraging context social information seems to play a role in some corvid species: When in close proximity to foraging family members, Florida scrub jays (*Aphelocoma coerulescens*) learned to forage at a novel food patch (Midford et al. 2000); rooks choose to land and forage where others are already foraging (Waite 1981) and choose the same novel food as a social partner (Dally et al. 2008); both hooded crows (*Corvus cornix*) and ravens seem to be able to pick up information on the location of food at roosts that act as 'information centres' (Sonerud et al. 2001, Marzluff et al. 1996); and in experimental studies, ravens that had observed others opening a food box approached and opened the box more readily than non-observers (Fritz & Kotrschal 1999).

In *Chapter 3* I presented a study with jackdaws that show that they employ social learning: Observers were more successful at opening a food box and foraging from it than non-observers. The study of *Chapter 3* was conducted using a classical 'one-to-one' setting, with a trained demonstrator performing an action and one observer watching that demonstrator. Afterwards, the observer was tested in an individual test session. This was repeated for all individuals of the observer group. A different way of testing species for social learning abilities is presenting the task in a group setting.

With chimpanzees, various cases of differences in behaviour between populations that were attributed to social learning have been documented (Boesch & Tomasello 1998, McGrew 1992, 2004; Whiten et al. 1999). The existence of traditions and/or culture was also established in other species, such as meerkats

(Thornton & Malapert 2009), orang-utans (*Pongo abelii*; van Schaik et al. 2003), rats (*Rattus rattus*; Terkel 1996) and cetaceans (Krutzen et al. 2005, Noad et al. 2000; Rendell & Whitehead 2001).

In those cases, alternative explanations ascribed to genetic or environmental influences have been rejected, because variation was found even between groups that live in close vicinity. Thus, the existence of traditions or even culture (repeated transmission of behavioural traits through social learning) in chimpanzees was concluded. An extensive study at 14 different sites in Africa detected across-site variation in army-ant-eating by chimpanzees (Schöning et al. 2008). By looking into various possible environmental influences, researchers found interactions between ecology and culture, i.e. the presence of ecological determinants but also cultural variation. The availability of army ants and alternative animal prey could not explain the presence or absence of different ant-eating techniques. The similarities and differences in techniques and tool properties seemed to be only partly driven by characteristics of the ants. The authors therefore concluded that army-ant-eating by chimpanzees varied culturally.

However, the possibility of undetectable environmental influences on social learning and traditions remains. Although observations in the wild provide us with an insight into naturally occurring behaviours and the spread thereof, they do not allow for exploring phenomena under controlled conditions. Two types of compromises of letting behaviours emerge naturally under somewhat controlled conditions have been found: experiments in the wild and observations in captivity. As an example for the former, novel materials could be introduced to a free-living group of apes, thus creating a kind of 'outdoor lab' (Biro et al. 2003, Matsuzawa 1994). This was conducted with chimpanzees at a field site, who were introduced to an unfamiliar species of nuts for research into nut-cracking behaviour at Bossou, Guinea (Biro et al. 2003). The researchers found an age effect and an effect of demonstrator identity. Juveniles were more likely to explore the nuts, and individuals seemed to be selective at choosing whom to learn from, with subjects preferentially watching models of the same age or older.

On rare occasions, it has been possible to observe and document the emergence of novel behaviour in captivity. This was the case for handclasp grooming at the Yerkes National Primate Research Center, Atlanta (Bonnie & de Waal 2006, de Waal & Seres 1997), which was first documented in the high mountains of Tanzania (McGrew & Tutin 1978). Nevertheless, to this day only experiments in captivity allow experimenters to include control conditions, e.g. to test a group of naïve subjects that were not allowed to observe a demonstrator performing a certain behaviour before being tested on that behaviour. The study conducted by Whiten and colleagues (2005) with chimpanzees is a well-known captive study that combined a two-action task (Dawson & Foss 1965) with a group setting to create a powerful set up for testing social learning and cultural processes. Two demonstrators were trained to use one of two alternative tool use techniques and were then reintroduced to their group, where they opened a test apparatus by either ‘poking’ or ‘lifting’ in the presence of their conspecifics. A control group was exposed to the apparatus without a model present. Whereas individuals in the control group failed to solve the task, the novel behaviours seeded by the two demonstrators spread differentially in the two experimental groups. In a follow-up study, it was found that ‘ghost conditions’, in which the apparatus was operated automatically rather than by a chimpanzee demonstrator, were not sufficient for learning to occur in the chimpanzee observers (Hopper et al. 2007). It therefore seems that the social stimulus of a conspecific opening the apparatus was vital and that the studies are indeed evidence for traditions in chimpanzees.

Very few studies have shown evidence for social learning in natural corvid groups. In a field study, white-throated magpie-jays (*Calocitta formosa*), were found to acquire a novel foraging skill via social learning (Langen 1996).

Following up from *Chapter 3*, I conducted further experiments on social learning in jackdaws, using a two-action task. Here, the novelty lies in the way the task was presented. Using a similar procedure to the chimpanzee studies (Hopper et al. 2007, Whiten et al. 2005), jackdaws were introduced to the apparatus in a naturalistic group context. Both observation and test sessions were conducted in the group. Two groups were tested consecutively with the same jackdaw as a demonstrator. The demonstrator was trained to open an apparatus by 'lifting' and then later re-trained to open it by 'pushing', before he was introduced to the second group.

Studying social learning in a group context has important implications from the perspective of the factors influencing the spread of novel skills and the establishment of traditions and should provide researchers with additional insight into the social learning abilities of jackdaws.

4.3 Methods

4.3.1 Subjects and housing

Three groups of jackdaws participated in this experiment, 2 of which were used as observer groups (Group 1 = Lift Group [n = 8 juveniles] & Group 2 = Push Group [n = 10 adults]), 1 as a Control Group (n = 10; Table 1). For reasons of feasibility, the age groups could not be mixed to create two observer groups that contained both adult and juvenile birds. The demonstrator (Dohli) was a female bird that hatched in 2006 and was housed together with the Control Group (not during the experiment). All birds apart from !Khosa and Poldi had been hand-raised.

Table 19. Details for (a) the Lift Group (juveniles), (b) the Push Group (adults) and (c) the Control Group.

(a) Group 1

ID	Name	Sex	Hatched
Ap	Apache	f	2008
Ba	Balu	m	2008
Ch	Cheyenne	m	2008
He	Heinrich	f	2008
Ka	Kaja	f	2008
My	Maya	f	2008
Mp	Mapuche	m	2008
Si	Sioux	f	2008

(b) Group 2

ID	Name	Sex	Hatched
Ce	Cheeky	f	2003
Co	Choucas	m	2003
Ja	Jackomo	f	2003
Kk	Krakehl	f	2003
Kw	Krawall	m	2003
Mn	Mono	f	2003
Mk	Mokka	m	2003
Rd	Radja	m	2003
Rn	Rani	f	2003
Xe	Xenia	f	2003

(c) Control Group

ID	Name	Sex	Hatched
Cs	Csoka	f	2004
Ja	Jacki	f	2007
Ka	Karacho	f	2003
Kh	!Khosa	m	2006
Po	Poldi	m	2007
Sp	Spinni	m	2005
Ts	Tschok	m	2004
Zu	Zulu	f	2003

For individual identification, the birds were banded with coloured leg rings. The 3 groups were housed in different parts of an outdoor aviary measuring 6 m x 5 m (Lift Group), 10m x 9 m (Push Group) and 15 m x 9m (Control Group) in Starnberg, Germany. The three parts of the aviary could be visibly separated by drawing opaque curtains between them. The aviary was equipped with nest boxes, branches, bushes, perches, poles, rocks and toys. Food was provided ad libitum after experimental sessions (cereals, cooked rice, curd, dried insects, dry cat food, eggs, various types of fruit, mealworms, *Tenebrio molitor*, and minced beef heart) and water to drink and to bathe in was available at all times. During the experimental phase, mealworms were removed from the diet to ensure motivation during test trials. Morio worms, *Zophobas morio*, were used as a reward in the experimental trials.

4.3.2 Apparatus and experimental set up

I conducted all experimental sessions in the outdoor aviaries and the demonstrator training indoors. Each group was worked with in the part of the aviary they were housed in. They were tested in test compartments in their respective parts of the aviary. All birds had been worked with almost every day prior to the experiment and were therefore well habituated to the presence of experimenters in their aviaries. For observation sessions, the demonstrator was released into a cage (96 cm x 50 cm x 65 cm) containing the test apparatus (Fig. 32a) at a spot clearly visible to the whole group (the demonstrator could access the cage through a door measuring 20 cm x 30 cm). During observation sessions, two experimenters were present: experimenter 1 (IG Federspiel) sat approx. 2 m from the cage, operating the video camera (Canon Digital Camcorder, Model MD101 Pal), a Dictaphone and the remote control with which the apparatus could be opened and closed (see below); experimenter 2 (AMP v Bayern) sat next to the demonstrator bird to ensure motivation (but did not provide any cues). For test sessions, the test apparatus was placed at the same spot in the aviary, but without the cage, and only experimenter 1 was present.

The test apparatus consisted of a wooden box (18 cm wide, 16 cm deep and 33 cm high; Fig. 32) with a treadle (5.5 cm x 11 cm x 1.5 cm) mounted horizontally on the front of the apparatus (5cm from the floor and 3 cm from the left side).

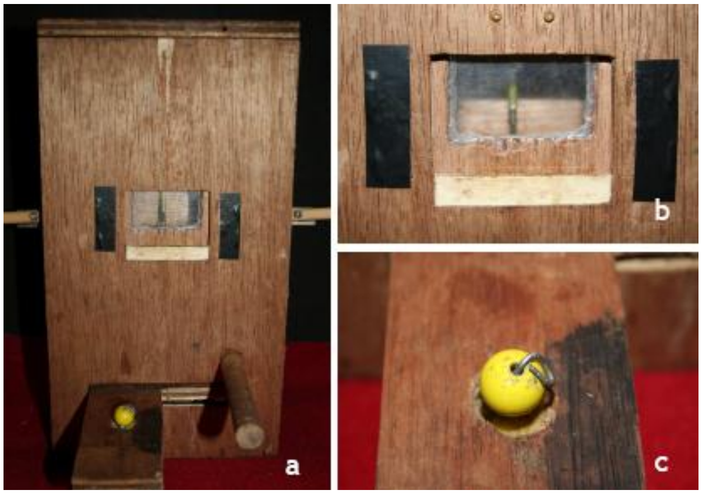


Figure 32. The test apparatus (a) and detailed pictures of the feeder opening (b) and the yellow wooden ball (c).

A yellow wooden ball (1 cm^3) with a wire stuck through the centre was attached to the centre of the treadle (6.5 cm from the edge, Fig. 32c). The ball could be pulled up 2.5 cm, or pushed halfway into the treadle (Fig. 33).

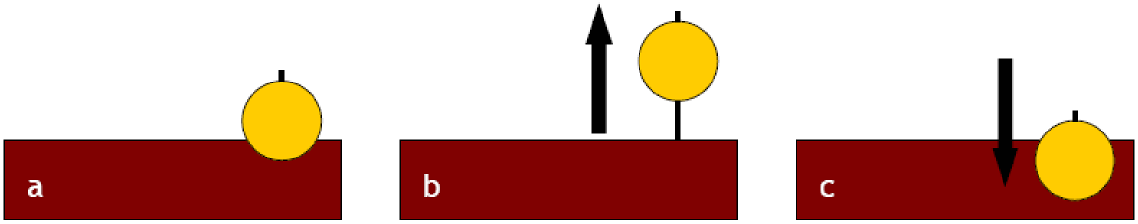


Figure 33. The actions that could be performed at the yellow ball (a) of the test apparatus: lifting (b) or pushing (c).

Next to the treadle, at the same height and 4 cm from the right side of the apparatus, a perch (11.5 cm long, 1.5 cm thick) was attached to the apparatus, enabling the birds to sit while operating the ball (and potentially feeding afterwards). A feeder opening (6 cm x 4.5 cm x 4 cm, Fig. 32b) was cut out of the centre of the apparatus, at the jackdaws' eye-level. The opening to the apparatus was baited with Morio worms in view of the subjects and could be opened and closed by a wooden sliding door with a Plexiglas window, operated by a remote control ('Digital Proportional Radio Control System Zebra 2 AM'), which controlled a motor connected to the sliding door on the inside of the apparatus. Immediately after the trained response (either lifting in the Lift Group or pushing in the Push Group; Fig. 33), experimenter 1 opened the sliding door, and the jackdaws could then feed from the opening. This was performed in the demonstrator training trials and the observation trials (only the trained action was performed by the demonstrator in the observation trials) or after either one of the two possible actions (lifting or pushing) in observer and non-observer testing trials.

For the habituation phase, I used two apparatuses that were slightly different to the test apparatus, both of them lacking the treadle with the yellow wooden ball: a functional and a non-functional habituation apparatus (Fig. 34).

Figure 34. The functional (a) and non-functional apparatus (b) for the habituation phase.

The birds could feed freely from the functional habituation apparatus. The window of the non-functional habituation apparatus was blocked and the jackdaws could therefore not feed from this apparatus. Only one of the two apparatuses was presented at a time. To make it possible for the birds to distinguish between the two, I stuck black tape next to the feeder opening of the non-functional apparatus. During the test phase, the black tape was also stuck onto the test apparatus. The reason for this was to habituate the birds to two different conditions of the apparatus so they could learn that they could not get worms from the non-functional apparatus. The birds stopped approaching the non-functional apparatus after a few trials and only sat on the perch of the functional apparatus to feed from the opening.

The next step after they had learned that they could not gain worms from the non-functional habituation apparatus was to introduce them to the test apparatus in the actual testing sessions. They should now have learned that they would not be able to feed freely from the apparatus. The additional parts at the apparatus (treadle and ball) provided them with an alternative around the problem of not being able to access the apparatus. Although the test apparatus also had black tape stuck on it, the birds appeared to notice the treadle and the wooden ball. Having observed the demonstrations, the subjects could learn that the seemingly non-functional apparatus was not exactly 'non-functional' when the tape, but also the treadle with the ball were attached to the apparatus. The logic behind this is that they should then attempt try to avoid the potential blockage of the apparatus by utilising the yellow ball to open the apparatus.

4.3.3 Procedure

The study was conducted from November 2008 to January 2009. To avoid influences of demonstrator identity ('socially biased learning', Fragazy & Visalberghi 2004), the same bird (Dohli) acted as a demonstrator for both groups. The study was divided into a demonstrator training phase, a habituation phase for observers (Lift Group and Push Group) and non-observers (Control Group), an observation phase consisting of 30 min sessions for the two observer groups, and a test phase consisting of 30 min sessions for all groups. The demonstrator was first trained to lift up the yellow ball and then demonstrated the action to the Lift Group in observation sessions. Subsequently, the Lift Group was tested (without the demonstrator present) and the demonstrator was re-trained to push the ball. The Push Group was then provided with observation sessions and test sessions. Therefore, each group observed a different demonstrated action. Finally, the Control Group was tested without observation sessions.

4.3.3.1 Demonstrator training phase

For training sessions, the demonstrator was separated from the group and taken indoors. The demonstrator was habituated to the apparatus by placing a Morio's worm in the feeder opening with the sliding door open and letting the demonstrator eat it. The cage was introduced only when the demonstrator was comfortable with approaching the apparatus and was reliably opening the apparatus. The demonstrator could then enter and leave the cage through the cage door, and as a final step, the door was closed after putting the demonstrator into the cage. Training on the apparatus was conducted using a method of stepwise approximation, starting off with the wooden ball being held in a slightly raised position, but as soon as the bird started pulling the ball upwards, it was initially positioned at lower and lower levels over the course of training sessions. Experimenter 1 opened the door of the apparatus via the remote control every time the ball was pulled up, from the first correct response onwards. Experimenter 2 was present at all times to ensure motivation. Training was complete when the demonstrator responded consistently by pulling up the ball without any preceding explorative actions and immediately feeding from the apparatus opening.

Training the demonstrator on the other opening technique was conducted in a similar manner, shaping the exploratory pecking behaviour into a forceful vertical stabbing movement at the centre of the ball that pushed the ball into the treadle (which was determined by observing a thin line that was drawn on the ball). The two opening techniques were defined by the outcome, i.e. the final position the ball reached after having been manipulated by the demonstrator. Technique 1, which was shown to the Lift Group, was lifting up the ball. It was counted as complete when the ball had been lifted up at least 2 cm (approx. twice the length of the ball itself). Technique 2 was pushing the ball into the treadle. It was counted as complete when at least a third of the ball had been pushed into the treadle (force was needed to achieve this, and the normal exploratory pecking behaviour was not sufficient). It took the demonstrator 12 sessions of approx. 20 minutes to learn the opening Technique 1 and apply it in a consistent and smooth manner and 6 sessions of approx. 20 minutes to learn Technique 2.

4.3.3.2 Habituation phase: observers and non-observers

Prior to the observation trials, all three groups were habituated to the following, in order to rule out neophobia as an explanation for differences in the behaviour between observers and non-observers: the yellow wooden ball (detached from the apparatus), the video camera and tripod, the remote control, the cage and a non-functional version of the apparatus (without the door or the treadle; Fig. 34) that had been baited. Those objects were placed into each of the three parts of the aviary in a randomised order and left until the birds ceased to show neophobic reactions towards them, had all touched the wooden ball and fed from the non-functional apparatus. To control for a possible influence of neophobia towards the test apparatus, the non-observers were also habituated to the test apparatus. Whereas the observer groups were able to observe demonstrations, the non-observers were only able to look at the test apparatus, without a demonstrator bird interaction with it, and without the opportunity for manipulating it. For that purpose, the apparatus was placed into the non-observers' aviary and the demonstrator cage that was used with the other birds in the observation phase was put over it. This was repeated for a few days to ensure approximately the same time span of habituation that the observer groups received in the observation phase.

4.3.3.3 Observation phase: observers

Once habituated to the apparatus, the observers were given approximately 20 blocks of 1-10 demonstrations per day, depending on the demonstrator's motivation. Demonstrations were continued until each individual had observed at least 30 openings and consecutive feeding events. A demonstration was only counted as 'observed', if the head of the given jackdaw was oriented in a way that suggested paying attention (towards the demonstrator). Prior to the observation trials, the cage and the apparatus were positioned in the aviary, and the test group was visually isolated from the other groups by drawing the dark curtains. At the beginning of the observation trials, the group and the demonstrator were shown a Morio worm, which was then placed into the feeder opening of the apparatus, the door of the apparatus was closed and the demonstrator was released into the demonstrator cage. Recording started as soon as the cage door was closed. The observers could either watch the demonstrations from 'near' (on top of the cage or on the ground, within 2 body lengths from the cage) or 'far' (on one of the wooden perches above the cage, at a distance of approx. 2.70 m in the Lift Group and at 2.50 m in the Push Group), as defined by the location.

4.3.3.4 Test phase: observers and non-observers

After the observer birds had each observed at least 30 demonstrations, they were tested during 30 min sessions using the same set up as the observation phase, but with the freely accessible test apparatus. The non-observers were tested without having seen any demonstrations. Experimenter 1 baited the apparatus in sight of the birds and they were then able to approach the apparatus (Experimenter 2 was not present). The experimenter operated the sliding door of the apparatus when a bird had acted upon the yellow ball appropriately, and the experimenter re-baited the apparatus straight after a bird had swallowed the worm. If the birds did not approach the apparatus for 5 min, the experimenter re-baited the apparatus in sight of the birds. All trials were videotaped for later analysis. If a bird had performed at least 40 openings (depending on which number was reached by the end of the session in which the given bird had performed its 40th opening), it was excluded from any further sessions. This was done to avoid monopolisation of the apparatus by a single or a few dominant birds and to allow equal opportunities for all test subjects.

4.3.3.5 Establishment of dominance hierarchy

I conducted daily 20 min observation sessions during which I coded the frequency and direction of displacements (an animal retreats after having been approached by another) between group members as a measure of dominance. This was only possible for the group of juveniles (Lift Group), as the adult birds of the Push Group interacted less frequently; thus not enough data for a calculating a dominance hierarchy could be taken. Data for the Lift Group were then arranged in matrices and a dominance hierarchy was established. Based on random permutations (10,000) of the displacement matrices, I calculated Landau's linearity index (h) using MatMan 1.0 (Noldus Technologies, Wageningen, The Netherlands).

A measure of 1 indicates a linear dominance hierarchy; a measure of 0 indicates a non-linear hierarchy (see e.g. Appleby 1983, Hemelrijk 1990, de Vries 1993). The directional consistency index (*dci*) showed the consistency of the hierarchy (1 = consistent, 0 = not consistent) (for a more detailed description of MatMan 1.0 see *Chapter* 2).

4.3.3.6 Data analysis

The test sessions were scored using two methods, by defining 'states; (times spans) and events (one-off behaviour). I included two sets of mutually exclusive states: set 1 for the presence (within 2 body lengths of the apparatus) or absence of a bird; set 2 for defining where exactly the bird was in relation to the apparatus, in case the bird was present (sitting on top of the apparatus, sitting on the perch, sitting on the treadle, not sitting on the apparatus). Events were as follows: looking at the apparatus (orienting the head in a way that suggested a close look at the apparatus), manipulating any part of the apparatus apart from the wooden ball (with beak or feet), lifting the wooden ball (not high enough to open the apparatus), pushing the wooden ball (lacking sufficient force to open the apparatus), manipulating the ball (in any other way, e.g. pecking it from the side), opening the apparatus, either by lifting the ball or by pushing it into the treadle, watching a conspecific opening the apparatus, feeding from the apparatus (after opening or after somebody else had opened).

Videotapes of the experimental sessions were coded using the behavioural analysis program The Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands) and data were analysed with STATISTICA 7 (StatSoft Inc., 1984-2004). In the observation phase, I noted which birds observed any given demonstration and whether they observed it from 'near' or 'far'. In the test phase, I scored time spans the birds spent present at the apparatus (and at which part), latencies to first approach the apparatus and first touch and/or first open the apparatus and events of closely looking at the apparatus (defined by an animal orienting its head in a certain way, namely tilting it slightly to the side or lowering it), manipulating the yellow ball or other parts of the apparatus (i.e. touching these parts with the beak or the feet), lifting or pushing the ball, but not high or hard enough to open the apparatus, opening the apparatus, either by lifting the yellow ball or pushing it into the treadle, watching a bird perform an opening, and taking the worm.

I used non-parametric statistics to analyse the data on the basis of tests for normality. All tests were two-tailed, and alpha was set at 0.05. Trends were reported for $0.10 > \alpha > 0.05$. For technical reasons (damaged video tapes due to cold weather), I were unable to retrieve data on durations and latencies of time spent at the apparatus and sitting on parts of the apparatus, manipulations and looks for sessions 8 and 10 of the Lift Group (juveniles) and session 20 of the Push Group (adults). Data on openings, individuals observing the openings and worms gained were available (dictaphone). To control for the missing data I therefore excluded data from the respective other groups from the analysis accordingly, e.g. when comparing the time the animals of The Lift Group and 2 spent at the apparatus, I excluded data for sessions 8 and 10 of the Push Group and data for session 20 of the Lift Group. I compared the overall time and the median durations the individuals of the two observer groups and the Control Group spent at the apparatus and their latency measures, as well as events of looking at, manipulating and opening (where applicable) the apparatus with Mann-Whitney U tests. Adjusted p-values were given for tests including data with two or more ties, i.e. equal values in both groups (Siegel 1956). For comparing the number of actions the animals performed at the apparatus, I analysed both the difference in total numbers and frequencies (total number per time spent within 2 body lengths of the apparatus) with Mann-Whitney U tests. I examined the influence of the dominance hierarchy on the behaviour of our subjects at the apparatus by performing Spearman rank correlations of the ranks (1 to 8, with Mp being the highest-ranking bird and hence number 1) with total and median measures of durations and latencies and total number of actions. Since I excluded animals from session 9 onwards and was unable to use data for session 8, I only included data for sessions 1 through to 7. Furthermore, I examined whether the observers used the same opening technique as the demonstrator.

I predicted that longer durations spent at the apparatus by the observers compared to the non-observers would indicate a social learning effect, and matching of the techniques of the demonstrator and the observers would point towards imitation as an underlying social learning mechanism, whereas a mixture of techniques in both the observer groups would suggest stimulus enhancement. Similar responses in the two observer groups would indicate the natural occurrence of the observed behaviour (i.e. opening technique), even without the birds having seen the behaviour just before performing it. Differences in the latency to approach the apparatus between observers and non-observers, with observers being quicker, might indicate the presence of neophobia in the non-observers.

I analysed possible influences of the number of observed openings performed by others, the number of own manipulations performed and the number of worms that were gained before performing the first opening oneself by correlating both of the former measures with the number of sessions and the number of trials (number of openings performed by the birds during a 30 min session) an individual participated in before performing the first opening. To look at the influence of possible transmission processes within the Lift Group, I calculated how many individuals opened the apparatus for their first time, i.e. how many 'new' demonstrators became available, in each session and correlated that data with the total number of openings per session.

4.4 Results

4.4.1 Dominance hierarchy of the Lift Group

Analysis of a total of 154 displacements revealed a stable, linear dominance hierarchy in the Lift Group ($h = 0.964$, $dci = 0.935$, $P < 0.001$). With Mp being the highest in dominance rank, the order was as follows: Mp > Ba > Ch > Ka > He > My > Si > Ap.

4.4.2 Experiment

4.4.2.1 Time spent at the apparatus

Groups differed in the time they spent at the apparatus (Kruskal-Wallis ANOVA: N = 26, H = 21.605, P < 0.001). Both groups spent more time at the apparatus than the Control Group (Mann-Whitney U tests: Lift Group: N_1 = 8; N_2 = 8; Z = 3.361, P = 0.001; Push Group: N_1 = 10; N_2 = 8; Z = 3.554, P < 0.001). Of the Control group, only one individual ever got within 2 body lengths of the apparatus: Zulu stayed close to the apparatus in session 20 for 6.3 s.

Individuals of the Lift Group spent more time at the apparatus than members of the Push Group (Mann-Whitney U test: N_1 = 8; N_2 = 10; Z = 3.199, P = 0.001; Fig. 35).

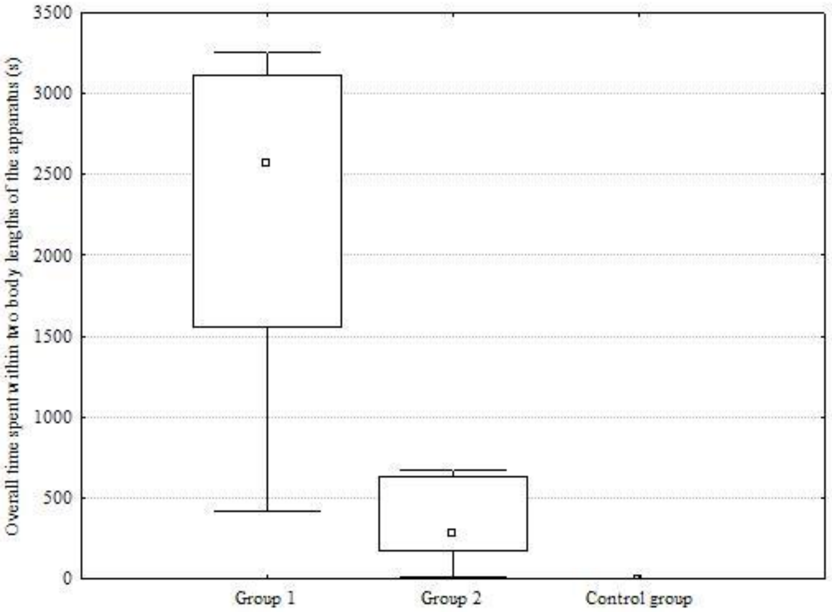
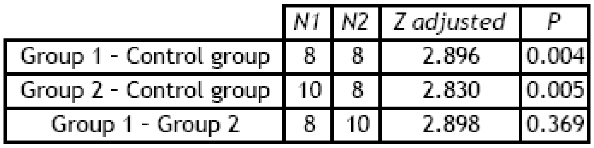


Figure 35. Box and whisker plots for the total time spent at the apparatus by members of all 3 groups. Boxes show the interquartile range; the square in the centre of the boxes stands for the median value. Whiskers indicate the largest and smallest value.

A similar result was found when looking at the median times the subjects spent at the apparatus: the groups differed (Kruskal-Wallis ANOVA: $N = 26$, $H = 17.993$, $P < 0.001$); post-hoc analysis revealed that the Lift Group spent more median time at the apparatus than the Push Group (Mann-Whitney U tests: Table 20).

Table 20. Results of Mann-Whitney U tests of the median times the animals spent at the apparatus.



	N1	N2	Z adjusted	P
Group 1 - Control group	8	8	2.896	0.004
Group 2 - Control group	10	8	2.830	0.005
Group 1 - Group 2	8	10	2.898	0.369

4.4.2.2 Time spent at relevant parts of the apparatus

Groups spent different amounts of time at the parts of the apparatus from which an opening could be performed (Kruskal-Wallis ANOVA: $N = 26$, $H = 15.600$, $P = 0.014$). The Lift Group spent more time on any part of the apparatus than the Control Group (Mann-Whitney U tests: overall time: $N_1 = 8$, $N_2 = 8$, $Z_{adjusted} = 3.590$, $P < 0.001$), but also more than the Push Group (Mann-Whitney U tests: overall time: $N_1 = 8$, $N_2 = 10$, $Z = 3.110$, $P = 0.002$).

As the individuals of the Control Group were almost never present and never touched or looked at the apparatus, I excluded their data from latency analyses.

4.4.2.3 Latency to approach and touch the apparatus

The Lift Group was faster at getting within 2 body lengths of the apparatus than the Push Group (Mann-Whitney U tests: $N_1 = 8$, $N_2 = 10$, $Z = -2.843$, $P = 0.004$; Fig. 36).

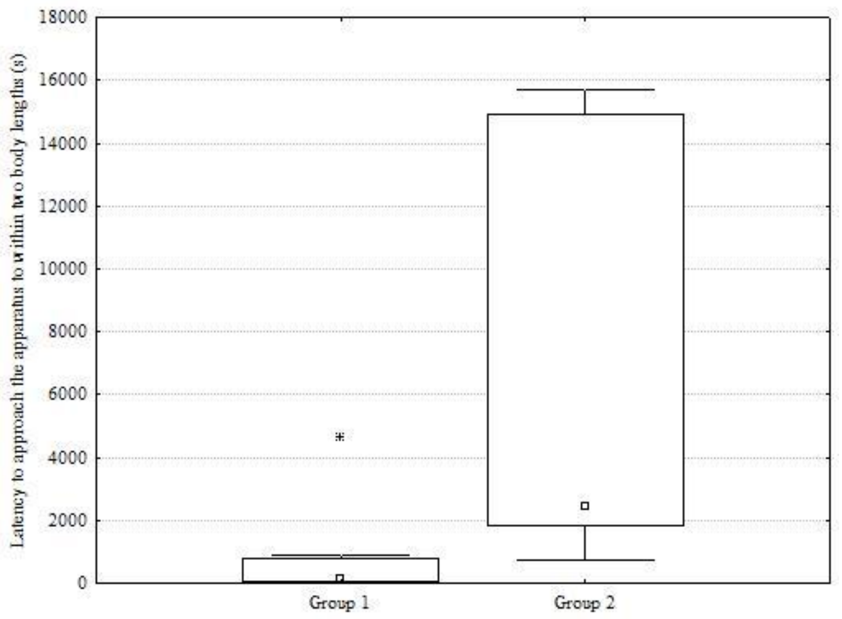


Figure 36. Box and whisker plots for the latency to approach the apparatus in the Lift Group and the Push Group (the Control Group is not included, as only one individual of that group ever approached the apparatus).

The same pattern was found for first touching the apparatus (Fig. 37), either by manipulating it, opening it or sitting on it, and looking at the apparatus closely (Mann-Whitney U tests, Table 21).

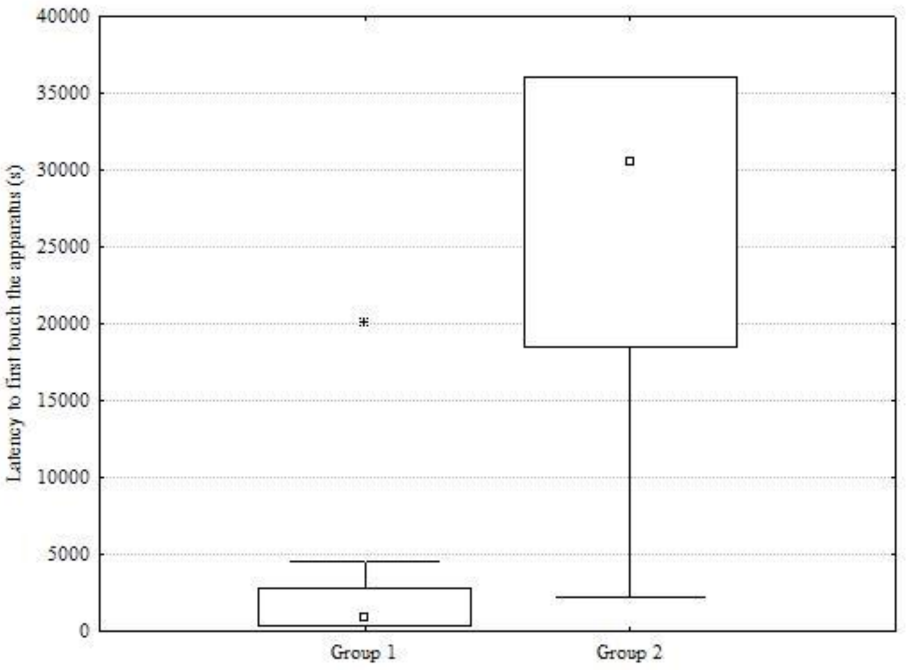


Figure 37. Box and whisker plots for the latency to touch the apparatus in the Lift Group and the Push Group.

Table 21. Results of Mann-Whitney U tests for the latency to touch and first look at the apparatus in the Lift Group and the Push Group.

First touch	*N1*	*N2*	*Z*	*Z adjusted*	*P*
Group 1 - Control group	8	8	-3.361		0.001
Group 2 - Control group	10	8		-2.249	0.025
Group 1 - Group 2	8	10	-3.199		0.001

First look	*N1*	*N2*	*Z*	*Z adjusted*	*P*
Group 1 - Control group	8	8	-3.361		0.001
Group 2 - Control group	10	8	-3.199		0.001
Group 1 - Group 2	8	10	-2.754		0.006

Subjects of the Lift Group sat on the perch or the treadle sooner than subjects of the Push Group (Mann-Whitney U tests: $N_1 = 8$, $N_2 = 10$, $Z = -3.288$, $P = 0.001$).

4.4.2.4 *Total number of actions at the apparatus: looks, manipulations and openings*

Because the Control Group did not perform any looks, manipulations or openings, their data were excluded from this part of the analysis. The Lift Group looked at and manipulated the apparatus more than the Push Group (Mann-Whitney U tests, $N_1 = 8$, $N_2 = 10$: looks: $Z = 3.288$, $P = 0.001$; manipulations of apparatus: $Z = 3.288$, $P = 0.001$), and also manipulated the yellow wooden ball more often ($Z = 3.110$, $P = 0.002$).

When I took into account the amount of time the animals were present and looked at the frequencies of performed actions, I found that the above results held for manipulations at the apparatus and the wooden ball, with the Lift Group performing more of both (Mann-Whitney U tests, $N_1 = 8$, $N_2 = 10$: apparatus: $Z = 2.044$, $P = 0.041$; ball: $Z = 3.110$, $P = 0.002$). Members of the Push Group never performed any attempted openings by lifting or pushing and never achieved any actual openings. Overall, the Lift Group performed 256 openings (range per bird = 0-67, median = 32.00, 95% confidence intervals = -17.80/+72.17; Table 22), only one of which was a push opening.

The first opening was a lift opening that was performed by the highest-ranking bird Mp in the first test session, after 12 minutes and 31 seconds, 12 performed manipulations at the apparatus and 1 ball manipulation. The only peck opening was performed by the mid-ranking He during the 13th session, after having been present for a total of 381 minutes and 40 seconds. Before the opening, he had performed 26 manipulations of the apparatus and 59 at the ball and observed 22 openings, all of which had been lift openings by 5 different birds.

Apart from Mp and He, 4 other birds performed openings. They first opened the apparatus in their 1st (Ka), 2nd (My), 3rd (Ch) and 7th (Ba) session (see Table 22). When individuals had performed 40 openings, I excluded them at the end of the session during which they had reached this number in order not to interrupt the ongoing session and to give other individuals the opportunity to also approach the apparatus thereafter (for details on the exclusion of animals see Table 22).

Table 22. Descriptive statistics for manipulations, openings and the exclusion of individuals of the Lift Group.

	N	Sum	Mean	Min	Max	Std. Dev.
Total number of openings per individual	8	256	32	0	67	27.09
No sessions (trials) before session with first opening	6	21 (304)	3.5 (50.67)	0 (0)	12 (217)	4.72 (86.46)
No apparatus manipulations performed before first opening	6	195	32.5	9	86	27.93
No ball manipulations performed before first opening	6	111	18.5	0	59	23.66
No openings observed before performing first opening	6	67	11.17	0	42	17.37
No worms gained before first opening	6	13	2.17	0	6	2.99
No openings performed before exclusion	4	208	52	46	67	10.03
Session before which excluded	4	-	10.25	8	12	2.06

The number of observed openings performed by others and the number of times the individuals manipulated the apparatus did not appear to have an influence on when the first opening was performed (Spearman rank correlations: Number of sessions before session with own first opening & number of openings observed before performing first own opening: $R = 0.770$, $N = 6$, $P = 0.073$; Number of sessions before session with own first opening & number of apparatus manipulations before performing first own opening: $R = 0.637$, $N = 6$, $P = 0.173$).

4.4.2.5 Influence of dominance hierarchy on actions

The longer the animals spent within 2 body lengths of the apparatus, the more time they spent on the treadle or the perch (Spearman rank correlations, N = 8: $R = 0.7881$, $P = 0.004$) and the more they manipulated the apparatus ($R = 0.810$, $P = 0.015$) and the ball ($R = 0.605$, $P = 0.002$). The birds that were present at the apparatus most frequently were typically higher-ranking animals, occupying the treadle and the perch at the apparatus (Spearman rank correlation: $R = -0.786$, N = 8, $P = 0.021$, Fig. 38).

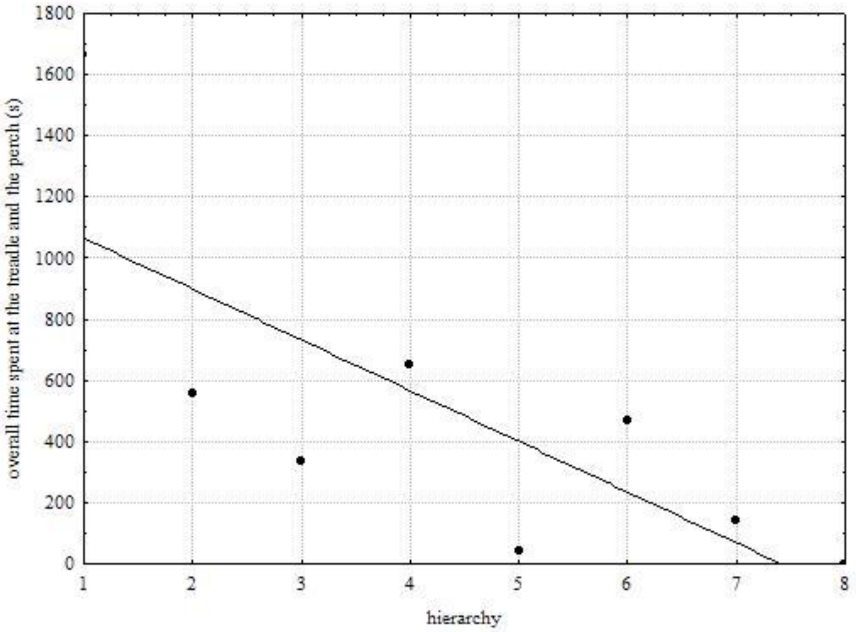


Figure 38. Scatter plot for the time the animals spent at the perch and treadle depending on the hierarchy (1 = highest-ranking animal).

Furthermore, higher-ranking animals manipulated the apparatus and the ball more frequently (Spearman rank correlations, *N* = 8: total numbers: apparatus: *R* = -0.857, *P* = 0.007; ball: *R* = -0.738, *P* = 0.037; but see also frequencies of manipulating the ball: *R* = -0.905, *P* = 0.002, Fig. 39) and watched more openings performed by others (*R* = -0.714, *P* = 0.047).

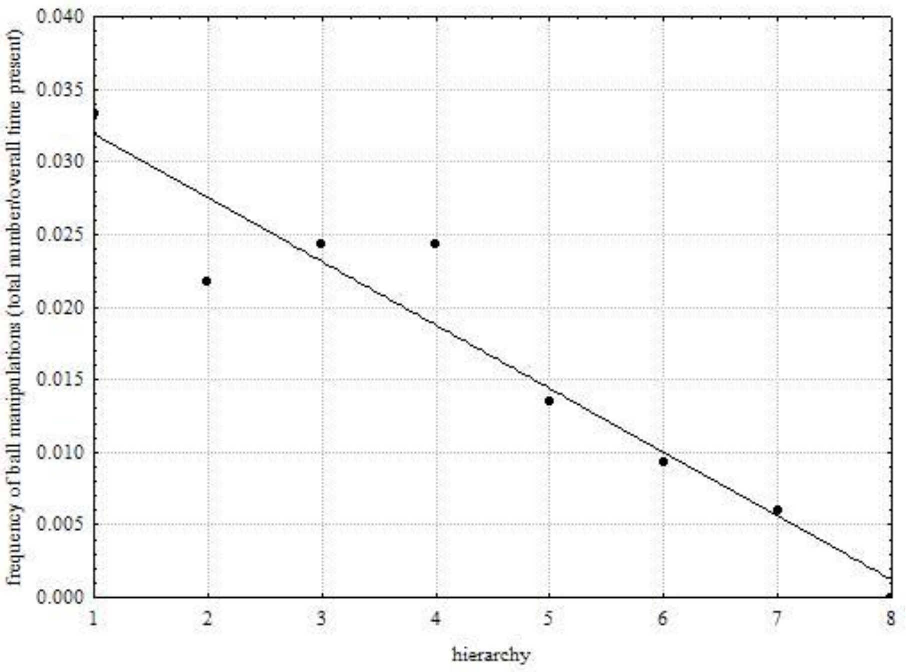


Figure 39. Scatter plot for the frequency of ball manipulations and the dominance ranks.

4.4.2.6 Individual learning vs social transmission

By examining how many individuals had opened the apparatus at least once prior to each session and would therefore become available as additional demonstrators, I found a relatively steady increase across sessions (Spearman rank correlation: session number & number of knowledgeable individuals per session: $R = 0.950$, $N = 20$, $P < 0.001$; Fig. 40).

The rate with which additional individuals acquired the novel opening technique was negatively correlated with the session number (session number & increase in number of knowledgeable individuals per session: $R = -0.548$, $N = 20$, $P = 0.012$). The same result was found when I correlated the trial number instead of the session number with the number of knowledgeable individuals ($R = 0.900$, $N = 258$, $P < 0.001$) or the increase of number of knowledgeable individuals ($R = -0.161$, $N = 258$, $P = 0.010$).

In session 13, the last additional individual adopted the new opening technique. The number of openings performed before the end of session 13 did not correlate with the increase of knowledgeable individuals per session (*R* = -0.371, *N* = 13, *P* = 0.212).

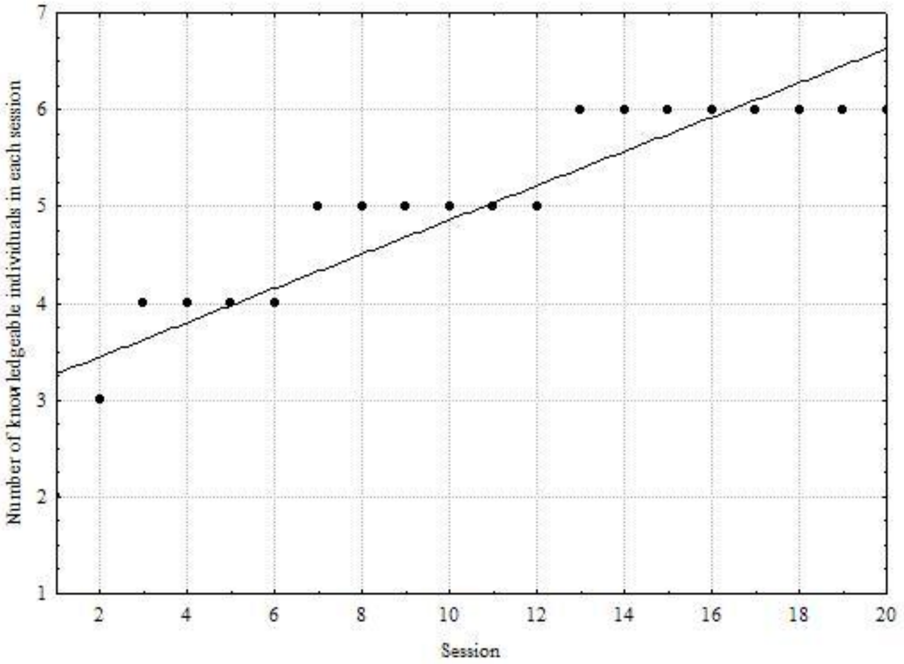
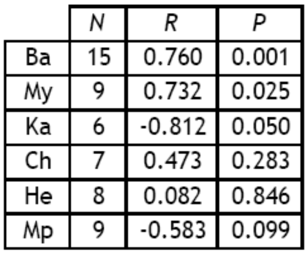


Figure 40. The number of knowledgeable individuals that were available as additional, new 'demonstrators' per session.

In terms of performance over time, I observed inconsistent results: Two of the birds (Ba, My) improved their performance across time (Spearman rank correlations: fraction of successful manipulations, i.e. those leading to an opening, of the wooden ball & no of sessions participated in), one worsened (Ka), for 3 I found no effect (Ch, He, Mp), and 2 never opened the apparatus (Ap, Si) (Table 23).

Table 23. Results of Spearman rank correlations of the fraction of successful manipulations of the wooden ball and the number of sessions the individual had participated in.



	N	*R*	*P*
Ba	15	0.760	0.001
My	9	0.732	0.025
Ka	6	-0.812	0.050
Ch	7	0.473	0.283
He	8	0.082	0.846
Mp	9	-0.583	0.099

4.5 Discussion

4.5.1 Time spent at the apparatus

I found that both observer groups spent longer at the test apparatus than the non-observers. Individuals of the Lift Group also spent more total time at the apparatus than members of the Push Group. The non-observers hardly ever approached the apparatus. This indicates a social learning effect, as the only difference between observers and non-observers was the social stimulus, i.e. the demonstrator opening and feeding from the apparatus. All groups had been habituated to a non-functional version of the apparatus before the test sessions, which I predicted would lead to the non-observers approaching the apparatus as well and potentially trying to gain some reward from the food opening.

Surprisingly, they did not do so. Three different factors might have influenced the non-observers' behaviour: First, the lack of a social stimulus at the apparatus may have led to them being reluctant to approaching it. In addition to acquiring social information, the observers may have learned that because a conspecific was interacting with the apparatus, it was safe to do so. Without that information, the non-observers may have been more cautious and so avoided the apparatus. However, the fact that all the non-observers had previously eaten out of the food opening of the non-functional apparatus seems to render that explanation unlikely. Second, the test apparatus differed from the habituation apparatus and may have therefore elicited a neophobic response. Instead of categorising the functional test apparatus as ‘the non-functional apparatus with an attachment’ (the wooden treadle with the ball), the jackdaws may have perceived it as a whole new object and therefore reacted to it with fear. Also, without ever moving close to the apparatus and looking through the window properly, the birds may not have learned that there was food inside. In my opinion, this is unlikely, as the subjects seemed to be capable of transferring between similar apparatuses and usually did not display strong neophobia to small changes in their environment (von Bayern, personal communication).

Finally, the season may have had an influence on their behaviour. The experiment was conducted shortly before the onset of the breeding season, and it is possible that the birds were experiencing hormonal changes that resulted in a motivational shift (although this would have most likely affected all the birds). However, food seems to be the jackdaws’ main concern in their daily lives; even more so during the breeding season. Furthermore, the birds were not collecting sticks yet at the time, a behaviour that usually denotes the beginning of the breeding season, so it is unlikely that this could have indeed affected the birds’ behaviour. To look into the observed phenomenon, I would suggest testing an additional jackdaw group as a control to determine whether the experiment itself or environmental factors influenced the behaviour of the Control Group.

4.5.2 Latency to approach the apparatus, looks, manipulations & openings

Whereas both observer groups readily approached the apparatus from trial 1, only one group, the Lift Group, opened the apparatus. This was also the group that was faster at approaching and touching the apparatus from the first presentation, closely looked at the apparatus more frequently and performed more manipulations of the apparatus. This difference between the two observer groups is most likely due to the age difference between the groups. The Lift Group consisted of individuals that were almost 5 years younger than the individuals of the Push Group and in their first summer of life. Jackdaws, as most corvids, typically go through an exploratory phase as fledglings before experiencing a switch to becoming neophobic during their first summer of life (Katzir 1981). Although both groups approached the apparatus, it seems that individuals of the Lift Group were more explorative, which indicates that lower neophobia levels had an effect.

Individuals of the Lift Group started to lift the ball over the course of the test sessions. Due to the lack of a baseline (manipulations by the non-observers), it is difficult to say whether lifting the ball was simply the more natural behaviour of the two (lifting and pushing) or whether observers imitated the opening technique they had observed.

One of the three explanations for the observed opening behaviour in the Lift Group points towards individual trial-and-error learning following an initial effect of stimulus enhancement by the demonstrator as an underlying mechanism. A similar sequence of events has led to the milk bottle opening of three different titmice species in the United Kingdom (Fisher & Hinde 1949, Fisher & Hinde 1951; see *Chapter 1*). The phenomenon is thought to have started with one or a few tits opening the metal caps of milk bottles to get to the cream on top of the milk, and others watching that behaviour. The attention of the observers was drawn to the metal caps of other, similar looking milk bottles, resulting in the birds' landing and manipulating the caps. However, they did not copy the exact actions that they had observed to open the caps, but employed their own actions. The authors concluded that trial-and-error learning proceeded by stimulus enhancement led to the subsequent spread of the behaviour throughout Great Britain.

Another explanation for what I found in this experiment is underlying social influence of the demonstrator on the observers. Those mechanisms could involve social facilitation (the observer's behaviour is influenced by the mere presence of a conspecific that has an influence on the observer's motivation, Zajonc 1965), contagious behaviour (unlearned, species-specific behaviour is 'released' upon the sight of others engaged in that behaviour, Thorpe 1963), or response facilitation, a term that was used to describe an alternative mechanism to imitation in two-action tasks (the presence of a conspecific performing an act, often resulting in reward, increases the probability of an animal which sees it doing the same, Byrne 1994). Considering the methods used in the current study, we believe mere social influence as the mechanism guiding the lifting behaviour should be ruled out, as the birds were never tested immediately after an observation session; thus, observation sessions and test sessions were separated in time and rendered facilitation effects unlikely. Although it is not known how long a facilitation effect can last and how long the interval between observation and tests sessions thus would need to be (Hoppit et al. 2007), I believe conducting test sessions on the next day after observation sessions would have introduced a salient delay.

The final possible explanation for the observed effect is more complex forms of social learning, such as imitation or emulation. At this stage, it seems difficult to disentangle the various different explanations for the observers' behaviour. However, taking into account other actions performed at the apparatus in addition to openings, I will discuss all the potential alternative mechanisms in the next section.

4.5.3 Social learning mechanism

Since the observers did not appear to know how to open the apparatus from the first trial, it is likely that they had only learned about the location of the food from the demonstrator (enhancement effect). As summarised in the previous section, three different forms of social learning could account for the observed effect: imitation, emulation or a localised form of enhancement, i.e. the conspecifics' actions at the yellow ball may have drawn the others' attention to that ball.

Whereas during observation sessions from a distance, the observers could have learned something about the apparatus, upon coming closer and arriving at the apparatus, and after watching conspecifics opening the apparatus by lifting up the ball, the birds could have learned something about a particular part of the apparatus, which may have led them to approach that part of the apparatus and then employ their own opening technique (although restricted to lifting or pushing).

Three other factors may have played a role during the acquisition of the novel opening technique: demonstrator identity, proximity to the conspecifics that opened the apparatus and the opportunity to scrounge. In some species, the demonstrator's identity and the relationship between demonstrators and observers has an effect on whether social learning is employed (age in house mice, *Mus domesticus*: Choleris et al. 1997, kinship in ringdoves, *Streptopelia risoria*: Hatch & Lefebvre 1997; social status and foraging success in laying hens, *Gallus gallus domesticus*: Nicol & Pope 1999, familiarity in guppies, *Poecilia reticulata*: Swaney et al. 2001; sex and feeding activity in zebra finches, *Taenopygia guttata*: Katz & Lachlan 2003; age in Norway rats, *Rattus norvegicus*: Galef & Whiskin 2004; affiliation in chimpanzees, *Pan troglodytes*: Bonnie & de Waal 2006). In jackdaws, a recent study showed that the birds preferred learning socially from non-affiliated individuals (Schwab et al. 2008). However, as the demonstrator was usually housed with the Control Group, but not during the experimental phase, I believe that 'uneven social dynamics' (i.e. socio-positive relationships between the demonstrator and the observers with varying intensity) did not play a role in the current study.

In most social learning experiments, and also in my initial observation phase, the observers are (were) tested for social learning during passive observation of a conspecific performing a certain action. In my subsequent test phase, the animals were able to approach the new 'demonstrators', i.e. the animals that had already acquired the novel behaviour, and stay in close proximity while those demonstrators were opening the apparatus by lifting up the wooden ball. This proximity and opportunity to interact with the new demonstrators at the apparatus may have had an influence on the type and amount of social information gained (Coussi-Korbel & Fragaszy 1995). I found that the high-ranking birds in the Lift Group spent more time at the apparatus than the low-ranking ones and monopolised the parts from which an opening could be performed: the treadle and the perch. They also manipulated the ball more than the lower-ranking individuals. Some of the close observers were able to scrounge (benefit from the conspecific's action and take the reward before the actor could) on some of the trials, which may have facilitated social learning (Caldwell & Whiten 2003, see *Chapter 1*).

Various social learning mechanisms could account for behaviour that is transmitted between individuals. In imitation, animals learn something about the action sequence that they observe and typically copy that action in a relatively exact way (for a review on social learning mechanisms see Whiten et al. 2004, Zentall 2004 or *Chapter 1*), although it has not yet been defined how exactly an animal has to copy an action for that copied action to qualify as an example of imitation. It appears that certain species are capable of copying actions to a very detailed level, for example, imitative behaviour in common marmosets, *Callithrix jacchus*, which was revealed using frame-to-frame analysis (Voelkl & Huber 2007).

Social learning tasks that use action sequences bypass that problem by adding an additional level to the behaviour that has to be copied: not only the actions, but also the order in which the actions are performed have to be copied in order to qualify the behaviour as imitation (e.g. Whiten 1998). With jackdaws, using a sequence task would have been very tricky, as they exhibit short attention levels (Scheid et al. 2007) and would have therefore most likely not observed the whole sequence performed by the demonstrator; I thus opted for a two-action task. A further distinction between 'true imitation', in which some sort of intention sharing between the demonstrators and the observers may be involved (found in great apes in the 'limited sense of copying for its own sake divorced from normal behaviour', Byrne & Tomasello 1995; for examples in common marmosets see Bugnyar & Huber 1997, Voelkl & Huber 2000), and 'mimicry' or 'blind imitation' (e.g. in pigeons, *Columba livia*: McGregor et al. 2006) makes pinpointing the mechanism even more difficult.

Nevertheless, for the current study, the level of intention or understanding involved in opening the apparatus only played a minor role. I expected that when imitating, the animals would apply the same technique as the animal they had observed from the first test trial on and subsequently use that technique (almost) exclusively (if successful). Judging from my data, this does not appear to be what the jackdaws did. Each individual performed a number of manipulations on the apparatus and the yellow ball before they first opened the apparatus and also continued to manipulate the apparatus and ball after having performed the first opening. Thus, not every manipulation led to a successful opening.

Furthermore, I looked at the rate of adopting the new behaviour, i.e. how many individuals were using the lifting technique for the first time in each session, as a potential measure of the underlying social learning mechanism. The number of individuals that utilised the new behaviour increased steadily until session 13. Two individuals never opened the apparatus. The rate of recruitment to the new behaviour slowed down over time. According to Galef (1992), this 'rate of recruitment to a behaviour' - in our case the number of additional new demonstrators of the lifting technique that became available per session - should be 'positively correlated with its frequency of occurrence', in our case, the number of openings performed in total per session, 'until saturation occurs'. In session 13, the last demonstrator picked up the new behaviour. After that, no additional individuals started opening the apparatus (only two individuals failed), which means saturation was reached in session 13. I found no correlation between the rate at which new demonstrators became available and the number of openings performed. Our results thus suggest individual trial-and-error learning, preceded by stimulus enhancement that led to the difference between observers and non-observers.

4.5.4 Spread of a novel opening technique?

In Japanese macaques the spread of a novel behaviour, namely potato washing, was observed (Kawai 1965). Within 3 years of one individual washing potatoes, a tradition was established, with 40 percent of the group members washing potatoes as well. Although some authors think that imitation is the only mechanism that can lead to the establishment of traditions and subsequently the formation of culture (although see Heyes 1993, Galef 1988), given the slow and steady increase in the number of potato-washing animals, it seems likely that the behaviour observed in the macaques was transmitted via enhancement followed by individual learning, between members with socio-positive bonds (see 'socially biased learning' Fragazy & Visalberghi 2004; 'who strategies', Laland 2004; for an example in chimpanzees: Bonnie & de Waal 2006; for another example of a behaviour that spread in the same group of Japanese macaques with an even slower rate, 'wheat-washing', see Kawai 1965 or Nishida 1987; for an example of a socially transmitted behaviour, namely termite-fishing in chimpanzees see Goodall 1970 or McGrew et al. 1979).

It seems likely that as the number of demonstrators available increases, the behaviour should spread faster if imitation was employed, but that was not the case with potato washing. Galef (1992) has stated that the original data reveals that "the pool of potential learners remained essentially constant over the years, the number of demonstrators rose dramatically, yet the rate of recruitment to the behaviour did not increase" and that the data therefore do not suggest imitation as the underlying mechanism (see also Galef 1990; and for further details on models of social learning and the acquisition rate of socially transmitted behaviour: Boyd & Richerson 1985).

However, Huffman & Hirata (2003) examined 12 different traditions and discovered that not all behaviours exhibited by group members were relevant to others and that the behaviours therefore spread at different rates during the transmission phase. The authors concluded that the acquisition rate might not be an ideal measure to determine the underlying mechanism. In the current study, I only looked at one type of behaviour and I could not compare the two observer groups and thus two different behaviours (e.g. 'lifting' or 'poking' in chimpanzees, Whiten et al. 2005; 'pushing' or 'pulling' in common marmosets, Pesendorfer et al. 2009).

In the group in which individuals opened the apparatus, the number of knowledgeable individuals increased steadily over sessions; however, the increase of knowledgeable individuals slowed down, meaning that as time went on, fewer individuals acquired the novel behaviour per session. This effect seems intriguing, because more demonstrators, i.e. individuals other could learn from, became available over time, but the rate of picking up the new behaviour did not increase. However, it is possible that this effect was a consequence number of individuals remaining that could adopt the methods as a percentage of the total group size (which is limited by the number of captive animals in that group).

By examining the number of demonstrations that each jackdaw had observed before opening the apparatus, it is clear that the first action the jackdaws performed when manipulating the yellow ball was not a goal-directed one. Only after a few manipulations did the birds manipulate the ball successfully and thus open the apparatus. The first animal to lift up the ball high enough to open the sliding door of the apparatus required 12 manipulations to achieve an opening. Given the first bird's slow application of the successful technique and the number of observed openings (performed by conspecifics within the group) and own manipulations of the ball by every subsequent bird that learned how to open the apparatus, I conclude that imitation was not the mechanism that led to the observed phenomenon, but that – as stated in an earlier section – stimulus enhancement followed by individual trial-and-error learning accounted for the observed phenomenon.

4.6 Conclusions

Observers appeared to be drawn to the box, indicating a social learning effect. Having arrived at the apparatus, individuals of both observer groups manipulated the apparatus, but only the individuals of one group were ever successful at opening it. This group almost only performed openings with a topography that matched the demonstrator's actions. However, it appears that the individuals of this group learned how to open the apparatus individually, as evidenced from the actions that were performed at the apparatus. Within the group, I discovered an influence of scrounging and own manipulations. I therefore conclude that an initial stimulus enhancement effect accounted for the difference between observers and non-observers.

As a second step, individual learning is likely to have accounted for the young birds' learning how to open the apparatus. Overall, I have shown that jackdaws can learn some information socially and that their performance is influenced by various social factors, such as the dominance hierarchy and age, but is possibly also effected by neophobia in the adult birds. To determine the social learning mechanism with certainty, the experiment needs to be replicated with mixed-age groups. However, to shed more light on the influence of age and neophobia, an additional study with different age groups would be also be useful. Future studies could also involve a ghost control to investigate the degree to which the social stimulus in social learning processes is important. It may also be important to examine the influences of scrounging using a diffusion design without the restriction of a demonstrator in a cage.

Chapter 5. Testing social learning in rooks using video playback

5.1 Abstract

A well-known, intrinsic problem in social learning tasks is coordinating the timing of demonstration and observation during observation trials. One possible way to bypass this problem is to use videos of the demonstrated actions. Video playback has been used to examine visual perception and cognition in various species, and in this study I used this relatively new technique to test social learning skills in rooks. Test subjects were shown videos of demonstrators opening an apparatus by unlocking two locking devices (sequential two-action task) and were then tested with the actual test apparatus. Only three birds approached and touched the apparatus, two of which also opened it. The successful individuals did not use the social information provided in the video, but applied their own techniques. I introduce a five-step model to social learning from videos and discuss at which stage the rooks might have failed. Possible reasons for not learning socially are also discussed.

5.2 Introduction

In the previous two chapters I have used a two-action task to test corvids' ability to imitate. Another way of testing for imitation (or emulation) is using a sequence task, where animals have to perform a single, individual action. This is followed by another action. A more complex version of a sequence task is a 'sequential two-action task' (e.g. Whiten et al. 1996), where individuals have to choose between two actions that start at the same part of the test apparatus. This is then followed by another decision between actions at a different part of the test apparatus.

One fundamental, well-known problem in these research methods is that coordinating the timing of demonstration and observation during observation trials is difficult to achieve. After training multiple (usually two) demonstrators to perform a certain action, they are then supposed to perform the action while an observer is watching. However, corvids have short attention spans (Scheid et al. 2007) and some species will not sit in the same spot for more than a few seconds (e.g. jackdaws, rooks; Federspiel, personal observations). In a number of cases, this combination leads to the demonstrator displaying the action to be copied when the observer is not watching or the observer closely monitoring the demonstrator's behaviour when the demonstrator is occupied in another behaviour aside from the desired action. This has negative consequences on different levels. First, it is not desirable for the researcher to deal with a long observation phase extending any given experiment. Second, these long time spans may have a detrimental effect on the observer's memory of the observed action, the demonstrator's performance or both.

One possible way to potentially bypass this problem is to use videos of the demonstrated actions. This allows a loop of demonstrations to be presented for as long as required until the observer reaches a set criterion (i.e. number of observed demonstrations). Furthermore, the observer's performance is less dependent on the demonstrator's motivation to perform the action or on the observer's attention during the short time that the demonstrator is performing the relevant action (i.e. interacting with an apparatus). Using videos instead of live animals also allows the experimenter to control various parameters, such as the length and the frequency of demonstrations and the manner in which they are performed.

With new technical advances emerging, it is now also possible to address common problems with digital media more appropriately. For example, using photographs of birds interacting with an apparatus has the disadvantage of the lack of movement that may be vital for an observer bird to ‘understand’ the action that is demonstrated (Dittrich & Lea 1993; for a review on picture recognition in animals and humans see Bovet & Vauclair 2000). Also, the difficulty of transferring from the image of a 2D object represented in a photograph to a real 3D object (i.e. real apparatus) is an obvious obstacle one would like to avoid to challenge one’s subjects with. Both factors mentioned may still play a role when cathode-ray tube monitors are used to play the videos, as most bird species have higher flicker fusion frequencies than humans (humans ~ 60 Hz, birds > 100 Hz), which may cause the birds to perceive the videos as a series of images rather than a continuous video, however such problems can be overcome by using LCD TFT monitors which do not refresh at 60 Hz, unlike traditional cathode-ray tube monitors (Bird & Emery 2008). Using high definition (HD) video equipment rather than standard video cameras to create the demonstration videos and playing them back using HD monitors should further address the potential transfer problem between an image and its real-life counterpart. HD technology yields finer grained images than standard equipment due to the greater number of lines of resolution with which videos are recorded and played back, and thus further contributed to a better transfer between 2D and 3D. In the future, this issue will be enhanced even further through the use of proper 3D technology currently employed in the movie industry.

Although using an LCD TFT monitor enables the birds to see a moving bird operating an apparatus rather than a series of static images, one cannot pinpoint with certainty what aspects of the stimulus the demonstrator actually perceives (D’Eath 1998, Fleishman & Endler 2000, McGregor 2000). The 2D apparatus may look completely different to a bird when compared to the 3D version of it, even though humans can usually easily make that transfer. Colour and depth perception, brightness, contrast, lumination, movement and distance from the screen can all influence how birds perceive images presented on video (Oliveira et al. 2000, Bird & Emery 2008).

Video playback has been used to examine visual perception and cognition in a number of species, including chickens, *Gallus gallus domesticus* (D'Eath & Dawkins 1996, Patterson-Kane et al. 1997) and budgerigars (Mui et al. 2008). Rooks also appear to be able to distinguish individuals in videos (Bird & Emery 2008). This is crucial for the present study, since it indicates that rooks perceive a conspecific presented in a video as another rook. In a study with 11 rooks, it was found that they preferred to look at a live conspecific rather than an empty compartment, but more importantly, this preference was also elicited when the subjects were shown a museum model of a rook, static images and videos, but not a control object with the same amount of black as a rook but with no shape information. When the rooks were presented with either their partner or a non-affiliated conspecific (either live, as a static image or video), they preferred to look more often at their partner than a non-affiliated conspecific, but only when presented live or on video, not as a static image (Bird & Emery 2008). This result indicates that rooks can recognize individuals in videos when those videos are presented on a screen with a high resolution and in the absence of flicker. Furthermore, in the latter study and in a few others before, a peep hole was used, so the birds had to look through the hole to watch the video (Bird & Emery 2008), causing them to exhibit a particular head movement that indicated switching from frontal to lateral view (Dawkins 2002, Range & Huber 2007, Scheid et al. 2007). This behaviour is usually shown when birds examine something in more detail and thus allows the experimenters to determine attention levels by looking at the head movement of the study subject.

The previous two chapters focused on social learning in jackdaws. As outlined in *Chapter 1*, not much is known about social learning in other corvid species. Only a few studies have focused on how rooks use social information in a foraging context. In an observational study, it was found that rooks' foraging decisions are influenced by the use of social information. Rooks flying over fields in search of food resources were more likely to land and forage where others were foraging in larger and denser flocks. Those kinds of flocks usually occurred in areas of high earthworm density; rooks thus increased their potential food intake by using social information (Waite 1981). In this case, a simple mechanism seemed to account for the choice of place: local enhancement drew individuals to where others were and hence facilitated learning about a food resource.

A different mechanism plays a role when it comes to the amount of food that is consumed, the preference for different food types and the acceptance of novel foods (Dally et al. 2008). Tested individually in a dyadic setting with a conspecific in the next door compartment, rooks ate more when a conspecific was present in an adjacent compartment, indicating social facilitation as the underlying mechanism. Novel foods were never eaten by any of the twelve rooks tested when they were alone. When the rooks were given novel and familiar food types to consume in the presence of a conspecific that was also feeding, they made choices based on the novelty of the food. If given two novel foods, they chose the same food as the conspecific; however, if they were given two familiar foods, i.e. foods that they had consumed before, they chose independently of what the demonstrator was eating. When the food was covered by a feeder, the rooks did not choose the same feeder as their conspecific in the adjacent compartment (Dally et al. 2008).

Differential use of socially and individually acquired information is found in many animals (Kendal et al. 2005). This is in line with Boyd and Richerson’s prediction (1985) that social information should be used when the costs of acquiring individual information are higher than the benefits, and to avoid risks, for example when faced with novel, potentially poisonous food resources. Witnessing a conspecific eating a novel food shows that the food is palatable and hence not dangerous.

Further exploring social information use in a foraging context further but using a new technique, Bird (2009) investigated rooks’ behaviour with video playback. Nine rooks were shown videos of a conspecific feeding from one of three differentially coloured and shaped cups and were then allowed to choose one of those cups to feed from. This was based on an earlier study which showed that rooks could recognize their partner in a video and could respond appropriately to actions others displayed in a video (Bird & Emery 2008; Bird & Emery, in revision). In the 2009 study, a rook was trained as a demonstrator and videos were recorded of it feeding from each one of three cups (green-oval, red-square, round-yellow). Subjects watched one of the videos and were then given access to the real cups. In order to solve the task, rooks should have used the social information presented in the video, as it showed the ‘correct choice’ (i.e. the location of the reward).

However, this is not what the birds did. Rather, they showed a tendency to persevere and adopted a win-stay, lose-shift strategy; meaning that if they were successful with a certain cup, they chose it again on the next trial until they did not get a reward. When that happened, they shifted their choice to a different cup. When one of the cups (the green one) was removed to decrease the potential memory load, the subjects were still not successfully using the social information presented. Moreover, the rooks’ performance did not improve when static images or real cups were presented instead of videos. Bird (2009) interpreted the findings as a problem of attention in the sense that the rooks had difficulties either with the position of the stimuli or with shifting their attention from the actual cups (where the reward would have been obtained from) to the screen. Two other possible explanations for the subjects’ poor performance included the lack of ‘punishment’ (the rooks incurred no real costs when making the wrong choice, because they had not been food-deprived) and a lack of inhibition, which may have led to them turning over the first cup they approached.

Although I cannot entirely dismiss the influence of satiation and hence a lack of motivation to work for food, I believe that using a preferred food as a reward should be salient enough for the rooks to participate in an experiment. Using the above described findings and methods as a foundation for the experiments reported here, the objectives for the current study were (1) to further test the feasibility of the relatively new technique of video playback for social learning research in corvids and (2) to determine whether rooks would be able to learn from others' actions (rather than choices) and use that information when tested with the same apparatus as the demonstrator in the video. For that purpose, the test subjects were shown videos of demonstrators opening an apparatus by unlocking two locking devices (sequential two-action task). They were then tested with the actual apparatus, and matching of their and the demonstrators' response topography was analysed.

5.3 Methods

5.3.1 Subjects & Housing

The subjects were 12 adult rooks of Group R2 (see *Chapter 2*, Table 2).

5.3.2 Apparatus & Experimental Set up

The apparatus used was a clear Perspex box that could be opened by manipulating various release mechanisms to gain access to a food reward (Fig. 41). The box was made of two discrete, but complementary sections mounted on a platform (31 cm x 15 cm): a vertical and a horizontal one (measurements: horizontal: 20 cm x 11 cm x 5 cm; vertical: 15 cm x 11 cm x 5 cm). In order to obtain a food reward, a bird had to manipulate a release mechanism on both the vertical and then the horizontal construct. The mechanisms had to be unlocked in this sequence in order to open the box successfully.

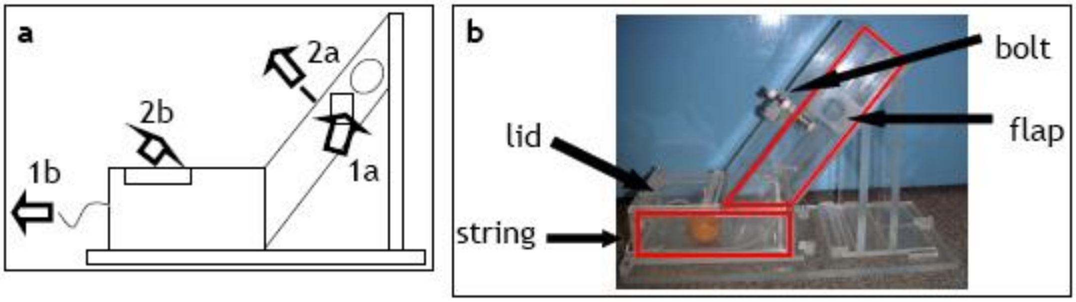


Figure 41. A diagram (a) and photograph (b) of the test apparatus. (a): Letters and arrows indicate the two different actions on each of the two parts of the apparatus; numbers represent demonstrators 1 and 2. The circle shows where the Kinder egg was placed at the beginning of each trial. (b): Bold red lines show the two parts of the apparatus: vertical and horizontal. Arrows point at the release mechanisms that had to be manipulated.

In order to release the food reward from the vertical section of the apparatus into the horizontal section, the subject had to either (a) push a flap on the side of the box (5 cm x 3 cm; accessible through a circular hole, diameter 2 cm), or (b) move a horizontal spring-loaded bolt located on the front of the box to the side (5 cm x 0.5 cm; accessible part 2cm long). Subsequently, to then obtain the food from the horizontal section, the bird had to either (a) pull a string (6 cm) to open a drawer (13.5 cm x 9 cm x 3,5 cm), or (b), slide open a drawer lid (6 cm x 11 cm). Once the unlocking sequence had been completed, the bird could access and consume mealworms as a food reward, which, as in previous experiments (Seed et al., unpublished data), was placed inside a yellow Kinder egg. As the rooks were familiar with receiving food rewards encapsulated in a Kinder egg, the egg was likely to be a salient and motivating stimulus for the birds.

All observation sessions were conducted either in an outside run adjacent to one of the testing compartments or inside a testing compartment, which contained three platforms: a central one and one on either side of the wire mesh of the adjacent compartment (Fig. 42). For half the observation sessions (‘peep hole condition’, PH), a 24” TFT monitor (Samsung LCD SM244T, Samsung Electronics, South Korea) was placed onto a platform inside the test compartment, adjacent to one of the outside runs. A High Definition (HD) camcorder (Sony HDR-

HC1E, Sony Corp. Tokyo, Japan) was connected to the monitor to play the demonstration videos from HDV tapes (see ‘Video stimuli’). A 2cm diameter peep hole was cut out in the centre of the wooden wall of the compartment. When sitting on a perch (1.65 m high) in front of the wall, the birds could thus look through the hole, which was at their eye level, and watch the video. For the other half of the observation sessions (‘platform condition’, PF), the monitor was placed behind a box and put onto a platform in a compartment adjacent to the test compartment. From the test compartment, the birds could see the whole monitor and thus watch the video without looking through a peep hole.

I chose to present the videos in two different conditions to ensure high levels of motivation (PH condition; in a previous study rooks were found to be highly motivated to look at stimuli if they were presented behind a wall with a peep hole; Bird & Emery 2008), quantifiable by measuring the number and duration of looks the birds directed towards the monitor through the peep holes, and to give the birds the opportunity to see the whole video without obstruction (PF condition), and thus probably also from the corner of their eye and for longer than in the PH condition. All trials were recorded onto DV tapes for later analysis of the behaviour of the birds and of which parts of the videos they had watched. Subjects were also monitored by the experimenter on a screen in a building adjacent to the aviary, which was connected to cameras (‘Atom Dome’, Model AHC, CSP Technology Ltd, Scunthorpe, UK) at the back of each one of the testing compartments.

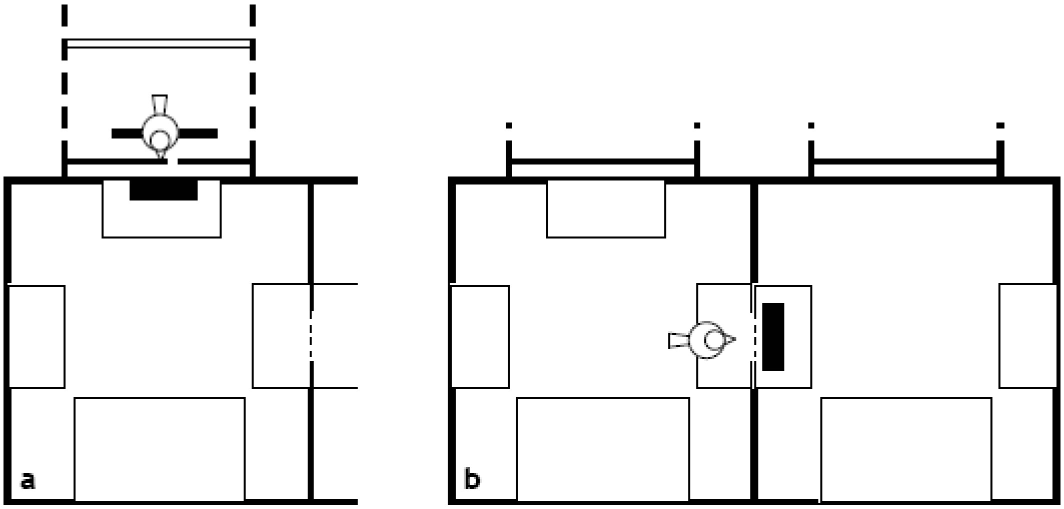


Figure 42. The set up for the PH condition (a) and the PF condition (b). Thick lines indicate wooden walls and hatches leading to the runs (top of drawing); thin lines show platforms and the door that was closed behind the subjects in the PH condition, and dashed lines stand for wire mesh. The video screen is depicted as a black square. Drawings not to scale.

5.3.3 Video Stimuli

Videos of the two demonstrator birds were recorded in HD 1050i format (1440 x 1080 resolution) at the end of the training phase (see 'Procedure'). They were filmed in the same test compartment with the same test apparatus, but with the demonstrator opening the apparatus in one of two different ways. Videos started with the bird flying onto the platform containing the apparatus and continued with the bird opening the apparatus and taking out the Kinder egg. Each demonstration was clipped to a length of 13s, and the sound was removed (using Sony Vegas video editing software); then the video clips were rendered in a loop with 1 sec in between the clips, thus resulting in two 30 min videos in MPEG2 HD format.

5.3.4 Procedure

The experiment was conducted between February and July 2008. It was divided into four phases: a habituation phase for all the birds (February to May 2008), a training phase for the demonstrators at the end of which the two videos were recorded (April & May 2008), and an observation (June & July 2008) and test phase for all the observers (June & July 2008). To reduce potential stress, the partner of the subject was placed into either an outside run adjacent to an inside compartment or into a compartment, depending on where the subject was in each of the phases, so that it could hear, but not see the subject (and the subject could hear their partner).

5.3.4.1 Habituation phase

During this phase, all the birds were re-familiarised with the Kinder eggs and habituated to a non-functional version of the apparatus. For the non-functional apparatus, the lid and drawer were removed, and the bolt and flap were blocked by a hook and a screw, respectively. The first half of the habituation phase was conducted in the aviary. A few Kinder eggs were placed inside the apparatus; the apparatus was then placed on the feeding platform in the aviary. This was continued until all the birds were observed feeding from the platform, opening the eggs and feeding on the mealworms. Subsequently, the non-functional apparatus was filled with Kinder eggs and placed into one of the testing compartments, with the hatch left open. Habituation was complete when all the birds had flown into the compartment and opened the Kinder eggs.

5.3.4.2 Demonstrator training phase

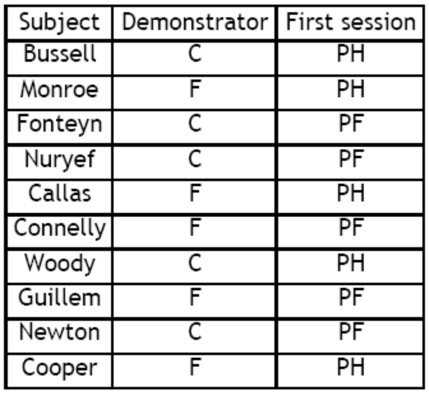
The two birds that in previous experiments had proven to be the most manipulative and the fastest to approach new apparatuses were chosen as demonstrators. They were individually trained on one of the two possible sequences by successive approximation (as described below). Cook (C) was trained on pushing the flap (vertical section) and pulling the string (horizontal section); Fry (F) had to move the bolt (vertical section) and then slide the lid (horizontal section). Both of the demonstrators were first trained to execute the action on the horizontal section only, with the vertical section not in place; the vertical section was then mounted on top of the horizontal one, and the birds were then required to incorporate the action for the vertical section to what they had learned before. Thus, in order to obtain the Kinder egg, the demonstrators now had to first release it from the vertical section by pushing the flap on the side of the box or by moving the bolt, before opening the drawer.

To ensure each demonstrator only learned one sequence of actions, the alternate opening mechanisms were locked. Pulling the string seemed to be quite straightforward and needed no extra encouragement. However, in the first few sessions, the flap and the hole that one of the demonstrators had to put their beak in to slide the lid open were made more obvious by painting a black circle around it; a piece of wire was attached to the bolt. After the birds had learned to perform the required actions, these ‘visual aids’ were removed again. Training was terminated when the demonstrators opened the box successfully in a consistent and smooth manner. At the end of the training phase, both of the demonstrators were recorded on HDV tape with an HD camcorder.

5.3.4.3 Observation phase

Observers were randomly assigned to observe one of the two demonstrators (see Table 1).

Table 24. Demonstrators the subjects were assigned to (Cook, C: flap & string; Fry, F: bolt & lid) and the type of session that they first experienced (PF or PH).



Subject	Demonstrator	First session
Bussell	C	PH
Monroe	F	PH
Fonteyn	C	PF
Nuryef	C	PF
Callas	F	PH
Connelly	F	PF
Woody	C	PH
Guillem	F	PF
Newton	C	PF
Cooper	F	PH

Each of them was presented with at least 1 session of each of the two different observation conditions: the PH condition and the PF condition. The order in which the birds received the two conditions was counter-balanced. Criterion to complete each condition of the observation phase was that the subject had to look at the video at least 15 times. As it was found that the looks that rooks direct towards a monitor are relatively short (Bird & Emery 2008), we used the number of looks rather then their durations as a criterion in the PF condition. A look was defined as turning the head towards the screen (the head had to be turned in a way that it was directed towards the screen with an angle between 0 and 180 degrees). In the PH condition I was able to score the number of looks directed at the video by counting the number of times the observers looked through the peep hole.

At the beginning of a test session, the video presentation was initiated, and the bird could sit on the platform or the perch and watch the demonstrations. A session ended after 30 min or after the bird had looked at the screen or through the peep hole 15 times. The subject was then released from the compartment or the run. If the criterion had been reached, the bird was tested immediately afterwards (see ‘Test phase’) and then participated in the other condition the next day. If criterion was not reached within 30 min, the bird received up to two more observation sessions of 30 min on the next two consecutive days. If within a total of three consecutive days the criterion was not reached, the bird moved on to the other observation condition on the following (4th) day without being tested in that condition. If the bird never reached criterion on any of the two conditions, the bird was excluded from further testing.

5.3.4.4 Test phase

Subjects were presented with the test apparatus in a test compartment. If they completed the observation session of one condition (e.g. PF), they were tested in one session of 5 trials. They then participated in the next observation session (e.g. PH) and a second test session thereafter. In each of the test sessions, the hatch to the outside run was left open in the first trial, so that the bird could fly outside and see its partner, which was placed in the adjacent run. This has and previously made the birds more willing to participate in experiments (Bird, Federspiel, Helme & Seed personal observation).

A trial was terminated when the bird fed from the Kinder egg or when it had not approached the apparatus for 10 minutes. If it gained a reward from the apparatus, the subject was given the next test trial immediately afterwards, until it had received 5 test trials in total; if it had not touched the apparatus, it was given the next test trial with a Kinder egg close to the apparatus. Not touching the Kinder egg or the apparatus in the second test trial led to the bird being shut in the third test trial. If it still did not approach the apparatus, the test session was terminated. Without completing that observation session, the birds then received observation trials in the other observation condition. If the birds touched the apparatus in either the second or third test trial, the next test trial was then of the same nature as the 1st test trial.

5.3.4.5 Afternoon test phase

After running both of these conditions, all the birds were tested in a final condition (‘afternoon PF’), which was very similar to the PF condition and designed to motivate the birds to participate. The apparatus was placed into the same compartment as the monitor, and the hatch to the outside run was left open. The partner of the subject was shut into the adjacent compartment and visually (but not acoustically) isolated. Thus, the difference to the previous test phase is that the birds could choose whether to come into the compartment and that they had access to the video and the apparatus simultaneously.

5.3.4.6 Data analysis

Videotapes were scored using The Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands) and analysed with STATISTICA 7

(StatSoft Inc., 1984-2004). In the observation phase, I scored measures of looking behaviour, i.e. the number and duration of looks through the peep hole (PH condition) or directed at the screen (PF condition) and time spent on the perch in front of the peep hole (PH) or on the platform in front of the screen (PF). In the test phase, I examined the motivation to approach and the interest in the apparatus by scoring the latency to enter the compartment, to land on the platform with the apparatus, to touch the apparatus and the time spent on the platform with the apparatus. In terms of successful openings of the apparatus, I recorded the latency to first touch the Kinder egg and whether the response topographies of demonstrators and observers matched. Furthermore, I analysed the actions qualitatively (detailed protocols of the observers' actions in the test phase can be found in the results section). I used non-parametric statistics to analyse my data. All tests were two-tailed, and alpha was set at 0.05. To determine the influence of individual shaping processes at the apparatus, I analysed the latencies across the 5 test trials in the successful birds using Spearman rank correlations.

5.4 Results

All but 1 of the 10 observers (Gu) reached the criterion in their observation session for their first condition and were therefore tested after completing the observation sessions for the first condition they were assigned to (observation phase: Table 25, test phase: Table 26). Gu was tested after the 2nd observation session only.

Table 25. Observation phase: assigned demonstrator and number of looks for each subject in each of the sessions (1 to 6) of the two conditions. Numbers stand for numbers of consecutive observation sessions. Repeated conditions indicate that the criterion was not reached in the previous session. Boxes include observation phases 1 and 2, with a maximum of three sessions per phase. Italics indicate that the individual failed to reach criterion in that observation phase. Abbreviations stand for Cook (C), Fry (F), platform (PF) and peep hole (PH).

Subject	Demo	1	Looks	2	Looks	3	Looks	4	Looks	5	Looks	6	Looks
Bussell	C	PH	20	*PF*	*0*	*PF*	*0*	*PF*	*0*				
Fonteyn	C	PF	21	PH	20								
Newton	C	PF	15	PF	6	PH	21						
Nuryef	C	PF	0	PF	0	PF	20	PH	6	PH	8	PH	9
Woody	C	PH	2	PH	3	PH	12	*PF*	*3*	*PF*	*0*	*PF*	*0*
Callas	F	PH	20	PF	20								
Connelly	F	PF	20	PH	20								
Cooper	F	PH	20	*PF*	*1*	*PF*	*2*	*PF*	*1*				
Guillem	F	*PF*	*3*	*PF*	*3*	*PF*	*2*	*PF*	*1*	PH	23		
Monroe	F	PH	15	PF	2	PF	6	PF	13				

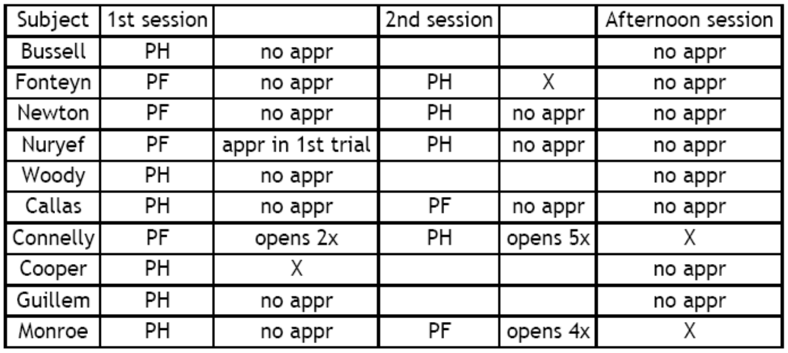
5.4.1 *First Test Session*

Testing with Cooper was terminated after he became too stressed to complete the test session. Out of the other 11 birds, only 2 approached the apparatus in their test trials (Connelly and Nuryef, both PF condition). Whereas Nuryef approached the apparatus in her second trial, but only pecked the string and then flew off, Connelly opened the apparatus twice in her first and second trial (Table 27).

5.4.2 *Second Test Session*

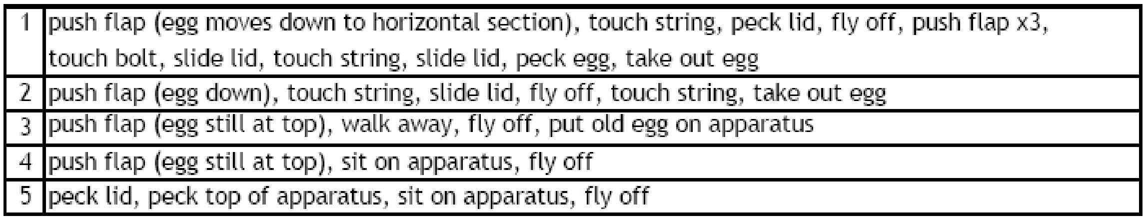
Six birds (Fo, Ne, Nu, Ca, Co, Mo) reached the criterion for the 2nd second condition (Table 25) and were thus tested in the 2nd test session (for 2 birds, the 2nd condition was a PF condition, for 4 it was a PH condition; Table 26). The other birds were excluded from testing due to not having watched a sufficient number of demonstrations. Two birds touched and subsequently opened the apparatus and fed from the Kinder eggs (Table 26; for a detailed protocol of the test sessions of the successful birds, see Tables 28 and 29).

Table 26. Test phase: Protocol for the first and second test session for all subjects. Type of condition (PF or PH) as well as approach behaviour ('no appr' = never approached the apparatus; 'appr' = approached; 'X' = session interrupted due to animal getting too stressed) and opening success are indicated. Empty cells show that the subject did not reach criterion.



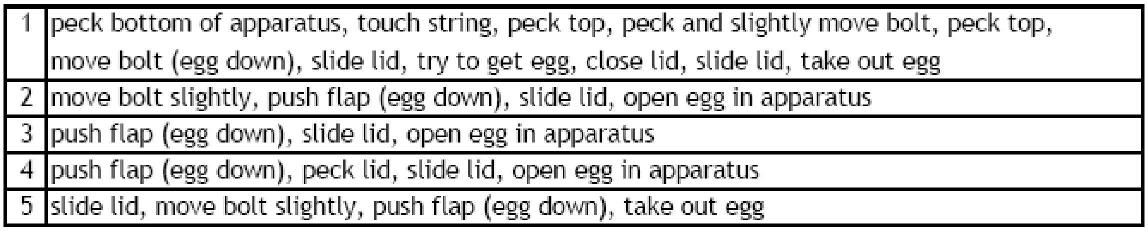
Subject	1st session		2nd session		Afternoon session
Bussell	PH	no appr			no appr
Fonteyn	PF	no appr	PH	X	no appr
Newton	PF	no appr	PH	no appr	no appr
Nuryef	PF	appr in 1st trial	PH	no appr	no appr
Woody	PH	no appr			no appr
Callas	PH	no appr	PF	no appr	no appr
Connelly	PF	opens 2x	PH	opens 5x	X
Cooper	PH	X			no appr
Guillem	PH	no appr			no appr
Monroe	PH	no appr	PF	opens 4x	X

Table 27. Test phase: Detailed protocol of Connelly's 1st test session (5 trials; demonstrator: Fry). Comments in brackets indicate the position of the Kinder egg after the given action performed by the subject.



1	push flap (egg moves down to horizontal section), touch string, peck lid, fly off, push flap x3, touch bolt, slide lid, touch string, slide lid, peck egg, take out egg
2	push flap (egg down), touch string, slide lid, fly off, touch string, take out egg
3	push flap (egg still at top), walk away, fly off, put old egg on apparatus
4	push flap (egg still at top), sit on apparatus, fly off
5	peck lid, peck top of apparatus, sit on apparatus, fly off

Table 28. Test phase: Detailed protocol of Connelly's 2nd test session (5 trials; demonstrator: Fry).



1	peck bottom of apparatus, touch string, peck top, peck and slightly move bolt, peck top, move bolt (egg down), slide lid, try to get egg, close lid, slide lid, take out egg
2	move bolt slightly, push flap (egg down), slide lid, open egg in apparatus
3	push flap (egg down), slide lid, open egg in apparatus
4	push flap (egg down), peck lid, slide lid, open egg in apparatus
5	slide lid, move bolt slightly, push flap (egg down), take out egg

Table 29. Test phase: Detailed protocol of Monroe's 2^{nd} test session (5 trials; demonstrator: Fry).

1	no appr
2	push flap (egg down), slide lid, touch string, peck lid, slide lid, sit on apparatus and peck lid, slide lid, take out egg
3	push flap (egg down), peck lid, pull string, sit on apparatus and peck lid, touch string, peck lid, pull string (drawer open), peck egg, open egg in apparatus
4	push flap (egg down), peck lid, pull string, peck lid, slide lid, peck lid, slide lid, open egg in apparatus
5	push flap (egg down), peck lid, slide lid, sit on apparatus, peck lid, slide lid, open egg in apparatus

Table 30. Test phase: Protocol for the four subjects that approached and touched and/or opened the test apparatus. Demonstrators were Fry for Monroe and Connelly and Cook for Nuryef. Latencies (s) from the beginning of a trial (the experimenter shuts the test compartment after having positioned the apparatus on the platform) to approach the platform ('present'), to touch the apparatus and to touch the egg and total time spent at the platform are given for each of the five test trials (in seconds). If the subject did not approach, 'n/a' is stated. Top row indicates whether the subject was tested after the first or second observation session and the type of session (PF or PH).

Monroe (after 2nd session: PF)

Trial number	Present	Touch apparatus	Touch egg	Time at platform
1	n/a	n/a	n/a	n/a
2	6	7	44	61
3	5	10	52	82
4	3	5	22	57
5	2	4	32	75

Connelly (after 1st session: PF)

Trial number	Present	Touch apparatus	Touch egg	Time at platform
1	112	114	285	72
2	5	7	21	25
3	28	31	n/a	88
4	n/a	n/a	n/a	n/a
5	n/a	n/a	n/a	20

Connelly (after 2nd session: PH)

Trial number	Present	Touch apparatus	Touch egg	Time at platform
1	433	435	648	172
2	94	95	116	73
3	18	19	25	36
4	10	12	21	39
5	11	14	20	26

Nuryef (after 1st session: PF)

Trial number	Present	Touch apparatus	Touch egg	Time at platform
1	11	17	n/a	8
2	n/a	n/a	n/a	n/a
3	n/a	n/a	n/a	n/a
4	n/a	n/a	n/a	n/a
5	n/a	n/a	n/a	n/a

Overall, the subjects approached the platform and the apparatus faster in the later trials than the earlier ones and also touched the egg earlier (Table 30). The faster performance at the apparatus also seemed to have led to shorter time spans at the apparatus. However, only data for 2 individuals could be analysed due to lack of data for the other individuals/test sessions. The effect was only significant for 1 individual out of the 2 (Monroe, Connelly after 2nd observation session): Connelly approached the platform faster, touched the apparatus earlier and spent less time at the platform over the course of the 5 trials (Spearman rank correlations: platform: $N = 5$, $R = -0.90$, $P = 0.037$; apparatus: $N = 5$, $R = -0.90$, $P = 0.037$; time present: $N = 5$, $R = -0.90$, $P = 0.037$).

Both rooks that opened the apparatus (Connelly and Monroe) had Fry as their demonstrator, who moved the bolt and slid the lid open to open the apparatus. Both birds followed the same *sequence* as the demonstrator, but did not consistently use the same *technique* at the release mechanisms as the demonstrator. At the vertical part of the apparatus, they mainly used the flap to release the egg; at the horizontal section they slid the lid open in most of the trials. Overall, the response topographies thus did not match the demonstrators' actions (see Tables 27 to 29). None of the birds approached the apparatus in the afternoon session.

5.5 Discussion

In this study I have shown that rooks do not appear to use social information they could have potentially gathered from watching a video of a conspecific opening an apparatus. This may be due to problems with the five main steps of gaining and using social information from videos, which will be analysed in detail below (Fig. 43).

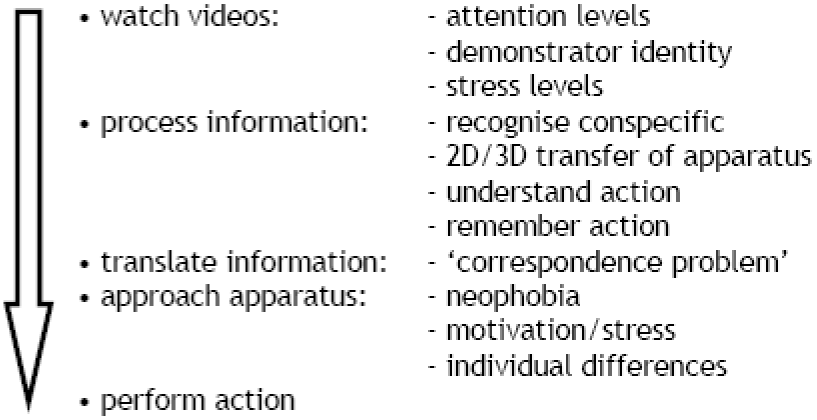


Figure 43. Five main steps involved in the potential social learning process the rooks would go through during this particular experiment, from having to observe then process information and then finally performing an action (left) and the obstacles they have to overcome (right).

First, the birds have to pay attention to the videos to be able to learn something from them. It has been demonstrated that ravens and jackdaws look through peep holes to watch conspecifics, although they exhibit relatively short attention spans (Scheid et al. 2007). Ravens spent more time watching a conspecific than jackdaws did, and they were also more selective in terms of when to watch, preferring to watch affiliated individuals (median: 3.8 sec) over non-affiliated ones (2.6 sec) and individuals engaged in foraging (3.7 sec) over individuals manipulating objects (2.7 sec). Jackdaws watched their conspecifics significantly less and were also not selective when watching others (attention span medians between 1.0 sec and 1.6 sec for the different contexts and not significantly different from each other).

In a few studies with the same rooks that were used in the present experiment, Bird & Emery (2008) revealed that rooks were willing to focus their attention on video or pictures with a conspecific in them behind peep holes. When allowed to watch their partner through a peep hole, the rooks looked for approximately 1.5 s at a time (Bird & Emery 2008). When confronted with pictures or videos of 'possible' and 'impossible' configurations of objects and supporting platforms in an expectancy violation task, rooks spent approximately 0.7 s to 1.3 s (medians for pictures) or 1.0 s to 1.6 s (medians for videos), respectively, looking through the peep holes. Overall, they only looked through the holes approximately 2 to 4 times (medians) both with pictures and videos in a session (16 min period, with each of the 4 stimuli presented in 4 different configurations for 1 min each) (Bird & Emery 2010; Bird 2009, *Chapter 6*).

In a different study, the same rooks were tested in a social learning setting, during which they had to watch rooks turning over coloured cups (although not through a peep hole, but on a screen) and then choose which cup to turn over themselves. Although no exact data on that was provided, it appears that the rooks watched the videos, but failed to copy the demonstrator's choice, suggesting that they could not transfer what they observed on screen to a real scenario (Bird 2009, *Chapter 5*). In the present study, all observers reached the criterion for their first observation session within 1 to 4 observation sessions. However, there is a slight chance that rooks might attend to the video, without processing featural detailed information. A human example of this is when a person looks at their watch but is still unaware of what time it is afterwards.

Another obstacle may be the identity of the demonstrator, in terms of the nature of their affiliation with the observer, their sex, and their position in the dominance hierarchy. Scheid et al. (2007) demonstrated that ravens were more attentive to close affiliates than jackdaws and Schwab et al. (2008) found that jackdaws seem to preferentially learn from non-affiliated individuals. In the current experiment, the two demonstrators were paired, thus, all the observers were non-partners; therefore it is not possible to make conclusions about the effect of affiliation in rooks. Of the two demonstrators, one was male, the other was female. They were both high-ranking individuals. There was only one male in the group of the observers. All of these factors make it difficult to test for the potential influence of dominance rank and sex on the use of social information. The higher stress level of the birds when they cannot be with their partner certainly affects performance. Hence, during testing, I enabled them to either hear or hear and see their partner. As it seems unlikely that rooks would not act upon available information on the location of food, and given that our rooks watch the videos that are shown to them and also pay attention to stimuli in other experiments, I think that this first step of the present experiment was successful and that the rooks did not fail to employ social learning due to a failure to pay attention to the demonstrator.

The second step in the social learning process involves various small steps contributing to processing the information gained from watching the videos: recognising a conspecific in the video; transferring from the 2D image of the apparatus to the real 3D apparatus; perceiving the performed action on the apparatus properly or even ‘understanding’ the action; and finally remembering the observed sequence until being able to manipulate the apparatus oneself. As discussed in the introduction, rooks are able to recognise a conspecific in video. Data from an expectancy violation study (Bird & Emery 2010; Bird 2009, chapter 6) suggests that the birds are also able to recognise objects in pictures or videos as they exhibited longer looking times when presented with a configuration of stimuli that appeared impossible, e.g. when objects in a picture seemed to be floating above or next to a supporting platform, or when presented in videos, an object was seen rolling up a slope. It thus seems unlikely that the same rooks would not perceive an object in a video as a 2D representation of a 3D object. Given that rooks appear to be able to both recognise conspecifics and objects in video, it also seems unlikely that they would not be able to perceive a performed action in a video.

Very little is known about a rook’s memory capacities. They are classified as moderate cachers (de Kort & Clayton 2006, Kallander 2007) and so need to remember the location of cache sites for extended periods, which indicated that they should be able to remember what they have observed.

Thirdly, in this study, the birds would have had to apply the observed and memorised actions at the apparatus. This involves probably one of the most difficult processes when applying socially acquired information: overcoming the ‘correspondence problem’ (Heyes 2001). The difficulty lies in translating observed actions into performed ones, i.e. activating the correct muscles to achieve a similar movement to the one observed (although when observing a conspecific, all that could be seen was the outcome of various muscle activations, not the activations themselves). Although a major topic in imitation and mirror neuron research, this issue still seems to be beyond our grasp (Brass & Heyes 2005). Mirror neurons might represent the underlying mechanism by which the correspondence problem is solved. Mirror neurons are neurons or networks of neurons that fire, not only when a certain action is being executed, but also when observing that same action being performed by another. These neurons become activated even when someone is heard performing the action, but not seen (for reviews on the topic of mirror neurons and imitation, see Rizzolatti et al. 2001, Rizzolatti & Craighero 2004). Discovery of this perception-action link has had a significant impact on various fields, as mirror neurons may not only be responsible for enabling animals to imitate, but may also be involved in empathy (Gallese 2003) and the development of language in children (Rizzolatti & Arbib 1998). Whereas some argue that mirror neurons have evolved for the purpose of social learning or even imitation, others take on a more general approach and argue that mirror neurons actually developed for a different purpose, but, as a by-product, aid in the process of imitating (Keysers & Perrett 2004). This generalist view suggests that the properties of mirror neurons have to be acquired through learning processes during the ontogeny, as a by-product of general associative learning (Bass & Heyes 2005). At this stage, I cannot rule out that the rooks struggle to overcome the correspondence problem and there is no evidence as yet, that rooks or any other bird species have mirror neurons that are equivalent to mammalian mirror neurons (for a different case for auditory-vocal mirror neurons, see Prather et al 2008).

In the fourth step, the birds had to approach the apparatus and perform the observed actions to open it. It is possible that neophobia played a role in the test trials, as most of the birds did not approach the apparatus, despite all subjects having been habituated in an earlier phase. Nevertheless, the parts that were added to the apparatus after the habituation phase to make it functional for the test phase could have elicited a negative response in some of the birds.

Furthermore, the birds may not have been motivated to approach the apparatus, either due to a general lack of interest or satiation; as discussed in the introduction, the rooks were not food-deprived and therefore did not have to rely on the mealworms in the Kinder eggs as food source. Having fear of the apparatus (although they have all been habituated to it), a lack of interest in the mealworms, and the stress of being in a compartment taken together may have lowered the rooks' motivational levels. If the birds were fearful of the apparatus or did not know how to open it, they could have been saving their energy and waiting for the food afterwards. However, the birds are usually very motivated to open Kinder eggs and gain an additional treat, and all of them opened the eggs when they were presented on the food platform in the main part of their aviary.

Individual differences might also have affected the way the rooks approached the apparatus, as some individuals seemed to be less shy to approach the apparatus than others (for individual differences along the bold/shy axis see *Chapter 6*).

The final stage of the social learning process is actually performing the action. When the successful animals approached the apparatus, they used the same sequence, but not necessarily the same actions as the demonstrators. Although it seems intriguing that the sequence of actions performed was the same as the demonstrators', the rooks may have just been following the egg and manipulated the parts of the apparatus the egg was closest to at any one time. One way of testing this in the future would be using an opaque test apparatus. The rooks in general seemed to be less motivated to participate in this experiment than the jackdaws described in *Chapters 3* and *4*, and the rooks appeared to only get motivated when they saw the Kinder eggs. Using an opaque apparatus might therefore be relatively difficult, but would contribute towards uncovering processes underlying the rooks' behaviour in a sequential social learning task.

Although in some trials the actions of the observers matched the demonstrators', they did not do so consistently, which indicates that they were not acquired via social learning (as switching between different mechanisms, such as imitation and emulation seems more difficult to achieve than just sticking to one method, I will disregard this possibility here and interpret the findings in the most parsimonious way).

Overall, it seems the successful subjects used individual rather than social information to open the test apparatus, which was acquired via trial-and-error learning. They were less shy to approach the apparatus and/or more innovative than the others. In their first trial, they manipulated various areas at the apparatus; in consecutive trials the birds' actions were much more goal-oriented and mainly directed at the release mechanisms. Also, the latencies to approach and manipulate the apparatus decreased across the five test trials, as did the latency to touch the egg (only significant in one individual). There could be two main explanations for the rooks not using social learning in this experiment. Firstly, similar to jackdaws (see *Chapters 3* and *4*), rooks may not need social learning mechanisms that are more demanding than local/social enhancement in their daily lives. Aspects of their ecology, such as their diet might influence their learning processes, such that enhancement provides rooks with all the information they need. If they do not need to gain more complex forms of social information, they would not employ costly processes such as imitation or emulation unnecessarily. The second reason that the birds might not have employed social learning in this study is that, as described by Bird (2009), an 'affinity' to innovation and/or rapid trial-and-error learning may override social learning processes in rooks.

Chapter 6. Individual differences in the exploratory behaviour of rooks, jackdaws and Eurasian jays

6.1 Abstract

Originating in human psychology, the concept of ‘personality’ or individual differences between humans has long been established. In recent years, it has become apparent that individual differences in behavioural traits also exist in non-human animals. Those differences are thought to be consistent across contexts, stable across time, irrespective of sex or age, and may also be related to differences in other behavioural traits. I investigated individual differences in exploratory behaviour in three corvid species: rooks, jackdaws and Eurasian jays. Birds were tested in two different settings: in a novel environment and a familiar environment with novel objects. I found differences between species, between the age groups of the same species and between individuals of each of the three species. However, individual differences were not stable across contexts. Some parameters within the two tests appeared to be associated, and physical condition (weight/tarsus length) also seemed to influence exploratory behaviour in the corvids. My findings have implications for cognition research with corvids in the sense that individual differences in exploration may lead to varying latencies to approach novel test apparatuses and therefore to differing task performance.

6.2 Introduction

The concept of personality has long been established in human psychology, and although there is still an ongoing debate as how to define personality (e.g. McCrae & Costa 2008; Eysenck 1992), the 'five-factor model' or the 'Big Five' has become a well-established model that is commonly used to explain the variation between individuals of the species *Homo sapiens* (for a review of human personality, see Nettle 2007). Different psychologists have used different labels for the five factors and different methodologies to determine them, causing confusion over naming the factors, which has even led to the organisation of symposia addressing the issue (Costa & McCrae 1992a). Originating with the NEO-I (Neuroticism-Extraversion-Openness Inventory), the NEO PI-R questionnaire has become the commonly used tool to measure human personality (for a general introduction to the five-factor model see McCrae & John 1992, for the NEO-FFI: McCrae & Costa 2004). With the NEO-FFI, a varying number (e.g. 30) of separate traits or 'facets' are determined, which are then organised by the model into the five factors Agreeableness, Conscientiousness, Extraversion, Neuroticism and Openness (see the revised NEO manual including six facets for each of the five factors, Costa & McCrae 1992b).

In recent years, individual differences in behavioural traits have been shown to also exist in non-human animals (see Boissy 1995, Koolhaas et al. 1999, Gosling 2001, Sih 2004, Réale et al. 2007 for reviews). These differences are consistent across contexts, stable over time, irrespective of sex or age, and are often related to differences in other behavioural traits (Sih & Bell 2008).

Although some researchers still apply the five-factor model to non-human animals (e.g. King et al 2008, Weiss et al 2000), a growing body of alternative literature shows that the predominant current approach is different: staying clear of anthropomorphism, researchers now mainly approach the topic of individual differences in non-human animals by defining factors that are more appropriately tailored to non-human animals. Instead of inferring characteristics, which may be clouded by the subjectivity of the observers, psychologists interested in animal personality have recently started to utilise behavioural factors that can be determined by observations and experiments rather than subjective scores or ratings. Factors that have been determined reliably in non-human animals using behavioural methods include activity, aggressiveness, boldness, exploration and sociability (Gosling 2001). Researchers in this area use many terms interchangeably such as *coping styles*, *temperament* or *personality*, to define individual differences, however there are subtle differences between these terms, particularly when applied to animals. Whereas the term *temperament* is commonly used to describe individual differences in emotional state that forms the basis upon which adult personality develops (Allport 1937, Buss et al. 1987, Budaev 1997, Box 1999, Clark & Wilson 1999), the term *coping styles* stands for individual differences in behavioural and physiological stress responses that may become adaptive (Koolhaas et al. 1999, Pfeffer et al. 2002). However, in this chapter I will use the most neutral of terms, *individual differences* (and have presented the human framework only for descriptive purposes).

Originating in human psychology, the field of personality research in non-human animals consists of a core of studies on apes and monkeys, with additional experimental work on various other species, ranging from mammals, such as dogs, cats, rats and pigs, to birds, fish and even octopus and butterflies (for a review see Gosling 2001). In birds, the great tit is a popular model for the study of individual differences in exploratory behaviour (Drent et al. 2003, Groothuis & Carere 2005; however for an example of individual differences in exploratory behaviour of starlings, see Minderman et al. 2009). In great tits, a genetic basis of individual differences in behaviour and thus the heritability of such differences has been established (Drent et al. 2003, van Oers et al. 2004b). However, although there is evidence for heritable components of individual differences and thus selection for a mix of different strategies in a given species, an alternative hypothesis takes into account behavioural tactics

(Dall et al. 2004). Also, a trade-off between current and future reproduction could result in a population with polymorphic structure (Wolf et al. 2007).

To date, not much is known about individual differences in corvids. A recent paper looked at differences between individuals of common raven (*Corvus corax;* Range et al. 2006). Ravens, a species well known for its behavioural flexibility and switching of strategies, is capable of social manipulation when recruiting others to food sources (Heinrich & Marzluff 1991) or even leading conspecifics away from food (Bugnyar & Kotrschal 2004). Ravens were also found to be able to switch from hiding ('caching') to stealing ('pilfering') food from others (Heinrich & Pepper 1998, Bugnyar & Kotrschal 2002). Social manipulation also seems to be subject to individual variation in ravens, as are object manipulation and learning abilities (Range et al. 2006). Connections between these three factors were found, with the faster learners in colour and position discrimination tasks engaging less often in social manipulation.

Using similar methods to those used with great tits (see Verbeek et al. 1994), I investigated exploratory behaviour in 3 different species of corvid: rooks (fledglings and adults), jackdaws (fledglings and adults), and Eurasian jays (fledglings only) (for examples of boldness and exploration in other species see Benus et al. 1990, Verbeek et al. 1996, Drent & Marchetti 1999; for a review on boldness and shyness see Wilson et al. 1994). Similar to many other corvids, these three species are said to be neophobic and thus wary of novel situations (Katzir 1981). Novel foods are only accepted slowly, unless eaten by a group member (e.g. rooks will eat the same novel food that a conspecific is eating; Dally et al. 2008). An unknown object in their environment will cause them to avoid that area for hours or even days before they begin to slowly approach the object (e.g ravens, Stoewe et al. 2006). Both rooks and jackdaws are well known for being highly social, whereas Eurasian jays are territorial birds that only associate with the opposite sex during the breeding season (Clayton & Emery 2007, Emery et al. 2007, von Bayern et al. 2007). Whilst I will not speculate on the difference in boldness and exploration between rooks and jackdaws in the wild, it is well documented that Eurasian jays are extremely secretive and shy in the wild (Coombs 1978). Individuals are rarely seen, hard to follow and can usually only be observed when looking for food or mates.

I recorded individual birds' responses to two different contexts of novelty: a novel environment and the presentation of two novel objects in a familiar environment. Animals were released into an unfamiliar room containing artificial trees ('novel environment test') and were subsequently given the opportunity to explore one of two unfamiliar objects in a familiar environment ('novel object tests', two sessions with two different objects). Originally designed to investigate emotionality in rats and mice (Hall 1934), the novel environment test has been used to test various other factors as well, such as timidity and activity (see Gosling 2001). My objectives were to establish individual differences in exploratory behaviour in two different contexts and to determine whether those differences would be consistent across the two contexts. Furthermore, I was interested in whether the physical condition of individuals would be a predictor of exploratory behaviour, i.e. whether it could influence how animals react to novel apparatuses in cognitive tasks and how fast or slow they are in exploring a novel set up. I compared responses to the two different contexts between individuals and also analysed differences between species and age groups, extending the original paradigm of *individual differences* (see Réale et al. 2007, p. 294). Results and their relation to the condition of individuals are placed into a broader framework of the current literature. Furthermore, I discuss implications of consistent individual differences for cognition research.

6.3 Methods

6.3.1 *Subjects and housing*

Subjects were adult and fledgling rooks, jackdaws, and fledgling Eurasian jays of groups R1, J1 and EJ1 (see *Chapter* 2, Table 2).

6.3.2 *Experimental Set up*

Birds of all three species were tested individually on their exploratory behaviour in two different tests based on the methods of Verbeek et al. (1994) with great tits (*Parus major*): a novel environment test and two novel object tests. The novel environment test was conducted first. In this test, conducted to examine the birds' spatial exploration, birds were released into an unfamiliar room measuring 6 m x 2 m x 2.5 m that contained 5 artificial trees (Fig. 44a). The trees consisted of 4 sided posts with a wooden perch 30 cm long, on each side, at a height of 1.40 m (Fig. 44b).

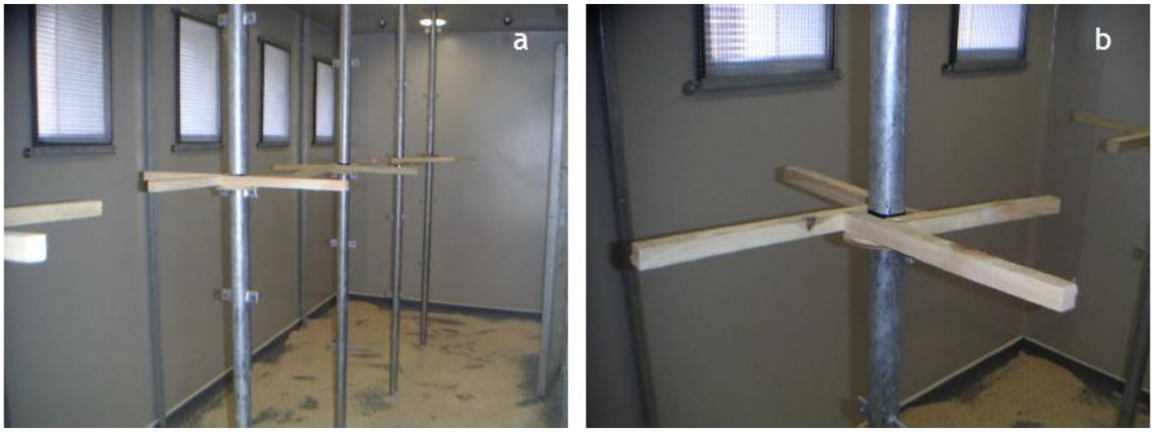


Figure 44. The set up for novel environment tests: a room containing 5 artificial trees (a) consisting of 4 sided posts (b).

Each bird was tested once for 20 min, starting immediately after the bird was released into the room. Sessions were recorded via overhead cameras (surveillance system Geovison ezCCTV). For each bird, I recorded latencies to approach the first and subsequent trees, as well as the number of trees visited.

In the novel object tests, birds were tested on object exploration by confronting them with novel objects presented in a familiar environment (Fig. 45).

Figure 45. The two objects for the novel object tests.

Two sessions (using two novel objects) were conducted to rule out the possibility that the animals' behaviour to a novel object was based on a reaction towards specific features of that particular object. Objects were chosen to be of similar size, but of different features. Object 1 was a red rubber ball with a diameter of 4 cm. Object 2 was a plastic Mickey Mouse™ figure measuring 5 cm x 3 cm x 1 cm. Fledglings were lifted into and tested in the pen that they had been hand-raised in, measuring 1.60 m x 1.80 m x 1 m, whereas adult birds were released into and tested inside test compartments measuring 1.6 m x 1.5 m x 3 m (4 yr old rooks & jackdaws) or 2.5 m x 2 m x 3 m (5 yr old rooks). Test sessions lasted for 10 min and were conducted on two consecutive days. The trial started when the birds were placed into the pen or entered the test compartment. The order in which subjects received the two objects was counter-balanced. All trials were recorded with 'Atom Dome' CCTV video cameras (Model AHC, CSP Technology Ltd, Scunthorpe, UK) that had been mounted at the back of each one of the testing compartments (both adult bird groups) or a Sony Handycam (Model CCD-TR840E; for the fledglings). Data taken to quantify the birds' behaviour were latency to approach the object within 1 m, 50 cm and 20 cm, whether the object was touched and the minimum distance to the object.

After conducting the novel environment tests, all birds were weighed and their beak and tarsus length was measured to determine their condition, i.e. 'fitness' (usually expressed as weight/tarsus length; see Verbeek et al. 1994). To acquire a measure that was as accurate as possible, tarsus length was measured three times, and the three measures were averaged.

6.3.3 Data scoring and analysis

Birds were given scores for each test. In the novel environment test, scores depended on how many trees the birds visited (0-5). In the novel object test, the birds were ranked on how close they approached the object. A score of 0 meant that they never approached the object in the 10min period; scores 1 to 3 were given for approaching the object within 1 m, 50 cm or 20 cm. Animals assigned a score of 4 touched the object with their beak. In order to compare individual performances, latency to approach the first tree or the object within 20 cm (within reach of the animal) was analysed in blocks of 200 s or 100 s, respectively. Animals that did not approach a tree or an object within 20 min or 10 min, respectively, were given the maximum time span in the data analysis, i.e. 1200 s or 600 s, respectively. Because I did not find significant differences between the data sets of the 4 yr old and the 5 yr old rooks, I analysed the two data sets as a whole (the two groups together will thereafter be classified as 'adult rooks'). To analyse individual differences consistent across contexts, I examined the relationships between scores of the two tests. I correlated these measures to the weight/tarsus length ratios for each individual to determine any possible influence of condition and compared to dominance ranks to examine any influence of dominance hierarchy. Furthermore, I compared measures to examine any effects of age and species on individual differences. Due to the highly skewed numbers of birds per sex for each species, we were not able to analyse sex differences.

Videotapes were coded using The Observer 5.0 program (Noldus Information Technology, Wageningen, The Netherlands) and analysed using STATISTICA 7 (StatSoft Inc., 1984-2004) and SPSS 17.0 (SPSS Inc., 1989-2008). We used non-parametric statistics. All tests were two-tailed and α was set at 0.05. Trends were reported for $0.10 > \alpha > 0.05$. I performed Kruskal-Wallis ANOVAs and post-hoc Mann-Whitney U tests to investigate species differences between the groups, i.e. species and age differences. Adjusted Z-values were stated if there were two or more ties in the two data sets that were compared. Spearman rank correlations were used to test for relationships between latencies in the two novel object tests, relationships between any measures of novel object and novel environment tests and links between any individual measures.

6.4 Results

I found effects of species, age and individual differences in the animals' responses to a novel environment and to novel objects, however many of the measures of the two tests did not correlate, nor surprisingly did the measures for the two novel object tests.

6.4.1 Age and species differences

6.4.1.1 Novel environment test

A trend towards differences between the five groups tested was found for the latency to approach the first tree in the novel environment test (Kruskal-Wallis test: $H = 12.41$, $N = 68$, $P = 0.064$). Post-hoc Mann-Whitney U tests revealed age differences between the young and old rooks, with the young ones being slower to approach (N_1 = 12, N_2 = 20, $Z_{adjusted}$ = 2.16, P = 0.031).

Bird groups also differed in the number of trees they visited (Kruskal-Wallis test: H = 25.16, N = 68, P < 0.001). Species differed in that adult jackdaws visited more trees than adult rooks (N_1 = 9, N_2 = 20, $Z_{adjusted}$ = -2.30, P = 0.021). I discovered age differences in both rooks and jackdaws, with the adult jackdaws visiting more trees than the fledglings (N_1 = 12, N_2 = 20, $Z_{adjusted}$ = -2.55, P = 0.011) and the adult rooks visiting more than the fledgling rooks (N_1 = 15, N_2 = 9, $Z_{adjusted}$ = -3.38, P = 0.001).

6.4.1.2 Novel object tests

There were differences between the groups in the latency to approach the novel object to within 20 cm in both the first (Kruskal-Wallis test: H = 18.53, N = 68, P = 0.001) and the second novel object test (H = 20.86, N = 68, P < 0.001). Post-hoc Mann-Whitney U tests revealed similar results in both novel object tests.

Both tests revealed age differences, with fledgling jackdaws being slower to approach the novel object within 20cm than the adults (N_1 = 15, N_2 = 9; first: $Z_{adjusted}$ = 3.26, P = 0.001; second: Z = 2.92, P = 0.003). In the second novel object test, I found a similar difference between the two age classes in the rooks (N_1 = 12, N_2 = 20, $Z_{adjusted}$ = 2.08, P = 0.037).

6.4.2 Individual differences

Individuals of all three species varied greatly in the latency to approach the first tree or a novel object, in the number of trees they visited and in how closely they approached the novel objects.

6.4.2.1 Novel environment test

Some individuals of all 5 groups never visited any of the trees. Only adult rooks and adult rooks visited all 5 trees (Fig. 46a). The first tree was usually visited in the first 3 min or never at all (Fig. 46b).

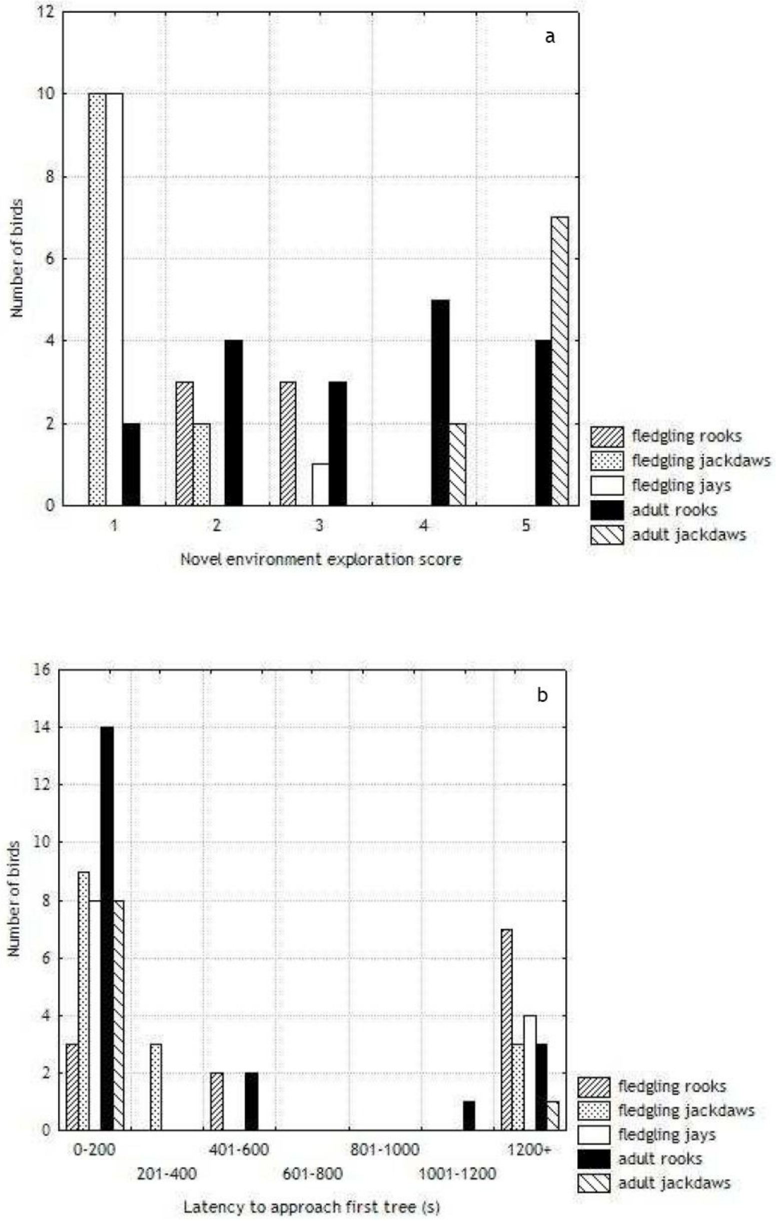
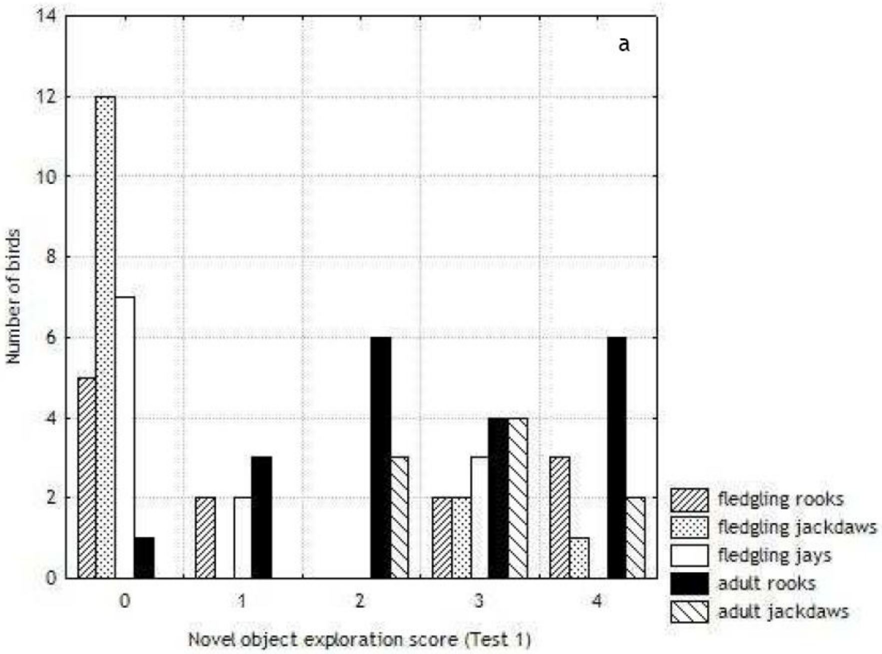


Figure 46. (a) Exploration scores and (b) latency to visit the first tree out of five in a novel room for 12 young and 20 adult rooks, 15 young and 9 adult jackdaws and 12 young Eurasian jays during a 20 min test period. Exploration scores were based on how many trees the birds visited (0 - 5).

6.4.2.2 Novel object tests

In the first novel object test, most young jackdaws did not approach the object, whereas all adult jackdaws approached the object within 50 cm. Individuals of the other groups could be divided into all categories (Fig. 47a). In the second test, most young birds of the three species never approached the object. Most adult rooks and jackdaws approached the object within 20 cm, and some birds touched the object (Fig. 47b).



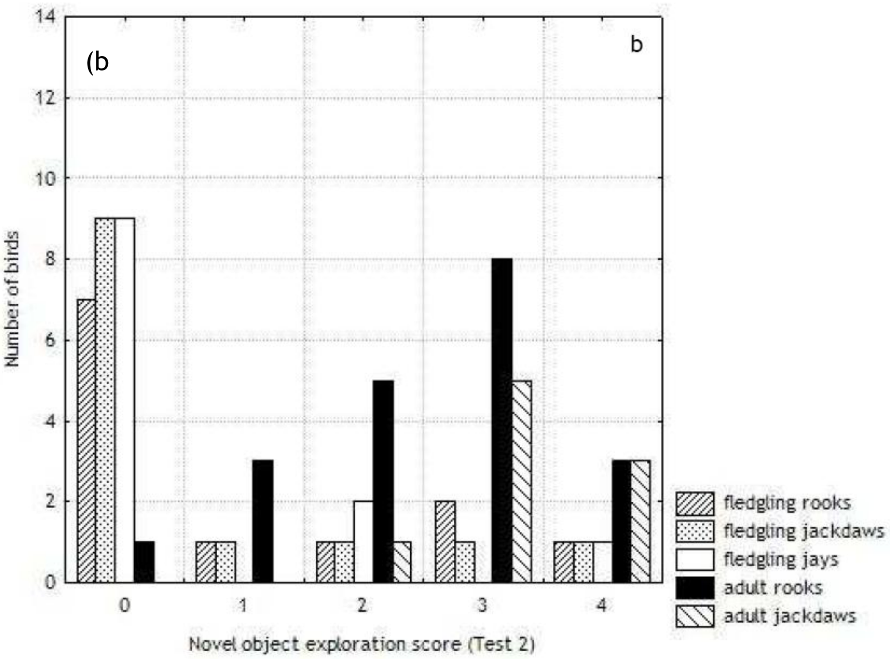


Figure 47. Exploration scores for 12 young and 20 adult rooks, 15 young and 9 adult jackdaws and 12 young Eurasian jays during a 10 min test period. Scores were based on how close the animals approached the novel object in the first (a) and second (b) test: 0 = no approach, 1 = to within 1 m of the object, 2 = to within 50 cm, 3 = to within 20 cm, 4 = touched the object with its beak.

Latencies to approach the object within 20 cm were similar in the first and second novel object test. Most animals either approached the object in the first 3 min or did not approach at all (Fig. 48). There was more variation in the latencies in the first than in the second test, with more individuals of each species approaching the object within 20 cm between 200 sec and 600 sec.

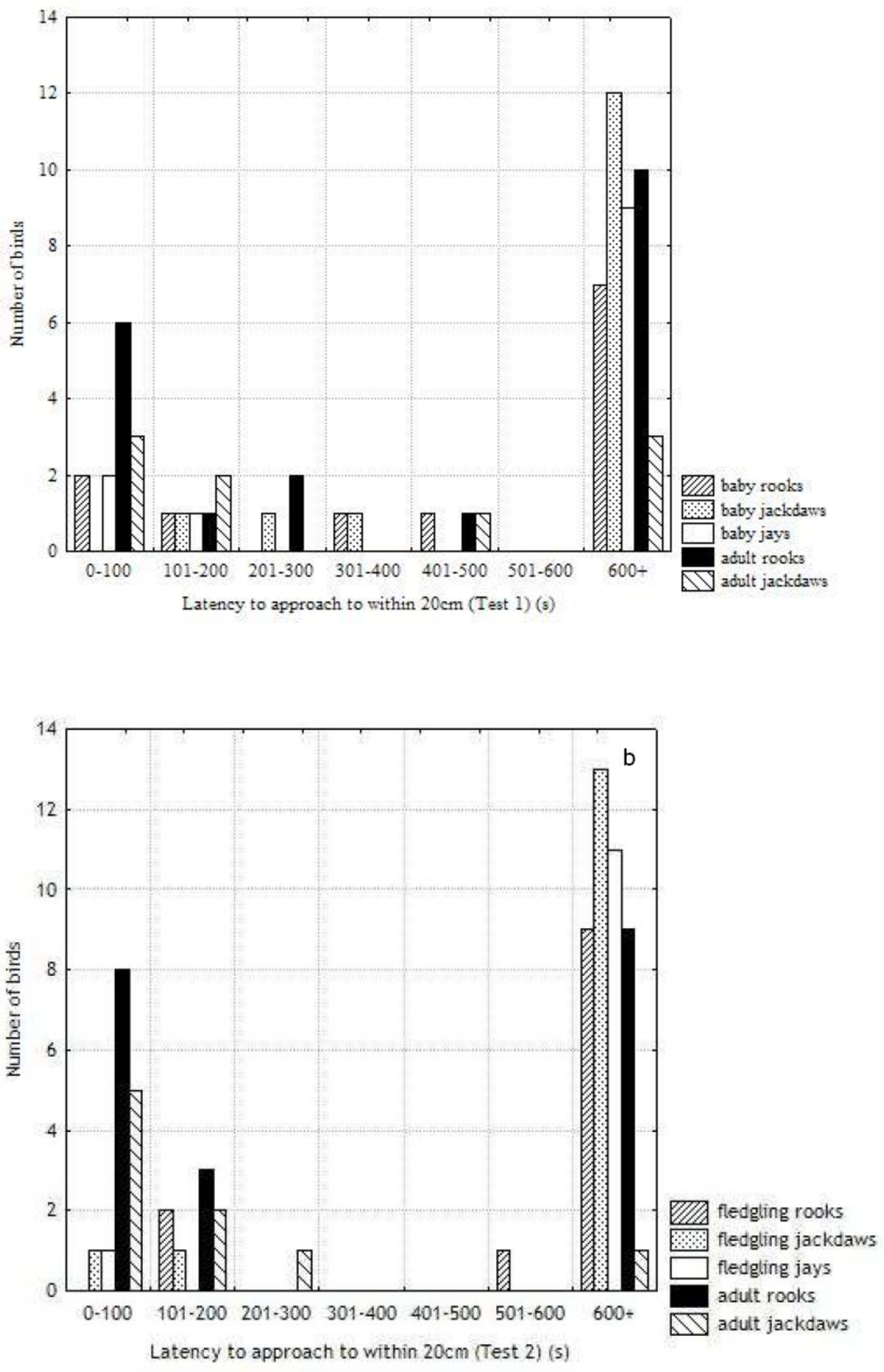


Figure 48. Latency to approach the novel object in the first (a) and second (2) test for 12 young and 20 adult rooks, 15 young and 9 adult jackdaws and 12 young Eurasian jays during a 10 min test period.

6.4.3 *Consistent individual differences?*

6.4.3.1 Correlations within test conditions

In both novel object tests, latencies to approach the object within 20 cm did not correlate in most of the groups, but there was a trend towards a correlation in adult rooks (Spearman rank order correlations: Table 31).

Table 31. Results of Spearman rank order correlations between novel object tests 1 and 2 to for latencies to approach the object within 20 cm.

	N	R	P
Fledgling rooks	12	0.409	0.186
Fledgling jackdaws	15	0.259	0.351
Fledgling jays	12	0.401	0.196
Adult jackdaws	9	-0.237	0.539
Adult rooks	20	0.407	0.075

In the Eurasian jays, the birds that were faster to approach the object within 50 cm in the first novel object test were the same individuals that were also faster in the second novel object test (Spearman rank order correlation: $R = 0.96$, $N = 12$, $P < 0.001$). A similar result was found for the fledgling jays and also the fledgling jackdaws for approaching the objects in the two tests within 1 m (fledgling jays: $R = 0.85$, $N = 12$, $P < 0.001$; fledgling jackdaws: $R = 0.57$, $N = 15$, $P = 0.027$).

Some measures of the novel environment test correlated in the fledglings of the three species (Table 32). In the adult jackdaws, only two measures correlated: the faster the birds were to approach the fifth tree, the more trees they visited in total. In the adult rooks, all measures correlated; the latency measures correlated positively, meaning that the faster the birds were to approach a tree, the faster they were to approach the next tree. Latency measures and total number of trees visited correlated negatively; a high latency to approach any of the 5 trees thus predicted a low number of trees visited (see Table 32).

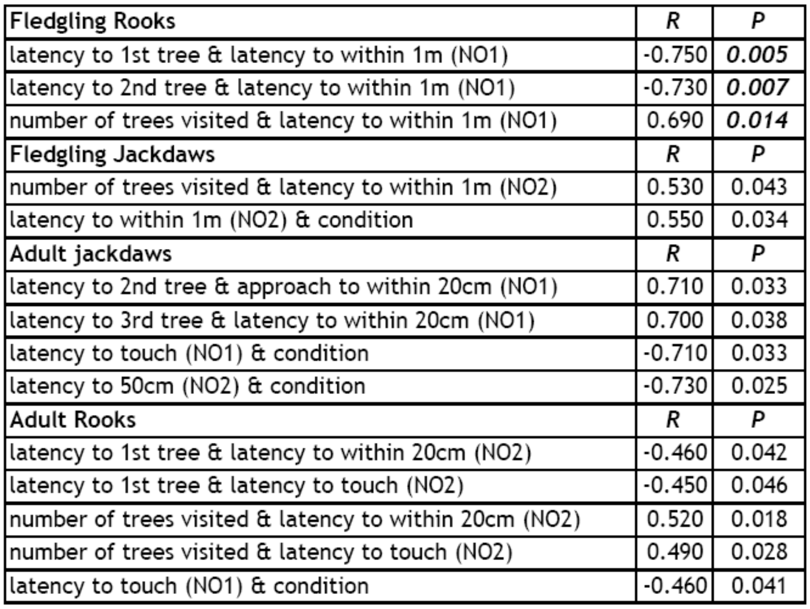
Table 32. Results of Spearman rank order correlations for measures of the novel environment test (20 min test period) for the 5 bird groups (12 young and 20 adult rooks, 15 young and 9 adult jackdaws and 12 young Eurasian jays). Latencies to approach each of the 5 trees and the total number of trees visited are correlated. Significant results and trends are reported. Empty cells represent calculations that were unfeasible, because of equal measures in the two groups (e.g. when all of the individuals reached the maximum latency of 1200 s for the second and third tree).

	Fledgling rooks		Fledgling jackdaws		Fledgling jays		Adult jackdaws		Adult rooks	
	R	*P*	*R*	*P*	*R*	*P*	*R*	*P*	*R*	*P*
1st & 2nd	0.960	<0.001	0.370	n.s.	0.400	n.s.	0.530	n.s.	0.750	<0.001
1st & 3rd	0.740	0.006			0.400	n.s.	0.560	n.s.	0.710	0.001
1st & 4th							0.480	n.s.	0.580	0.007
1st & 5th			-0.710	0.003			-0.070	n.s.	0.430	0.058
1st & no trees	-0.950	<0.001			-0.860	<0.001	-0.080	n.s.	-0.700	0.001
2nd & 3rd	0.660	0.021			1.000	<0.001	-0.560	n.s.	0.910	<0.001
2nd & 4th							-0.160	n.s.	0.660	0.002
2nd & 5th							0.160	n.s.	0.560	0.010
2nd & no trees	-0.920	<0.001	-0.710	0.003	-0.550	0.065	0.140	n.s.	-0.840	<0.001
3rd & 4th							-0.570	n.s.	0.740	<0.001
3rd & 5th							-0.130	n.s.	0.570	0.009
3rd & no trees	-0.840	0.001					0.110	n.s.	-0.840	<0.001
4th & 5th									0.720	<0.001
4th & no trees									-0.860	<0.001
5th & no trees							-0.820	0.007	-0.700	0.001

6.4.3.2 Correlations between test conditions

I analysed the association between measures of the novel environment test, the novel object tests and the condition (weight/tarsus length) of the birds using Spearman rank correlations. None of the measures correlated for the Eurasian jays. In the other species groups, various measures of the two tests correlated. In both jackdaw groups and the adult rooks, some novel object test measures correlated with body condition (Table 33).

Table 33. Significant results of Spearman rank order correlations of measures of the novel environment test (20 min test period), novel object tests (10 min test period each) and condition (weight in g/tarsus length in mm) for 12 young and 20 adult rooks and 15 young and 9 adult jackdaws.



Fledgling Rooks	*R*	*P*
latency to 1st tree & latency to within 1m (NO1)	-0.750	***0.005***
latency to 2nd tree & latency to within 1m (NO1)	-0.730	***0.007***
number of trees visited & latency to within 1m (NO1)	0.690	***0.014***
Fledgling Jackdaws	*R*	*P*
number of trees visited & latency to within 1m (NO2)	0.530	0.043
latency to within 1m (NO2) & condition	0.550	0.034
Adult jackdaws	*R*	*P*
latency to 2nd tree & approach to within 20cm (NO1)	0.710	0.033
latency to 3rd tree & latency to within 20cm (NO1)	0.700	0.038
latency to touch (NO1) & condition	-0.710	0.033
latency to 50cm (NO2) & condition	-0.730	0.025
Adult Rooks	*R*	*P*
latency to 1st tree & latency to within 20cm (NO2)	-0.460	0.042
latency to 1st tree & latency to touch (NO2)	-0.450	0.046
number of trees visited & latency to within 20cm (NO2)	0.520	0.018
number of trees visited & latency to touch (NO2)	0.490	0.028
latency to touch (NO1) & condition	-0.460	0.041

To determine whether either the weight (in g) or the tarsus length (in mm) could predict approach behaviour in the novel object tests, I conducted additional correlations with the novel object measures that initially correlated and just the weight or the tarsus length. In the fledgling jackdaws, both weight and tarsus length correlated with the latency to approach the object within 1 m in the second novel object test (Spearman rank correlations: weight: R = 0.64, N = 15, P = 0.010; tarsus length: R = 0.53, N = 15, P = 0.041).

In the adult jackdaws, only body weight correlated with the measures that originally correlated with condition (latency to approach the object within 1 m in the first novel object test: R = -0.71, N = 9, P = 0.032; latency to approach the object within 50 cm in the second novel object test: R = -0.68, N = 9, P = 0.032).

Whilst these measures correlated positively in the young jackdaws, they correlated negatively in the adult birds. When the latency to touch the novel object in the first test for the adult rooks was correlated with weight and tarsus length, the effect disappeared (weight: R = -0.34, N = 20, n.s.; tarsus length: R = 0.16, N = 20, n.s.).

6.5 Discussion

The aim of the study described in this chapter was to determine species, age and individual differences in three corvid species. I investigated the relationship of the responses in two novel contexts and linked the responses to body condition.

6.5.1 Age and species differences

Species differed in latency to approach trees and objects. Adult jackdaws were faster explorers in the novel environment test than young rooks and Eurasian jays and than the jays in the novel object tests. Adult rooks were more explorative than young jackdaws and jays in the novel environment test and faster explorers in the novel object tests than the young jackdaws and jays. However, these species differences may be confounded by the influence of age. In direct comparison, adult jackdaws were more explorative than adult rooks, which may reflect a difference based on ecological differences between the two species. Both species are highly social, roost and forage in groups and exhibit stable pair-bonding, usually for life (Emery et al. 2007).

The main difference between the two species lies in their foraging behaviour, with the rooks being classified as moderate cachers, whereas the jackdaws hardly ever cache, i.e. hide, food (de Kort & Clayton 2006). Having to find potential cache sites and to be vigilant towards others’ behaviours, one might expect cachers to be more explorative than non-cachers. However, the opposite may also be true. Rooks may take more time to observe their surroundings and pick a potential site, whereas jackdaws may simply explore their surroundings without having to pay attention to others and may therefore end up visiting more sites than the rooks. In an unrelated study, jackdaws were found to be less attentive to their conspecifics than ravens, which was suggested to be because there is less fierce competition over food in jackdaws (Scheid et al. 2007; for a description of social foraging in jackdaws see Röell 1978). However, rooks and jackdaws are often found to live in mixed groups and may therefore experience similar pressures when foraging. An alternative explanation is that there may be a more basic difference in the rooks' and jackdaws' information processing capabilities. Jackdaws appear to generally have great difficulties remaining in one place for long and lack concentration when trying to focus on cognitive tasks (personal observation). For example, when tested in a food-finding task, jackdaws performed worse than ravens in trials with long presentation times, suggesting that the jackdaws were worse at perceiving and/or processing information, which may be due to their short attention span (Mikolasch et al. 2009). Jackdaws, therefore, may lose interest quicker than rooks, which in turn may have lead to them being fast explorers, often shifting attention from one task to the next. Indeed, this would be important when capturing flying insects, their main source of food, compared to rooks who tend to spend longer foraging in soil.

Age differences were found for both rooks and jackdaws. Surprisingly, the adults of both groups visited more trees in the novel environment test and approached the novel objects faster than the fledglings. This study was conducted before the time during which these species naturally become more neophobic after fledging (i.e. late summer, personal observation). Before this major change occurs in the corvids' life, fledglings are thought to be much less neophobic than adults. A similar result has been found with Gouldian finches (*Chloebia gouldiae*), where younger birds were slower at approaching a familiar feeder that had a novel object attached to it (Mettke-Hofmann 2009). Two main factors could account for the age differences in rooks and jackdaws. First, younger birds may have been in a less agile phase of their development at the time the study was conducted than adult birds. Second, and perhaps more likely, living in captivity and the resulting experience of performing in experiments and manipulating various objects may have had an effect on differences between young and adult birds. Adult birds have lived in captivity for much longer than the fledglings and had therefore encountered many different experimental settings and been in contact with a range of experimental apparatuses and objects in their aviary. This may have led to a general habituation effect towards novel situations (Reale et al. 2007).

6.5.2 Individual differences

Great inter-individual variation was observed in each of the species for both the novel environment test and the novel object tests. Individual differences were found with how many trees the birds visited, how fast they approached the first tree and the objects and how close they approached the objects. Interestingly, various measures of novel environment exploration were associated for rooks and jackdaws, but not the jays, whereas measures of novel object exploration were not associated (with two exceptions). Novel object tests using two different objects were conducted to rule out different behavioural responses to objects based on reactions to specific features of one of the objects and to produce some level of repeatability, i.e. consistency over two similar contexts. However, small changes in an animal’s environment may elicit absolute differences in behaviour, rather than relative ones that would be stable over the two contexts. Hence, two contexts, which are seemingly comparable to an experimenter, may be perceived as different by animals. Two different objects in the same familiar environment may be perceived by animals as representing two different contexts altogether, thus ‘micro-environmental effects’ may change the expression of behaviour (Henderson 1990; but see Réale et al. 2007).

Furthermore, measures of the two novel object tests may not correlate due to the individuals’ differentially general habituation to novelty itself, thus demonstrating how fast they can adapt to the novel situation with experience, i.e. over 2 trials (Réale et al. 2007). If all the individuals' relative values had remained the same, then a general tendency to habituate to novelty may have been assumed, indicating an effect of experience or habituation on the response to the test situation (Réale et al. 2007; for a summary on whether experience can influence 'behavioural syndromes' see Sih et al 2004, p. 375). Since this does not seem to be the case here, it appears that individuals either differed in their ability to adapt to new situations - i.e. in their behavioural plasticity in this context - or the second novel object elicited different responses in the birds that - on a relative scale - were not similar to the responses to the first object.

In the novel environment test, a variety of measures correlated for most of the species. In the adult jackdaws, only the latency to approach the fifth tree seemed to be associated with how many trees they visited. By contrast, all measures that were analysed were found to correlate in the adult rooks. The most accurate predictor of exploratory behaviour in the novel environment test was the latency with which animals approached the second tree: the faster that tree was approached, the more trees were visited overall.

6.5.3 Consistent individual differences: correlations between measures?

Some of the measures of the two exploration tests correlated for the rook and jackdaw groups, but not for the Eurasian jays. The results roughly suggest that individuals that approached a higher number of trees also approached novel objects faster. In addition, subjects that were faster at approaching the first, second or third tree were faster at approaching novel objects. A similar result has been found for ravens, where individuals fell into two groups: slow and fast explorers (Range et al. 2006). A potential explanation for this may be the varying abundance of food resources, leading to selection, most likely acting in more than one direction (Roff 1997), giving rise to variation, i.e. individual differences, based on fluctuating selection pressures (Van Oers et al. 2004c) and thus differential fitness pay offs (Dall et al. 2004). Ravens, but also rooks and jackdaws experience varying levels of food abundance in their environment, which could lead to consistent behaviour and thus to the co-existence of slow and fast exploring individuals (Wolf et al. 2007).

Exploratory behaviour may also be influenced by varying levels of neophobia. Schneirla (1965) accounts for such responses to novel stimuli in his biphasic ‘approach/withdrawal theory’. By taking into account social and other stimuli, Schneirla discusses how stimuli in an animal’s environment are approached by individuals. Behaviours that appropriately increase or decrease the distance between an animal and a stimulus source are thought to be crucial for the survival of all species. Those behaviours may be selected by environmental influences for transmission over generations. An animal that is surviving and manages to look for food or mates, but also avoids potentially dangerous situations, has developed efficiencies in dealing with differences in the ‘stimulative intensities’ of the above mentioned different situations (Doyle 1989).

However, disentangling exploration from neophobia or even shyness/boldness has proven to be a difficult endeavour, with authors disagreeing over the issue whether exploration and boldness are identical or just influence one another, or whether they are even two different categories (for a review see Réale et al. 2007). In a classic study by Verbeek (1994)on individual differences in early exploratory behaviour of great tits (*Parus major*), three different experiments (novel object tests, a novel environment test, and a test on ‘habits in foraging’) were conducted and yielded results that were interpreted as consistency in exploration, with the quick explorers in the novel environment exploring novel objects faster, but sticking to old feeding habits in the foraging task.

By looking at the repeatability and heritability of exploratory behaviour in great tits, Dingemanse and colleagues (2002) found that heritable variation in exploratory behaviour exists in wild great tits. In two further studies, the authors tested *boldness* by looking at novel object tests and *exploration* in a novel environment, combining them afterwards as early exploratory behaviour (van Oers et al. 2004a, 2004b). Réale and colleagues (2007) state in their review paper that ‘given the strong correlation’ of the two factors boldness and exploration, they ‘should be regarded as the same temperament trait’. Nevertheless, in their list of categories, shyness-boldness are described as a separate category to exploration-avoidance (alongside activity, aggressiveness and sociability; Réale et al., 2007). Whereas shyness-boldness is defined as an animal’s reaction to any risky situation, apart from new situations, exploration-avoidance is the reaction to a new situation, suggesting it could be examined using novel object and novel environment tests. Furthermore, the authors state that neophobia (or neophilia) is considered a part of exploration and would most likely also be the main target of selection (for a study on the influence of neophobia on individual differences in exploration see Greenberg & Mettke-Hoffmann 2001).

However, my results have to be observed with caution as not many of the measures were associated and also which measures were correlated seemed to be subject to differences between the species. Interestingly, none of the measures correlated for the Eurasian jays. For this species, the results paint a completely different picture. The lack of correlation between object exploration (novel object tests) and spatial exploration (novel environment test) suggest that exploratory behaviour in the two different ‘novel’ contexts was a result of two different underlying processes, at least in the jays.

From an anthropomorphic perspective, it seems likely that ‘fast explorers’ or ‘bold’ individuals would act similarly in both a novel environment and when confronted with a novel object in a familiar environment, thus acting on the basis of a *behavioural syndrome* (e.g. a suite of correlated behaviours reflecting between-individual consistency; Sih et al. 2004). However, corvids, and Eurasian jays especially, may have perceived the two contexts as completely different situations and may therefore not react in a similar way to them both (‘similar’ in a relative sense, i.e. the absolute values may change, but the relative scores of each individual stay the same).

It appears that the reaction of the birds to the two different contexts may be based on two different factors, rather than two separate traits, that would feed into the same factor (e.g. in humans, interest in sex, ambition, competitiveness, enjoyment of travel and desire to be famous are all correlated, which all feed into the factor ‘extraversion’; Nettle 2005).

6.5.4 Individual differences and physical condition

In both age classes of jackdaws and in adult rooks, physical condition was associated with the latency to approach novel objects. Whereas in rooks, the weight per tarsus length seemed to have an effect, in jackdaws the tarsus length and/or the weight itself also correlated with latency to approach. Interestingly, the heavier the fledglings were, the faster they approached the objects. In adult jackdaws, the effect was reversed.

6.5.5 Implications for cognition research with corvids

These findings may have implications for animal cognition research, as animals with different personalities may also react differently to the same treatment and solve tasks differently. Animals that are slow to approach novel objects or to explore a novel environment may also approach unfamiliar test apparatuses slower. Depending on what is important for a given task, one therefore has to be aware of the described effect and aim for a representative sample of test subjects out of an available pool of animals. Picking test subjects at random out of a group will lead to variation in approach latencies in cognitive tasks.

However, the following phenomenon is commonly observed: a few animals are selected from a group to take part in an experimental study based on favourable attributes, such as participation tendency. That alone could lead to skewed results, in the sense that animals that are more motivated and hence potentially more explorative are the ones that will participate, whereas the less motivated animals may not be part of the given study. Samples sizes would therefore not be representative for the whole species, but the chosen individuals would all be located at one end of the axis of exploration. Working with small sample sizes could give rise to the same problem (Taborsky 2010), hence working with captive animals and thus a restricted number of animals is likely to have an effect on results of experimental studies in terms of exploration measures. For example, when I evaluated studies conducted in our own lab using some of the 4 year old rooks that participated in the current study (Bird & Emery 2009a, b, Helme et al. 2006, Seed et al. 2006, Seed et al 2008, Tebbich et al. 2006), I found that the same 7 or 8 birds participated in these studies. This could have led to the above described effect (animals that are more motivated are the ones that will participate), had researchers been recording approach latencies or other measures of exploration, rather than, say, percentage success.

The animals that were chosen in those studies were roughly the ones that explored a high number of trees in the novel environment test of this study. By looking at other measures, such as the latency to approach a novel object, I could not pinpoint a difference between the individuals that participated in the studies and the ones that did not. However, tendency to explore may not just have an influence on how fast or how thoroughly a novel situation is explored, but may also have indirect effects on cognitive tasks, such as performance in discrimination experiments (e.g. ravens; Range et al. 2006). Choosing test subjects to participate in a study therefore seems to be the first crucial step that could greatly influence the outcome of a study - influenced both directly and indirectly by individual differences in exploratory behaviour.

Future work should therefore test in more detail how exploratory behaviour in the two different contexts (exploring a novel object and a novel environment) are related and in what other categories individuals of the same species may differ that could influence task performance in cognitive tests. To further determine the influence of individual differences in corvids on relevant behaviours in experimental studies, it would be interesting to study exploratory behaviour in relation to individual and social learning (suitable tasks have to be selcted, see *Chapter 7*), dominance ranks, aggressiveness, and other social factors. This could also lead to establishing potential predictors of exploratory behaviours, such as the physical condition of an individual, as discussed earlier.

Further work should also investigate to what extent individual differences are stable across time and contexts. Behavioural syndromes seem to limit behavioural plasticity (Sih et al. 2004) and would therefore influence an animal's behaviour in an experimental context, as well as individual fitness. From an adaptive perspective, fitness payoffs should depend on both the frequency of occurrence of competing strategies, such as bold and shy individuals, and an individual's behavioural history (Dall et al. 2004). We thus suggest that finally, future work should examine the levels of heritability of personality traits in corvids and their adaptive value to 1) reveal the significance of individual differences in these bird species for experimental work and 2) place individual differences in corvids within a framework of ecology and evolution.

6.6 Conclusions

In this study, I have established species, age and individual differences in three corvid species in response to two tests of novelty and exploration. However, those individual differences were not consistent across contexts. I would like to highlight the fact that different tasks, that appear to measure the same underlying processes, may be perceived very differently by animals. To human eyes, seemingly similar contexts may be processed by two distinct underlying mechanisms and therefore elicit different responses in the test subjects.

It may be vital as a first step to establish domain-specific individual differences (correlates of measures within contexts), before broader categories, i.e. correlations between the different contexts can be determined (D. N. Lee, personal communication). Individual differences in exploratory behaviour appear to have a direct effect on approach behaviour and thus potentially also an animals’ performance in cognitive tasks. Depending on what kind of behaviour is investigated in a given study, one should therefore consider not only which model species to choose to answer a research question, but also take into account other factors, such as the age of the test subjects and their physical condition.

Chapter 7. General discussion

7.1 Introduction

The overall objective of this thesis has been to investigate social learning in rooks and jackdaws, using different methodologies and analysing the findings within a framework of ecology, ethology and evolution. As sociality is often seen as a prerequisite to social learning, I studied the social structure in groups of the social rooks and jackdaws and the territorial Eurasian jays. Focus was the two main factors that contribute to structuring a group: social bonds and dominance hierarchies. Moreover, it seems likely that individuals within a species differ and that those differences influence their performance in cognitive tasks, such as social learning experiments. I thus determined individual differences between members of the same species along the bold-shy axis.

The important findings of this thesis are (1) the social structure is more complex in jackdaws and rooks than in Eurasian jays, (2) jackdaws learn socially and employ enhancement when doing so, (3) rooks seem to rely on individual learning more than social learning and (4) individual differences exist in all three species, but are not stable across contexts.

In the following sections, I will summarise the main findings of each of the studies and discuss them in the light of the species' ecology and the relevant literature. Furthermore, I will discuss methodological difficulties and strategies for overcoming them as well as future avenues of research on social learning and individual differences.

7.2 Summary and discussion of the main findings

In *Chapter 1* I introduced a new framework for studying social learning in animals. I emphasised the importance of integrating the various different approaches to the field, first and foremost the two main approaches: psychology and biology. When studying the underlying social learning mechanisms in a species, it is useful to consider its ecology (the constraints on cognition due to environment), its ethology (natural behavioural repertoire) and its evolutionary history. Considering these factors yields two advantages over using the classic approaches: (1) they lead to a more unified picture of the studied phenomenon, and (2) they add ecological validity to the proposed conclusions. Such an approach will thereby aid researchers when interpreting findings and designing experiments.

7.2.1 Sociality: Chapter 2

Chapter 2 provides what is to my knowledge the first long-term study of sociality in rooks and Eurasian jays (a comparable study on jackdaw sociality to the one presented here was conducted in 2006 (von Bayern 2008). In it I investigated the existing social bonds and dominance hierarchies in adult rook and jackdaw populations and their establishment in fledgling rooks, jackdaws and Eurasian jays. Relatively stable social bonds and dominance hierarchies existed from the onset of the study in adult rooks and jackdaws; fledgling rooks and jackdaws developed bonds and hierarchies over the course of the observation period, although only a few bonds seemed to become stable. Pair bonds were developed when jackdaws were approximately 8 to 10 months and rooks were 6 to 8 months old. The hierarchies never reached significant linearity. Eurasian jays did not form bonds or establish a hierarchy. Based on this finding, I conclude that the jays' social structure is less complex than that of rooks and jackdaws.

As summarised *Chapter 2*, Eurasian jays are territorial birds that defend their territory all year round and only spend time with members of the opposite sex during the breeding season. Rooks and jackdaws, on the other hand, are highly social corvids that form big groups with the mated pair as the core unit. Both species stay in life-long pairs, the members of which associate throughout the whole year (Coombs 1978, Cramp & Perrins 1994, Emery et al. 2007, Goodwin 1986, Lorenz 1970, Roëll 1978. Members of a pair exhibit paired affiliative behaviours, such as preening, food-sharing, displaying and post conflict third-party affiliation, and synchronise their behaviours (de Kort et al. 2006, Emery et al. 2007, Seed et al. 2007, von Bayern et al. 2007). They can also be observed performing joint activities, such as nest-site establishment, territory defence and provisioning of the young (Emery et al. 2007, Goodwin 1986, Katzir 1983, Marshall & Coombs 1957, Roëll 1978, Røskaft 1981). The cognitive abilities needed for maintaining those long-term pair-bonds have been named 'relationship intelligence' (Emery et al. 2007). Being in a relationship bears mutual benefits for both members of the pair (Kummer 1978, van Schaik & Aureli 2000). In captivity, where individuals of each sex are a limited resource, same-sex pairs are relatively common. I discovered same-sex pairs with stable social bonds in one of the adult rook groups and in the adult jackdaw group. This agrees with earlier studies of jackdaw groups (Katzir 1981, Roëll 1978, von Bayern 2008, Wechsler 1989) and indicates cases of homosexuality (Bagemihl 1998, Poiani 2010) or an effect of captivity.

Outside of the pair bond, jackdaws and rooks socialise with other group members when roosting, foraging and breeding (Coombs 1960, Emery et al. 2007, Røskaft 1980). Breeding takes place in huge colonies, but micro-territories are maintained within those colonies (Roëll 1978, Røskaft 1982). One reported winter roost of rooks consisted of 60,000 individuals (reported in Clayton & Emery 2007). Such high levels of sociality provide individuals with opportunities to learn from one another and might also facilitate social information use.

7.2.2 Social Learning: Chapters 3, 4, 5

In *Chapters 3, 4*, and *5,* I investigated social learning in rooks and jackdaws. For the first two chapters I worked with jackdaws and used two different methodologies: the experiments for *Chapter 3* were conducted in a classical 'one-on-one' setting, with one observer watching one demonstrator and individual test sessions after observation sessions; in *Chapter 4,* I used a more natural setting and conducted both observation and test session in a group. For *Chapter 5* I tested rooks with a relatively new technique, showing them videos of a rook demonstrator opening an apparatus and then testing them with the actual apparatus. I found that jackdaws use social learning and most likely employ enhancement, which is in line with previous findings (Schwab et al. 2008). Rooks do not seem to utilise social information, but rely on individual trial-and-error learning.

Chapter 3 was conducted with a relatively small sample size of four observers and four non-observers, which raises issues of statistical validity (Taborsky 2010) and makes it difficult to draw general conclusions about the social learning abilities of jackdaws as a species from the study. However, the study indicated which points to pursue and thus set the basis for a broader follow-up study (*Chapter 4*). The study in Chapter 3 involved a two-action task, in order to determine the social learning mechanism involved. Because both actions were performed at the exact same point of the apparatus and led to the same outcome, such a task should have allowed me to rule out simpler forms of social learning, such as local/stimulus enhancement and facilitation, provided preferential performance of one action (e.g. pecking) is found in one observer group and preferential performance of the other action (e.g. pecking) is found in the other group (Akins & Zentall 1996, Dawson & Foss 1965). Such a finding would indicate imitation as the underlying mechanism.

Therefore, over the course of a few months I trained two demonstrators on either pecking at or stepping on a wooden treadle to open an apparatus containing mealworms, which are the preferred food of jackdaws. After a few weeks, the demonstrator that was being trained on stepping refused to continue opening the apparatus and therefore had to be excluded from the study. In order not to further decrease the sample size I continued the experiment without that demonstrator and consequently used one observer group and one non-observer group instead of two observer groups. Both groups were habituated to the apparatus: observers watched the demonstrator opening the apparatus before they were given access to the apparatus and non-observers were allowed to 'watch' the apparatus plus the demonstrator in an adjacent compartment for the same amount of time. This was done to rule out the lack of social stimulus close to the apparatus as an influencing factor. I found that only one non-observer even opened the apparatus and seemingly not deliberately. All four observers opened the apparatus on their first attempt and on all subsequent trials and manipulated the apparatus more often than the non-observers. The observers did not only peck at the apparatus, but also stepped on the treadle. Thus, they did not consistently copy the exact action that was demonstrated in the demonstration sessions, i.e. pecking. I concluded that the employed mechanism could potentially be local/stimulus enhancement or emulation. Following the line of parsimony, it seemed more likely that the jackdaws would employ enhancement, but to be sure, I conducted a follow-up study.

For *Chapter 4* I conducted a similar social learning experiment, but in a group setting. I found a difference in performance between observers and non-observers which provided evidence for social learning in jackdaws and confirmed the findings of *Chapter 3*. Local/stimulus enhancement seemed to be the underlying social learning mechanism that was employed by the birds. For this study, I improved a few factors from the previous study. First, the sliding door of the apparatus was made transparent, so that the jackdaws could see the mealworms inside the apparatus at all times. Although the birds had seen the reward inside the habituation apparatus, it is possible that they were not able to transfer this information from the habituation apparatus to the test apparatus. Being able to see the worms ensured high motivation levels. Second, a perch was mounted next to the treadle. This change was included to encourage the birds to sit nearby and may thus have facilitated manipulation of the apparatus and/or opening attempts. Third and most importantly, the two actions that could be performed to open the apparatus were changed so that the birds now had to perform both actions with the same body part, the beak, by pushing or pulling. Information on actions performed with different body parts, e.g. the feet and the beak, might be processed differently, whether in the motor system in the case of an observer having to perform the action in the test sessions, or in the perceptual and memory system when the observers perceived the actions during the demonstration sessions. The fact that the feet were further away from the visual field than the beak when an action was performed could have also had an influence.

In addition to changing the two actions, I created a more natural situation with a change in the set up: I conducted this second experiment with the jackdaws in their group, which means that all birds could watch demonstrations at the same time and then gain access to the apparatus in the test session at the same time (in total, two observer groups were tested). This method, however, had the disadvantage of restricting access to the apparatus for the subdominant birds, since the dominant birds monopolised it at times. I therefore decided to exclude dominant birds from test sessions after they had opened the apparatus a fixed number of times.

I discovered that the observers spent more time close to the apparatus than the non-observers and that they also manipulated the apparatus more often than the non-observers, and therefore this provides evidence for social learning. Observer groups differed in that only one of the groups ever opened the apparatus. The individuals of that group opened the apparatus early on in the test sessions. There was seemingly no influence of the number of openings they had observed others perform before they opened the apparatus for their first time. Furthermore, the number of times they manipulated the apparatus did not affect how quickly they managed to open it. Two factors did have an influence on the time it took the animals to learn how to open the apparatus: the number of manipulations at the wooden ball that they either had to lift or push in to open the apparatus and the number of worms gained prior to opening the apparatus.

Some studies have found an influence of scrounging on social learning (e.g. marmosets: Caldwell & Whiten 2003), but in others scrounging seemed to hinder social learning (e.g. pigeons: Giraldeau & Templeton 1991). In the study in *Chapter 4*, dominant animals tried to monopolise the apparatus, spent more time at it and manipulated the relevant parts of it more often than lower-ranking animals. The individuals that learned how to open the apparatus exhibited different patterns in terms of performance over time: two improved, one worsened and three did not change. Overall, I concluded that an initial local/stimulus enhancement effect was followed by individual trial-and-error learning, which led to only one group learning how to open the apparatus.

In *Chapter 5*, I tested rooks' ability to use social information and found that they did not take advantage of it. One possible reason for animals not using social learning in experiments is related to attention. This study addressed one of the major problems that I encountered over the course of the previous two social learning studies, namely that observers do not always pay attention to demonstrators when they are performing the desired action. Additionally, demonstrators do not always demonstrate the action when the observers are watching. In the rook study, tried to bypass these problems by showing the subjects videos of demonstrators opening the test apparatus, a technique that has been used with birds (e.g. budgerigars: Mui et al. 2008, rooks: Bird & Emery 2008). Individuals watched the videos (which was clear due to cameras in the test compartments that enabled me to watch the rooks looking through a peephole when watching the videos), but subsequently failed to use the social information provided by them. Only two birds successfully opened the apparatus, but reached that goal by trial-and-error learning. In the discussion of *Chapter 5* I listed the steps involved in social learning from videos: watching the videos, processing and then translating the information they contain, approaching the apparatus and, finally, performing the action. The rooks could have failed at any one of those steps, and although some ‘errors’ seem less likely than others, one cannot completely rule them all out. Overall, it seems that the successful subjects used individual rather than social information, as indicated by the shaping process that could be observed over the course of the trials: although in the beginning the birds manipulated the apparatus at many different spots, in the later sessions, their actions became much more goal-oriented and were mainly directed at the release mechanisms. Furthermore, latencies to approach and manipulate the apparatus decreased. As an alternative to failing at one of the necessary steps involved, or even as an explanation for it, I would like to propose that rooks may not need to be able to employ complex social learning mechanisms. Instead of not being able to learn socially altogether, it is also possible that they are indeed capable of employing local enhancement, as was found in earlier studies (Waite 1981), but did not use it in this study, because of neophobia.

Chapters 3, *4* and *5* tell us that high levels of intelligence do not necessarily entail complex behaviours. One might question why, if jackdaws and rooks are indeed so ‘brainy’ (Clayton & Emery 2004, Emery 2006), they do not employ complex social learning mechanisms? This is where environmental influences come into play; costs and benefits of behaviours could actually influence which kind of social learning mechanism is used. If a certain type of behaviour is not needed in one’s day-to-day life, why should one be able to perform that kind of behaviour? Saving time and energy, one should perform *sufficient* behaviours (i.e. those that do not cost a lot of time and energy, but still fulfil the needs) and thus employ the social learning mechanism that is *sufficient* in a given situation.

As discussed in *Chapter 1* and *3*, the feeding ecology may play an important role here. Species that only need to locate food, but not learn how to process it, would not need a mechanism more complex than local/stimulus enhancement. Two more factors could play a role. First of all, as stated by Bird (2009), certain corvid species (in his case rooks) may be driven by some sort of affinity for innovation and rapid trial-and-error learning. This affinity could even override social learning and might have contributed to the rooks' impressive performance in other tasks (Bird 2009, Bird & Emery 2008, 2009, in prep.). Secondly, it would make sense that within a group, some individuals would learn socially, whereas others would 'concentrate' on individual information to ensure the spread of new, up-to-date information, especially in changing environments (Boyd & Richerson 1988). A balance of social learners and individual learners/innovators within a population would on the one hand guarantee passing on of new innovations, such as the location of a novel food resource, and on the other hand stop outdated information from spreading, since there would be innovators producing new information that could then be gained by conspecifics. Another potential influence on varying levels of social information use is individual differences, and therefore this was the subject of the next investigation.

7.2.3 Individual Differences: Chapter 6

In *Chapter 6* I investigated individual differences between members of the same species. I tested all six groups of rooks, jackdaws and Eurasian jays in two different experiments. Novel object tests were conducted to measure levels of exploration and neophobia to those objects in a familiar environment, and a novel environment test was conducted to measure differences in exploration and neophobia. I found that levels of exploration/neophobia varied between individuals in a species in both of those contexts (context here means the situation the birds faced in the novel environment test or the novel object tests). The results from the two contexts did not correlate, nor did the results from the two novel object tests with each other. Correlations would be expected if behavioural syndromes existed in the corvid species.

Such suites of correlated behaviours across situations can be found when investigating aggressive behaviour, for example, where some individuals are more aggressive than others across a range of different situations (Sih et al. 2004a). The prevailing view in current literature is still that different contexts of exploration/neophobia should be processed in similar ways and thus measures of those contexts should be correlated (Sih et al. 2004a). It makes sense that testing individuals in two contexts in which they explore a novel situation and have to overcome their neophobia should lead to results reflecting between-individual consistency across those contexts. But this was not the case in my study. Although such between-individual consistencies across situations of exploration/neophobia exist for some bird species (for a review see Sih et al. 2004b), we should not let our anthropomorphic view of the 'similarity' of those contexts lead us to believe that this is necessarily true for all (bird) species. In *Chapter* 6, I therefore proposed the following: the three corvid species I studied seem to have perceived the two seemingly similar contexts as two different situations, and the information was therefore processed by two distinct underlying mechanisms, which elicited different responses in the birds.

7.3 Future directions

The findings of this thesis have several implications, both in terms of potential future experiments and in terms of additional analysis of existing data. In the following section I will highlight what I see to be the most important future directions.

Much potential lies in the collected sociality data of *Chapter 2*. In that chapter, social bonds and dominance hierarchies were analysed and used to characterise the social relationships within the groups of the three species that were investigated. However, additional data was gathered that was not analysed since it goes beyond the scope of this thesis. (That data can now be analysed for future publication.) Analysing data on affiliative behaviours, play behaviours, displays and agonistic behaviours could contribute to a more complete picture of corvid sociality. Principal component and factor analysis could reveal which behaviours account for variability in the sociality data and could potentially verify the use of ‘social proximity’ as an umbrella for most affiliative behaviours in the analysis of this thesis. Additionally, a follow-up study could reveal stable pair bonds in the now mature birds that were fledglings during the time I took the data for this thesis. Looking at my data and the current pair bonds would show whether it is possible to accurately predict future pair bonds at an earlier stage in the birds’ life. Future studies should include intense data collection on displacements, as I have shown in *Chapter 2* that the number of displacements entered into data analysis has an impact on the calculation of the linearity of a dominance hierarchy. When more studies on sociality emerge, comparisons of levels of sociality and social complexity between groups of the same species would reveal potential population differences.

The social learning experiments with jackdaws indicated that this species used local/stimulus enhancement as a social learning mechanism when processing information gained by watching conspecifics access a food source. Additional controlled lab experiments with a bigger sample size would provide further clarity on the social learning mechanism. In the original study, the sample size was relatively small, and the second study was conducted in a group, so it did not include conditions as controlled as they would be in a laboratory setting. Moreover, the two-action task should be carried out with two demonstrators rather than with just one. In the second social learning study I found differences between the two observer groups, with only one of them learning how to open the apparatus. Although both of those groups were habituated to the apparatus prior to the experiment, the age difference between those groups might have had an influence. The group containing the younger birds was also the group that opened the apparatus. Lower levels of neophobia could have played a role. The study should therefore be replicated with two groups of birds of the same age. Replications of both studies would enable us to further look into how social relationships, tolerance between individuals and demonstrator identity (sex, age, dominance rank, etc.) influence social learning performance.

Rooks did not seem to learn socially. Future studies should try and achieve two things: (1) test each one of the steps in the social learning process listed in the discussion of *Chapter 5* and thereby (2) test the feasibility of using videos in social learning experiments. Additionally, ecologically more relevant experiments, i.e., with a more naturalistic test apparatus or in a group setting, could reveal the full potential of applied social learning mechanisms in rooks. Testing a larger sample size would address the issue of an ‘even’ distribution of individual and social learners within a population.

On a more theoretical level, the proposed framework of *Chapter 1* has to be extended to account for bird species, such as Japanese quail and pigeons, that employ imitation even when, ecologically, there seems to be no need for them to be able to do so (imitation in Japanese quail: Akins & Zentall 1996, Akins et al. 2002; in pigeons: Klein & Zentall 2003, Zentall et al. 2003).

To test the hypothesis that highly social animals should be better at social learning, future studies should include both social and less-social species. The Eurasian jay is an example of the latter. I was planning on conducting a social learning study with the Eurasian jays for my PhD, but the project turned out to not be feasible due to the available facilities and a few setbacks that my lab experienced during my time there. In a follow up study, similar experiments to the ones that have been conducted with rooks and jackdaws could be conducted with the Eurasian jays, and their performances could be compared. Alternatively, a whole new set of experiments could be conducted using methods that would be as similar as possible, but still within the framework of behavioural repertoire and ecological validity for each of the species.

I would like to stress the importance of adapting the methods of social learning experiments to a framework that takes the ecology, ethology and evolution of a species into account. Whereas the evolutionary influences on behaviour and underlying mechanisms might not be easy to determine, it seems relatively straightforward to include considerations of the ecology and ethology of a species when designing an experiment. For example, adding a set of experiments on individual trial-and-error learning would test whether social learning is an adaptive specialisation for group living (Klopfer 1959). When the social pinyon jays were compared to territorial Clark's nutcrackers in a social and a non-social task, the pinyon jays showed an enhanced performance in the social task compared to the non-social task. Such an enhancement of performance was not found in the Clark's nutcrackers (Templeton et al. 1999; but see also *Chapter 1*). It would be intriguing to conduct a similar study with the Eurasian jays for comparison to more social corvid species.

The studies on individual differences in rooks, jackdaws and Eurasian jays provided insight into the distribution of shy and bold individuals in each of the species. However, the results of the different tests did not correlate. This indicates that either the methods of those tests has to be improved, adapted better to the tested species or that novel object exploration and novel environment exploration are cognitively processed in different ways. Further novel object and novel environment tests and analyses for correlations between those contexts would shed light on this issue and contribute to the ongoing debate on the existence of correlations between different contexts of exploration/neophobia (i.e. 'behavioural syndromes').

A point that I would like to stress is the importance of a stepwise approach that researchers should take when investigating individual differences and behavioural syndromes. The investigation of individual differences should be the starting point of all studies into behavioural syndromes. Only when consistent individual differences in one context are established, can we go on to test for correlations between those and individual differences in potentially related contexts. For example, additional novel object tests would make correlations across a number of novel object tests possible and would consequently allow the establishment of domain-specific individual differences (i.e. correlations between repetitions of the same test with slight modifications, e.g. objects of different size, colour, etc.). Those differences can then be related to individual differences in novel environment exploration. If the measures for the two contexts are correlated, a 'new' type of behavioural syndrome for exploration/neophobia will have been established.

An additional intriguing aspect that could be investigated using a replication of this study is the influence of age. By definition, individual differences are stable over time, which means that a group of individuals could, for example, become less shy later in life, but in a relative sense the individuals of that group would remain as shy or bold as they were when they were younger. Testing the same birds again that I tested as fledglings for *Chapter 6* would reveal whether this is true for corvids.

The social learning experiments of my thesis did not allow correlations between social learning skills and individual differences, as they were not measured on a continuous scale, but rather in terms of 0 and 1. A battery of individual and social learning tests could be conducted to rate individuals on a number scale, for example 1 to 10. Experiments yielding more 'quantifiable' measures for social learning skills would enable correlation analyses. Furthermore, individual learning tasks similar to those conducted by Range et al. (2006) would allow interrelations between individual learning and individual differences to be analysed and the various influences of individual differences on individual and social learning to be compared.

7.4 Concluding remarks

This thesis has contributed to the field of animal behaviour through an investigation into three different topics - sociality, social learning and individual differences - using rooks, jackdaws and Eurasian jays. I investigated social bonds and dominance hierarchies in the three species. Furthermore, I highlighted the importance of social complexity as a basis for social learning and discussed how ecology may influence social learning skills. Whereas jackdaws seem to employ the most 'sufficient' social learning mechanism (local/stimulus enhancement), rooks revert to using individual information, which indicates species differences in the application of social learning and maybe even a more central role for individual as compared to social learning in the life of rooks. Existing individual differences, but not behavioural syndromes, further contribute to our understanding of the corvids' cognitive processing.

We now have a greater understanding of how corvids use social and individual information and how that information use is influenced by other life history factors, such as sociality and feeding ecology.

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Appendix

Examples of rook, jackdaw and Eurasian jay behaviour

Figure 49. Examples of rook behaviour: begging (a), preening (b), sunbathing (c), collecting nesting material (d).

Figure 50. Examples of jackdaw behaviour: sunbathing (a), scratching (b), collecting material for nest building (c) and a threat display (d).

Figure 51. Examples of Eurasian jay behaviour: calling (a), food caching (b) and object play (c).