



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

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

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

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

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

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

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

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

Affiliate social relations can be characterized on a number of levels (Bonnie & de Waal 2006), such as high levels of sociopositive and low levels of agonistic behaviours. Thereby, sociopositive behaviours are measured as social support, food sharing or allopreening and agonistic behaviours as approach–retreat interactions or fights. Because of our short focal period (four months) in this study we concentrated on spatial proximity as an integrative measure (Bonnie & de Waal 2006) for determining social dynamics between individuals. Close social spacing and behavioural coordination in space and time do not only need social tolerance between individuals but also include actively seeking spatial proximity of others and can therefore, be regarded as basic measures of affiliation. We first examined the social dynamics within our group of hand-raised ravens via behavioural observations. We then experimentally tested for the influence of social

dynamics on social learning performance in a stimulus enhancement task. Following Zentall's (1996, p. 229) definition 'the term stimulus enhancement is used when the activity of the demonstrator draws the attention of the observer to a particular *object*' and it is considered to involve relatively low cognitive capacities (Galef 1988). Unlike previous experiments on ravens (Fritz & Kotrschal 1999) model–observer dyads were tested in physical separation to control for effects of spatial proximity on social learning. Following the ravens' life history in nonbreeder-groups we expected that the social dynamics would not be randomly distributed in our group of juvenile hand-raised ravens. We predicted enhanced social learning performance when individuals in a model–observer dyad maintain affiliate relationships as compared with socially more distant dyads.

METHODS

Subjects and Keeping

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

Behavioural Observations

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

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

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

Composition of Experimental Model–Observer Dyads

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

Experimental Procedure

Experimental trials

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

tested twice with model and observer roles reversed and with the use of different sets of objects.

Demonstration phase

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

Test phase

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

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



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

Analysis

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

and compared between the sibling and the nonsibling condition.

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

Control trials

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

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

RESULTS

Behavioural Observations

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

Experimental and Control Trials

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

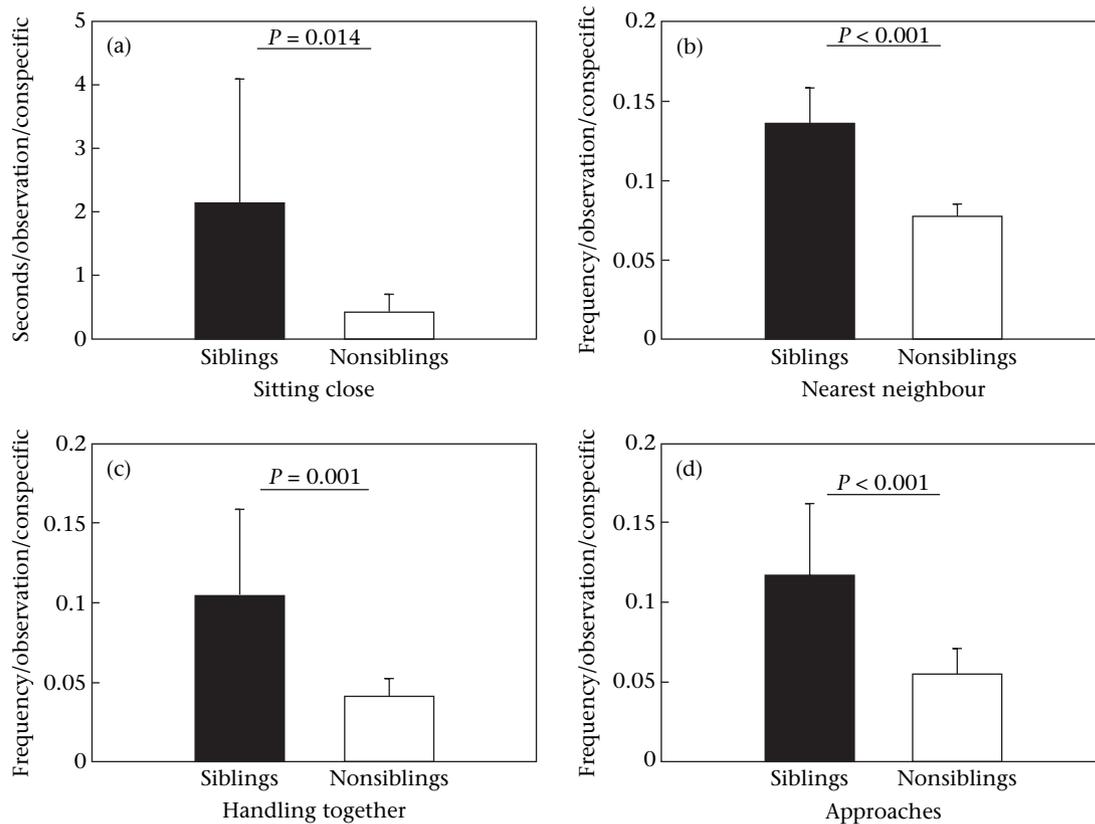


Figure 2. Behavioural observations of social interactions of birds in their social group. (a) Duration (s) birds sit close to each other, (b) frequency of being the nearest neighbour at the beginning of each observation, (c) frequency of birds handling an object together and (d) frequency of one bird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

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

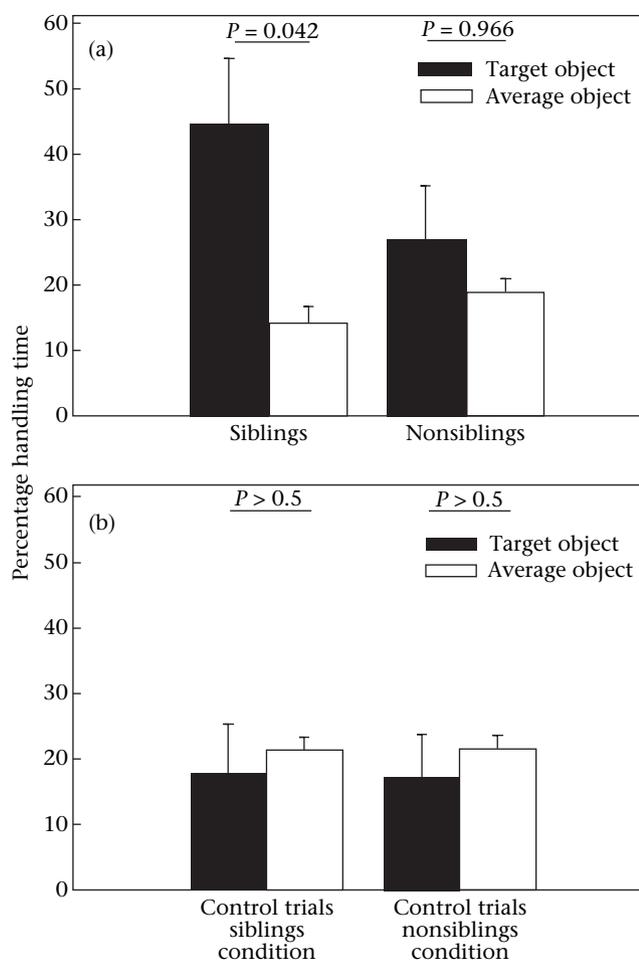


Figure 3. Percentage of time birds were handling the target object and an average of the other four available objects, both, in the sibling and in the nonsibling condition in test trials (a) and control trials (b). Black bars indicate birds' handling time of the target object while open bars indicate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

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

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

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

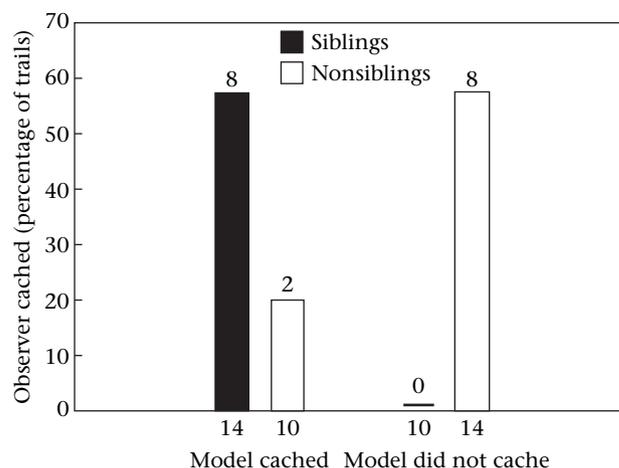


Figure 4. Caching behaviour of models and observers. Bars indicate the percentage of trials in which observers cached any object. Numbers below (models) and above (observers) bars represent the number of trials in which caching behaviour of models and observers occurred. Caching behaviour of the models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

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

DISCUSSION

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

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

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

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

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

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

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

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

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