

When, What, and Whom to Watch? Quantifying Attention in Ravens (*Corvus corax*) and Jackdaws (*Corvus monedula*)

Christelle Scheid
Université Louis Pasteur

Friederike Range and Thomas Bugnyar
University of Vienna

Complex social life requires monitoring of conspecifics. The amount and focus of attention toward others has been suggested to depend on the social relationships between individuals. Yet there are surprisingly few experiments that have tested these assumptions. This study compared attention patterns toward conspecifics in two corvid species, ravens (*Corvus corax*) and jackdaws (*Corvus monedula*). Birds were confronted with affiliated and non-affiliated conspecifics engaged in foraging and object manipulation. Visual access to the model bird was provided through two observation holes, which allowed measurement of exactly how often and for how long observers watched the other. Overall, ravens were more attentive to conspecifics than were jackdaws. Moreover, only ravens showed higher interest toward food-related than object-related behaviors of the model and toward close affiliates than non-affiliates by increasing the duration rather than the frequency of looks. These results are in accordance with predictions derived from the species' foraging biology and suggest that the facultative social, but highly manipulative, ravens use and value information from others differently than do the obligate social jackdaws.

Keywords: attention, corvids, social learning, social dynamics

One of the most important aspects of living in a socially complex society is paying attention to other group members, their interactions, and their behaviors. For example, only if an individual monitors the behavior of others with regard to affiliation, dominance, and tolerance will it be able to make the correct decisions of whom to solicit in agonistic conflicts (e.g., Noë, 1992; Silk, 1999; de Waal & Luttrell, 1986), whom to groom (e.g., Rowell, 1968; Seyfarth, 1980; Sinha, 1998), and whom to avoid (e.g. Busse & Gordon, 1983; Palombit, Cheney, & Seyfarth, 2001; Smuts & Smuts, 1993). Attention toward others and their actions is therefore a prerequisite for any form of behavioral adjustment

during cooperation, competition, communication, and social learning. However, because of time and/or habitat constraints, animals will seldom be able to monitor every other animal within the group or every action performed and thus will be selective with regard to whom and what to observe.

Whom to observe is likely to be dependent on at least two aspects: First, especially in larger groups, individuals might vary in the degree of importance. For example, monitoring a high-ranking female might be more important than monitoring a low-ranking female, because the behavior of the latter will have fewer consequences for the social dynamics within the group. In another example, monitoring an immigrating male might be more important than monitoring a resident male who is less likely to commit infanticide. However, both examples are also dependent on one's own status within the group (e.g. low-ranking, lactating). A second aspect that might influence selectivity is tolerance. Especially, if animals monitor others to acquire knowledge of new food resources, being able to approach an animal closely will highly influence to whom to attend. Both aspects are also highly dependent on the social structure of a particular species (egalitarian vs. despotic societies), which may determine the relative importance of individuals to one another and, hence, motives to which to attend in particular individuals (Coussi-Korbel & Fragaszy, 1995). Indeed, several studies to date have found that affiliate patterns, dominance status, sex, and age of the demonstrator affect how much individuals visually attend to others or even socially learn from others (e.g. Choleris, Guo, Liu, Mainardi, & Valsecchi, 1997; Choleris & Kavaliers, 1999; Nicol, 2004; Nicol & Pope, 1994; Valsecchi, Choleris, Moles, Guo, & Mainardi, 1996).

The frequency and duration of monitoring bouts may also depend on the context and on the type of information that is acquired. If monitoring is used to update old, status quo information, short, but evenly distributed looks might be sufficient. On the other hand,

Christelle Scheid, Equipe Ethologie des Primates, Department of Ecology, Physiology, and Ethology, Institut Pluridisciplinaire Hubert Curien, Université Louis Pasteur, Centre National de la Recherche Scientifique, Strasbourg, France; Friederike Range, Department for Behaviour, Neurobiology, and Cognition, University of Vienna, Vienna, Austria; Thomas Bugnyar, Konrad Lorenz Research Station, Grünau, and Department for Behaviour, Neurobiology, and Cognition, University of Vienna, Vienna Austria.

Thomas Bugnyar is now at the School of Psychology, University of St. Andrews, St. Andrews, Scotland, United Kingdom.

This work has received funding from the European Community's Sixth Framework Program (NEST 012929) and from the Austrian Science Fund (FWF Projects R31-B03 and P16939-B03). Research at the Karl Lorenz Research Station is supported by the Cumberland Stiftung and by the Verein der Förderer. We are grateful to K. Kotrschal and R. Noë for their advice and comments and to C. Schloegl, C. Schwab, and D. Ujfalussi for their help.

Correspondence concerning this article should be addressed to Christelle Scheid, Equipe Ethologie des Primates, Department of Ecology, Physiology, and Ethology, Institut Pluridisciplinaire Hubert Curien, Université Louis Pasteur, Centre National de la Recherche Scientifique 23 rue Becquerel, 67087, Strasbourg, France. E-mail: christelle.scheid@c-strasbourg.fr

if new information were gathered, for example, learning how to extract food items from small crevices with a stick, long observation bouts would be expected during the demonstrator's manipulation of the stick. In the human psychology literature, two attention processes are differentiated: the attention-getting and the attention-holding process (Cohen, 1972). The attention-getting process determines whether the subject will turn to look at the stimulus (frequency). The attention-holding process, on the other hand, determines for how long the subject will continue to gaze at the stimulus once it has looked at it (duration). The overall attention span is thus likely to depend on the identity of the model and on the context.

A few studies have measured attention toward conspecifics in different contexts in primates (vigilance: Alberts, 1994; Caine & Marra, 1988; social learning: Bugnyar & Huber, 1997; Day, Coe, Kendal, & Laland, 2003; Moscovice & Snowdon, 2006), but there is scarce research reporting detailed measures of attention levels in birds. One explanation for this lack of studies on attention to conspecifics might be methodological problems: birds have a spherical view (Fite & Rosenfield-Wessels, 1975) and thus it is difficult to measure where they are looking (but see Dukas & Kamil, 2000). Recently, Range and Huber (2007) introduced a method to quantify attention span in primates. In their approach, two animals (one observer and one model) are kept in two compartments separated by an opaque partition. Direct attention to the model is measured by providing only restricted visual access through two round holes in the partition, which allows for measurements of attention-getting and attention-holding processes. These authors' rationale for using a two-hole procedure is that if animals are interested in the actions of the model, they will look through one of the two holes during the demonstration. Two holes are provided to allow some flexibility for the observer with regard to the angle of vision as well as the position within the animal's own cage. This method can easily be applied to birds as well and allow measurement of attention/interest toward a particular conspecific and its actions.

We used this method of restricted visual access to examine attention span in two corvid species, ravens (*Corvus corax*) and jackdaws (*Corvus monedula*). Both species differ in their degree of sociality and in foraging style and diet. Ravens are facultative social animals and assemble particularly as nonbreeders for foraging, roosting, and playing (Heinrich, 1989; Ratcliffe, 1997). Competition for food is fierce, with birds showing elaborate tactics to gain access to and protect food from others, for example, recruiting others to overpower dominants at defended food sources (Marzluff & Heinrich, 1991), misleading dominants (Bugnyar & Kotschal, 2004), caching food and pilfering others' caches (Bugnyar & Kotschal, 2002; Heinrich & Pepper, 1998). Jackdaws, on the other hand, are highly social, breed in colonies, and forage in groups (Röell, 1978). As compared with ravens, they show moderate levels of scrounging and rarely cache food (Scheid & Bugnyar, 2007). Both species, however, form monogamous pairs and also establish valuable relationships ("friendship") with same and/or different sex partners (de Kort, Emery, & Clayton, 2006; Wechsler, 1988).

In the current study, we tested the birds' attention toward conspecifics that were engaged in a familiar manipulative task (destroying a tetra pack paper box) or foraging task (finding a hidden film canister containing food and removing its lid to get

access to food). Observers had either a high- or low-affiliate relationship with the models and were of same or different sex. In both species, we expected birds to pay more attention to conspecifics when these were foraging rather than manipulating objects. According to Coussi-Korbel and Fragaszy's (1995) prediction that in despotic societies, visual attention and social learning should occur more frequently between closely related and/or affiliated individuals, whereas in egalitarian social systems, information should spread more or less evenly through the group, we expected that the distribution of attention should be more asymmetric and more directed toward affiliates in ravens than in jackdaws.

Method

Study Site and Subjects

The ravens (*Corvus corax*) were housed in an outdoor aviary at the Cumberland Game Park Grünau in the Austrian Alps. They originated from three different nests (two from zoos, one from the wild) and were hand-raised at the Konrad Lorenz Forschungsstelle (KLF) in 2004. The enclosure consisted of an external aviary (about 200 m²) and an experimental portion (30 m²). The external aviary was equipped with perches, tree trunks, natural vegetation, and rocks. The experimental part was divided into five small compartments and contained only a floor of fine-grained sand. During this study, the group was composed of 9 birds, 8 of which (4 males, 4 females) participated in the experiment (Table 1). Individuals were identified with the help of colored leg rings. All

Table 1
List of Individual Birds, Indicating Sex and Kinship Relations (Numbers Refer to Nests), as Well as the Individuals' Combinations With Affiliates and Non-Affiliates of Same and Different Sex in the Tests

Individual	Sex	Siblings	Affiliated		Nonaffiliated	
			Male	Female	Male	Female
Ravens						
I	Male	1	Q	E	P	D
Q	Male	1	I	C	L	X
C	Female	2	Q	E	P	X
E	Female	2	I	C	L	D
L	Male	3	P	D	Q	E
P	Male	3	L	X	I	C
X	Female	3	P	D	Q	C
D	Female	3	L	X	I	E
Jackdaws						
N	Male	1		G		X
G	Male	1		N		U
X	Male	2		U		N
U	Male	2		X		G
E	Male	3		I		C
I	Male	3		E		B
R	Male	4		B		N
C	Male	4		S		E
S	Female	4		C		G
B	Female	4		R		I

Note. M = male; F = female.

ravens were well habituated to humans and familiar with experimental procedures (being called by name and temporarily separated from others in experimental compartments). Their social behavior ('who does what to whom') was routinely recorded every morning during standard observation sessions (5 min focus on each bird; 45 min in total). Birds had ad libitum access to water and were fed two times per day with meat, milk products, fruits, and bread.

The jackdaws (*Corvus monedula*) were housed in an outdoor aviary at KLF. They originated from six different nests and were hand-raised at KLF in 2005. As with the ravens, the aviary was divided into two parts: a large external aviary (90 m²) and an experimental portion (25 m²), which was composed of five small compartments. The external aviary was equipped with tree trunks, perches, and natural vegetation. The group was composed of 20 individuals, 10 of which (8 males, 2 females) participated in the experiment (Table 1). All experimental birds were well habituated to humans and had experience with individual testing. As with the ravens, they were subjected to daily observations on their social behavior (5 min/bird/session). Individuals were identified by colored leg rings. They were fed three times a day with a mixture of dried insects, milk products, eggs, and meat; occasionally they also received live insects, rice, potatoes, and fruits.

Experiments

The experiments were conducted in parallel with ravens and jackdaws from November to December 2005, when birds were 1.5 years of age and 6 months of age, respectively. (Ravens develop much more slowly than do jackdaws and may not start breeding until their 3rd year, whereas jackdaws may begin breeding in their 1st year.) Birds were tested in dyads in the experimental part of each aviary (Rooms B and C; Figure 1) in physical and visual isolation from the other group members. Dyads were composed of individuals with close affiliate relations and without affiliate relations, respectively. Affiliate relations between birds were characterized by high rates of socially positive behaviors (allopreening, contact sitting) and low rates of aggression (approach-retreat interactions, fights). They were calculated on the basis of the daily protocols and known before the onset of the study.

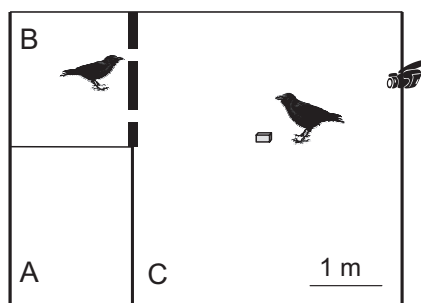


Figure 1. Sketch of the experimental set-up, showing the observer bird in front of one of the two observation holes in room B, the model bird next to the tetra pack box and in room C, and the position of the camera. Boldface lines indicate opaque walls.

Set-Up

The two rooms, Rooms B and C (see Figure 1) were divided by an opaque partition with two small holes at a height of 20 cm. The size of the holes was 10 × 10 cm for the ravens and 5 × 5 cm for the jackdaws; the two holes were approximately 20 cm apart. Both species were given the possibility of sitting on the sill of the door that separated the two rooms or on a perch directly in front of the holes (adjusted in height for the jackdaws) in order to have full visual access through the holes. Room B was assigned as observation compartment and Room C as a demonstration compartment. In order to see what was happening in Room C, a bird positioned in Room B had to approach the partition (<5 cm) and look through one of the holes.

All animals could observe a conspecific in two contexts, during object manipulation and while foraging. In the object manipulation task, models manipulated an empty tetra pack paper box (20 × 10 × 5 cm) containing small stones (so that shaking the box produced some sound). The tetra pack was placed on the ground and the birds would usually hold it with one foot and peck at it with the beak until it was destroyed. In the foraging task, models had to find a film canister (5 cm long, 3 cm in diameter) hidden in the sand floor of Room C and to then remove its lid in order to obtain a piece of cheese. The size of the cheese (1 × 1 × 2.5 cm) was such that birds had difficulties extracting it from the canister. Following the protocol of Range and Huber (2007), models but not observers were allowed to witness the hiding of the film canister. All birds gained familiarity with manipulating tetra pack boxes and opening lids of film canisters before the experiments started.

In each context (object manipulation, foraging), different observer-model combinations were tested. In ravens, models and observers were either close affiliates or non-affiliates and of same or opposite sex. In 4 birds, affiliate relations reflected kinship in the same- and different-sex dyads; in the other 4 birds, affiliate relations reflected kinship in the same-sex combinations but "friendship" in the different-sex combination (Table 1). Jackdaws were only tested in the affiliate and non-affiliate combinations because only two females participated in the experiments. Here, affiliate relations equaled kinship (Table 1). Each bird was tested once per day in a randomized order, with the object manipulation and foraging task being alternated between days.

Procedure

For each test, a dyad was isolated from the rest of the group and called into Room A of the experimental area (Figure 1). After showing the item (tetra pack or film canister) to both birds, the experimenter (Christelle Scheid) placed it into Room C and allowed the model bird to enter the room. As soon as the model was in Room C, the observer bird was allowed into Room B and data collection started. Each session started with the model entering Room C and lasted for 2 min.

The observing behavior of birds was recorded during the entire 2-min period of a trial with a digital video camera (Sony CCD-TR818) that was positioned opposite to the observation holes in the corner of Room C. From the tapes, we measured the duration (to the nearest second) and the number of looks of the observer bird (i.e., how long and often its head and eyes were visible behind the observation hole). In addition, the experimenter recorded the

activity of the models when the observers looked through the holes according to four categories: manipulating, feeding, walking, and resting. *Manipulation* was defined as being in physical contact with the object, that is, holding and/or trying to open the film canister during the foraging tasks or holding and pecking the tetra pack during the object manipulation task. *Feeding* was recorded only during the foraging task and defined as the bird being in physical contact with the cheese. *Walking* was defined as moving around the room on the ground without manipulating or feeding. *Resting* was noted when the model was sitting on a perch being inactive.

Although all ravens were confronted with the opaque cover between Rooms B and C a month before the experiment, some birds ($n = 5$) were still reluctant to approach the holes at the beginning of the experiment (in 9 out of 64 sessions). However, after one or two tests, depending on the individuals, all birds came at least once per session to observe the model. Thus, we repeated the first experimental sessions in which individuals refused to approach the holes (i.e., did not look even once). The jackdaws, in contrast, had been exposed to the opaque wall for a long time before the experiments started, and no neophobic reaction was observed.

Analysis

For each species, we compared the frequency and duration of looks (median, first and third quartiles) when the model was an affiliate or a non-affiliate, of same or opposite sex, and engaged in object manipulation or foraging. Moreover, we calculated the percentage of observation time by dividing the duration observers watched the models by the total duration of recordings (2 min). We also compared the attention measures obtained for the ravens with those obtained for the jackdaws. Individuals that failed to look through the holes in one of the conditions ($n = 1$ jackdaw during object manipulation, $n = 2$ jackdaws during foraging), were excluded from the analysis. Videotapes were analyzed by Christelle Scheid; a subset of 10 sessions were also analysed by a naïve observer. The interobserver reliability was 91%. Because the data were not normally distributed (Kolmogorov–Smirnov $p \leq .01$), we performed nonparametric statistics throughout. Wilcoxon and Mann–Whitney tests were used to compare durations and frequencies of looks for intraspecific differences (food–object, affiliate–non-affiliate, same sex—different sex) and interspecific differences, respectively. Friedman test and post hoc comparisons specific to Friedman tests (Siegel & Castellan, 1988) were used to compare the attention span for each activity of the model. Statistics were calculated by hand according to Siegel and Castellan’s procedure (1988). Probabilities were adjusted using the Benjamini–Yekutieli method (Benjamini & Yekutieli 2001). All tests were two-tailed, with $\alpha = .05$; corrected probabilities (α') are reported in the Results section.

Results

What to Watch: Object or Food Manipulation

In ravens, the median percentage of time observers looked through the holes was 21.67% (11.25, 22.92) during the foraging task, whereas it was only 10.62% (6.87, 16.46) during the object

manipulation task (Figure 2a). This difference was due to a longer duration of looks (Wilcoxon signed-ranks test: $T+ = 34$, $n = 8$, $p = .01$, $\alpha' = .02$) rather than to a difference in the frequency of looks ($T+ = 24$, $n = 8$, $p = .23$; Table 2).

In jackdaws, the median percentage of time observers looked through the holes was 2.92% (1.67, 5.83) during the foraging task and did not differ from the observation time of 2.92% (1.98, 5.83) during the object manipulating task (Figure 2a). Neither mean duration nor frequencies of looks were significantly different be-

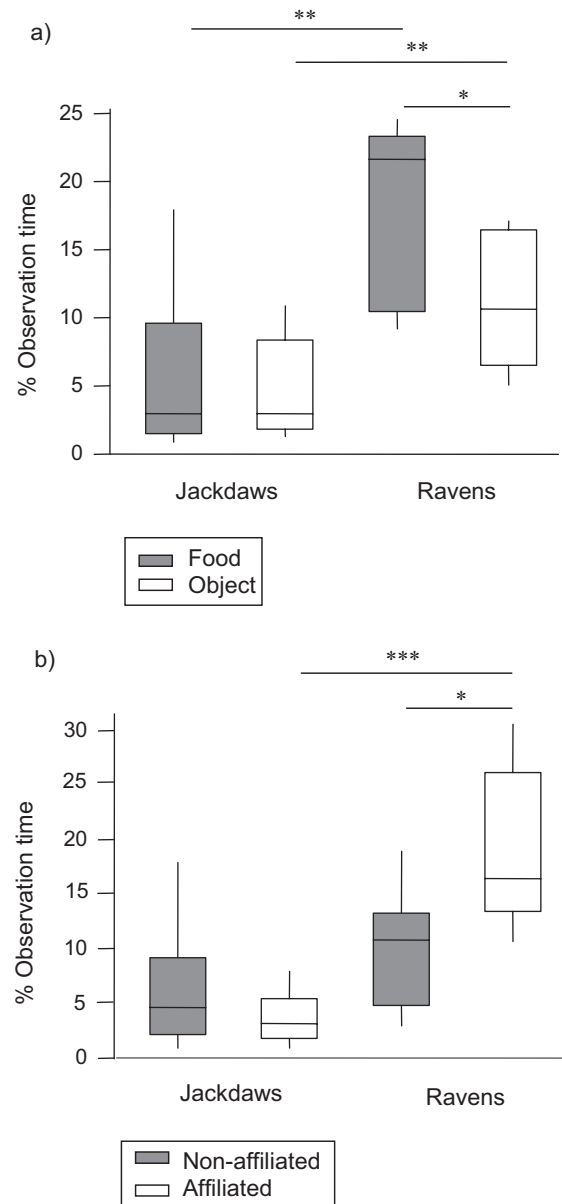


Figure 2. Percentage observation time of ravens and jackdaws in (a) the foraging and object manipulation task and (b) with affiliated and non-affiliated partners. Box plots show median and 25th and 75th percentile; whiskers represent $Q3 + 1.5(Q3 - Q1)$ and $Q1 - 1.5(Q3 - Q1)$, where Q = quartile. Significant results of Wilcoxon and Mann–Whitney tests are outlined above brackets. * $p < .05$. ** $p < .01$. *** $p < .001$.

Table 2
Median (and Quartiles 1 and 3) of Frequencies and Durations (in Seconds) of Looks in Ravens and Jackdaws in the Conditions With Food and Object, Affiliate and Non-Affiliate Model, and Same- and Different-Sex Model

Variable	Frequency		Median duration (s)	
	Ravens	Jackdaws	Ravens	Jackdaws
Food	6.5 (5.5, 7.3)	3.0 (2.0, 5.5)	3.7 (3.2, 4.4)	1.2 (1.0, 1.4)
Object	5.1 (3.2, 6.7)	2.8 (2.0, 4.6)	2.7 (2.1, 3.0)	1.4 (1.0, 1.6)
Affiliate	6.6 (4.6, 8.0)	2.5 (2.4, 5.8)	3.8 (3.1, 4.4)	1.0 (1.0, 1.2)
Non-affiliate	5.3 (3.6, 5.7)	3.5 (3, 6)	2.6 (1.8, 2.9)	1.6 (1.2, 1.7)
Same sex	5.0 (4.5, 6.9)		3.1 (2.2, 3.5)	
Different sex	5.9 (4.9, 7.2)		3.8 (3.1, 3.9)	

Note. Boldface indicates a significant difference between ravens and jackdaws.

tween foraging and object manipulating tasks (mean duration: $T+ = 14, n = 7, p = .53$; frequency of looks: $T+ = 15, n = 7, p = .47$; see Table 2).

In comparing ravens and jackdaws, we found that the percentage of time observers watched the model was higher in ravens than in jackdaws in both contexts (Figure 2a). The observed difference was due to a longer duration of looks in ravens as compared with jackdaws in both tasks (foraging: $c_u = 106, M = 8, n = 9, p = .0002$; object manipulation: $c_u = 96, M = 8, n = 8, p = .0009, \alpha' = .02$) rather than due to a difference in the frequencies of looks (foraging: $c_u = 87, M = 8, n = 9, p = .08$; object manipulation: $c_u = 83, M = 8, n = 8, p = .07$; Table 2).

Whom to Watch?

Affiliate or non-affiliate. In ravens, observers paid attention to the model 16.46% (13.63, 21.92) of the time when they were affiliated and 10.83% (6.46, 12.60) of the time when they were not affiliated (Figure 2b). Again, this difference was due to a longer duration of looks ($T+ = 34, n = 8, p = .01, \alpha' = .02$) rather than a difference in the frequency of looks ($T+ = 22, n = 8, p = .32$; see Table 2).

In jackdaws, the percentage of watching was 4.58% (2.92, 8.75) for nonaffiliates and 3.12% (1.98, 5.42) for affiliates (Figure 2b). There was no significant difference for the duration or for the frequency of looks between non-affiliated and affiliated dyads (duration: $T+ = 21, n = 7, p = .15$; frequency: $T+ = 17, n = 7, p = .34$; Table 2).

Comparing the two species, we found that ravens spent relatively more time than jackdaws watching affiliated and non-affiliated conspecifics (Figure 2b). In both conditions, ravens looked longer than did jackdaws (with affiliates: $c_u = 99, M = 8, n = 8, p = .0002$; with non-affiliates: $c_u = 105, M = 8, n = 9, p = .0003$), but they did not look more often (with affiliates, $c_u = 86, M = 8, n = 8, p = .03, ns, \alpha' = .02$; with non-affiliates: $c_u = 78, M = 8, n = 9, p = .30$).

Same or opposite sex. Overall, ravens showed a higher interest when the model was of the opposite sex than when it was of the same sex (Wilcoxon signed-ranks test: for duration, $T+ = 33, n = 8, p = .02, \alpha' = .024$; for frequency of looks, $T+ = 29, n = 8, p = .07$). Combining gender and social relation factors, dyads of the same sex watched affiliates for a relatively longer time than did nonaffiliates ($T+ = 33, n = 8, p = .019, \alpha' = .024$). However,

dyads of different sex did not differ in their observation time between affiliates and non-affiliates ($T+ = 27, n = 8, p = .13$).

When to Watch: Duration of Looks per Activity

In ravens, the mean duration of observers' looks was significantly affected by the model's activity (Friedman test: $Fr = 12.0, df = 2, p \leq .01$). Looks were longer when the model was feeding than when it was resting and walking (Figure 3). In jackdaws, the mean duration of looks was not significantly affected by the model's behavior (Friedman test: $Fr = 0.9, df = 2, p > .10$).

Discussion

In this study, we quantified the amount of attention ravens and jackdaws paid to affiliated and non-affiliated conspecifics that were engaged in a foraging task and an object manipulation task. We found striking differences between species, with ravens but not jackdaws being selective to when, what, and whom to watch. Moreover, interest in the model and/or its activity was expressed in

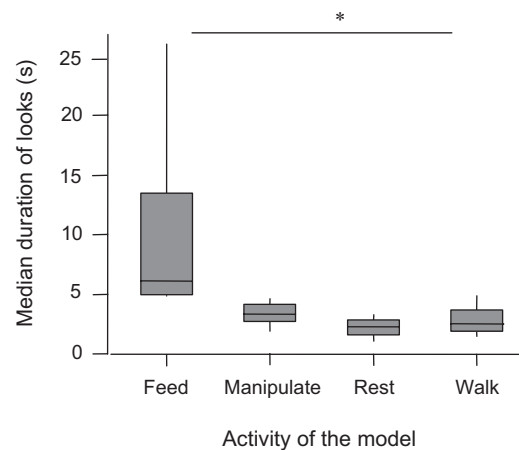


Figure 3. Median duration of looks (in seconds) by raven observers according to the model's behavior. Box plots show median and 25th and 75th percentile; whiskers represent $Q3 + 1.5(Q3 - Q1)$ and $Q1 - 1.5(Q3 - Q1)$, where Q = quartile. Significant results of post hoc comparisons that are specific to Friedman test are outlined above brackets. * $p < .05$.

the duration rather than in the frequency of looks, indicating effects on attention-holding rather than attention-getting processes.

The general difference in attention span between ravens and jackdaws could potentially be attributed to the size difference between the two corvid species. Ravens are three times larger than jackdaws (Heinroth & Heinroth, 1926) and thus slower in their movements and behaviors, causing them to spend relatively more time in front of the observation holes than jackdaws. However, unlike in the ravens, the attention measurements of jackdaws did not differ between the two contexts (foraging, object manipulation) or in regard to the model's behavior (e.g. feeding, manipulating vs. walking, resting), suggesting that they regularly checked the adjacent compartment but paid limited interest to what a conspecific was doing there. Possibly, in small birds like jackdaws, the attention-holding process is very short and our procedure was not sensitive enough to measure small differences in the birds' looking time. Still, common marmosets (*Callithrix jacchus*) are of similar size to jackdaws and they did show a clear differentiation of responses towards different conditions in this set-up (Range & Huber, 2007), rendering a methodological explanation due to body size unlikely. A possible confound in our set-up could have been that holes were relatively higher above-ground for jackdaws than for ravens and thus more easily accessible for the latter. However, all jackdaws regularly used the perch in front of the holes and, consequently, they did not differ significantly from the ravens in the frequency of looking through the holes in any condition.

Marmosets confronted with the foraging task looked most and longest when the model was manipulating the film canister, suggesting that they were mainly interested in how to obtain the food (Range & Huber, 2007). In contrast, ravens paid most attention to the "feeding" of a model, which could be interpreted as a motivational effect or an increase in arousal (Zajonc, 1965) rather than the acquisition of information about where to search and how to access food (e.g. Galef, 1988). Indeed, ravens have an accurate observational spatial memory (Bugnyar & Kotrschal, 2002; Heinrich & Pepper, 1998), which might facilitate finding a hidden canister and thus require little attention to the searching process of a conspecific. Moreover, our ravens were familiar with the type of film canister we used in the experiment as well as with the opening technique. Thus, the essential information for them to be extracted from the demonstration might have been the kind of hidden food (Forkman, 1991) and how to extract it from the canister (which we defined as feeding) rather than finding or opening the canister.

As predicted, the distribution of attention towards different models was more asymmetric in ravens than in jackdaws. These results are in line with Coussi-Korbel and Frigaszy's (1995) argument, relating social dynamics of groups and distribution of attention within conspecifics. Ravens engage in various types of cooperation, such as recruitment at roosts and food calling (Heinrich & Marzluff, 1991; Marzluff, Heinrich, & Marzluff, 1996), joint object exploration (Stöwe et al., 2006), and alliance formation (Loretto, Bugnyar, & Kotrschal, 2007), some of which appear to work on the basis of affiliate social relationships. Accordingly, they showed more attention toward friends than toward non-friends in the experiment. Moreover, ravens were more interested in the demonstration if the model was of opposite sex, which might reflect their interest in potential mates. Interestingly, jackdaws did not show higher interest in affiliates, but rather in non-affiliated individuals, which is slightly puzzling in relation to

the information we currently have about the social relationships of this species. Possibly, the interest in non-affiliates has to do with pair formation which occurred shortly after this experiment. However, recent data on social learning indicate that even pair-bonded jackdaws tend to pay more attention to non-affiliates (Schwab, Bugnyar, & Kotrschal, 2007).

The observed differences in attention patterns between ravens and jackdaws suggest that the amount and type of social information may be of differential importance for the two species. Socially foraging ravens may benefit from others by learning what to eat (Heinrich, 1999), whom to use and avoid for scrounging and pilfering (Bugnyar & Kotrschal, 2002), and, possibly, how to access and/or process food (Fritz & Kotrschal, 1999). Paying close attention to others (attention-holding process) may be critical for acquiring this information but constrained by the willingness of others to share information (Laland, 2004). Jackdaws may also benefit from social foraging (Röell, 1978), but their access to food appears to be less difficult, and competition over food that has been made accessible by others appears to be less fierce than in the ravens (Scheid & Bugnyar, 2007). Thus, their attention pattern of constant but short observation bouts may reflect the updating of information, such as where feeding is profitable and when to leave a foraging site (Templeton & Giraldeau, 1996). This updating process does not need to be restricted to certain individuals, and it may function to facilitate group cohesion.

Taken together, the two-holes-in-a-wall design proved to be a simple but useful method for testing visual attention patterns in birds. It should be incorporated in studies on social foraging and social learning, as understanding when, what, and whom to observe is critical for investigating the use of public information and the acquisition and transmission of novel skills.

References

- Alberts, S. C. (1994). Vigilance in young baboons: Effects of habitat, age, sex, and maternal rank on glance rate. *Animal Behaviour*, *47*, 749–755.
- Benjamini, Y., & Yekutieli, D. (2001). The control of the false discovery rate in multiple testing under dependency. *The Annals of Statistics*, *29*, 1165–1188.
- Bugnyar, T., & Huber, L. (1997). Push or pull: An experimental study on imitation in marmosets. *Animal Behaviour*, *54*, 817–831.
- Bugnyar, T., & Kotrschal, K. (2002). Observational learning and the raiding of food caches in ravens, *Corvus corax*: Is it "tactical" deception? *Animal Behaviour*, *64*, 185–195.
- Bugnyar, T., & Kotrschal, K. (2004). Leading a conspecific away from food in ravens (*Corvus corax*)? *Animal Cognition*, *7*, 69–76.
- Busse, C. D., & Gordon, T. P. (1983). Attacks on neonates by a male mangabey (*Cercocebus atys*). *American Journal of Primatology*, *5*, 345–356.
- Caine, N. G., & Marra, S. L. (1988). Vigilance and social organization in two species of primates. *Animal Behavior*, *36*, 897–904.
- Choleris, E., Guo, C., Liu, H., Mainardi, M., & Valsecchi, P. (1997). The effect of demonstrator age and number on duration of socially-induced food preferences in house mouse (*Mus domesticus*). *Behavioural Processes*, *41*, 69–77.
- Choleris, E., & Kavaliers, M. (1999). Social learning in animals: Sex differences and neurobiological analysis. *Pharmacology Biochemistry and Behavior*, *64*, 767–776.
- Cohen, L. B. (1972). Attention-getting and attention-holding processes of infant visual preferences. *Child Development*, *43*, 869–879.
- Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, *50*, 1441–1453.

- Day, R. L., Coe, R. L., Kendal, J. R., & Laland, K. N. (2003). Neophilia, innovation and social learning: A study of intergeneric differences in callitrichid monkeys. *Animal Behaviour*, *65*, 559–571.
- de Kort, S. R., Emery, N. J., & Clayton, N. S. (2006). Food sharing in jackdaws, *Corvus monedula*: What, why and with whom? *Animal Behaviour*, *72*, 297–304.
- de Waal, F. B. M., & Luttrell, L. M. (1986). The similarity principle underlying social bonding among female rhesus monkeys. *Folia primatology*, *46*, 215–234.
- Dukas, R., & Kamil, A. C. (2000). The cost of limited attention in blue jays. *Behavioral Ecology*, *11*, 502–506.
- Fite, K. V., & Rosenfield-Wessels, S. (1975). A comparative study of deep avian foveas. *Brain, Behavior and Evolution*, *12*, 97–116.
- Forkman, B. (1991). Social facilitation is shown by gerbils when presented with novel but not with familiar food. *Animal Behaviour*, *42*, 860–861.
- Fritz, J., & Kotrschal, K. (1999). Social learning in common ravens, *Corvus corax*. *Animal Behaviour*, *57*, 785–793.
- Galef, B. G. Jr. (1988). Imitation in animals: History, definition, and interpretation of data from the psychological laboratory. In T. Zentall & B. G. Galef, Jr. (Eds.), *Social learning: Psychological and biological perspectives* (pp. 3–28). Hillsdale, NJ: Erlbaum.
- Heinrich, B. (1989). *Ravens in winter*. New York: Simon & Schuster.
- Heinrich, B. (1999). *Mind of the raven*. New York: Harper Collins.
- Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others? *Behavioural Ecology and Sociobiology*, *28*, 13–21.
- Heinrich, B., & Pepper, J. W. (1998). Influence of competitors on caching behaviour in the common raven, *Corvus corax*. *Animal Behaviour*, *56*, 1083–1090.
- Heinroth, O., & Heinroth, M. (1926). *Die Vögel Mitteleuropas [Birds of Central Europe]*. Frankfurt/Main: Verlag Harri Deutsch.
- Laland, K. (2004). Social learning strategies. *Learning & Behavior*, *32*, 4–14.
- Loretto, M.-C., Bugnyar, T., Kotrschal, K. (2007, February). *Ontogeny of dominance relations and coalitions in juvenile common ravens (Covus corax)*. Poster presented at the Symposium der Ethologischen Gesellschaft, Grünau, Austria.
- Marzluff, J. M., & Heinrich, B. (1991). Foraging by common ravens in the presence and absence of territory holders: An experimental analysis of social foraging. *Animal Behaviour*, *42*, 755–770.
- Marzluff, J. M., Heinrich, B., & Marzluff, C. S. (1996). Roosts are mobile information centers. *Animal Behaviour*, *51*, 89–103.
- Moscovice, L. R., & Snowdon, C. T. (2006). The role of social context and individual experience in novel task acquisition in cottontop tamarins. *Animal Behaviour*, *71*, 933–943.
- Nicol, C. J. (2004). Development, direction, and damage limitation: Social learning in domestic fowl. *Learning & Behavior*, *32*, 72–81.
- Nicol, C. J., & Pope, S. J. (1994). Social learning in a small flocks of laying hens. *Animal Behaviour*, *47*, 1289–1296.
- Noë, R. (1992). Alliance formation among male baboons: Shopping for profitable partners. In A. H. Harcourt, & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp. 285–321). Oxford, England: Oxford University Press.
- Palombit, R. A., Cheney, D. L., & Seyfarth, R. M. (2001). Female–female competition for male “friends” in wild chacma baboons, *Papio cynocephalus ursinus*. *Animal Behaviour*, *61*, 1159–1171.
- Röell, A. (1978). Social behaviour of the jackdaw in relation to its niche. *Behaviour*, *64*, 1–12.
- Range, F., & Huber, L. (2007). Attention in common marmosets—Implications for social-learning experiments. *Animal Behaviour*, *73*, 1033–1041.
- Ratcliffe, D. (1997). *The raven: A natural history in Britain and Ireland*. London: T. & A. D. Poyser.
- Rowell, T. E. (1968). Grooming by adult baboons in relation to reproductive cycles. *Animal Behaviour*, *16*, 585–588.
- Scheid, C., & Bugnyar, T. (2007). *Observational spatial memory: Comparing jackdaws and ravens*. Unpublished manuscript.
- Schwab, C., Bugnyar, T., & Kotrschal, K. (2007). *Learning from non-affiliated individuals as relevant sources of information in jackdaws (Corvus monedula)*. Manuscript submitted for publication.
- Seyfarth, R. M. (1980). The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour*, *28*, 798–813.
- Siegel, S., & Castellan, N. J. (1988). *Nonparametric statistics for the behavioural sciences*. Boston: McGraw-Hill.
- Silk, J. B. (1999). Male bonnet macaques use information about third-party rank relationships to recruit allies. *Animal Behaviour*, *58*, 45–51.
- Sinha, A. (1998). Knowledge acquired and decisions made: Triadic interactions during allogrooming in wild bonnet macaques, *Macaca radiata*. *Philosophical Transactions of the Royal Society London*, *353B*, 619–631.
- Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in non-human primates and other mammals: Evidence and theoretical implications. *Advances in the Study of Animal Behaviour*, *22*, 1–63.
- Stöwe, M., Bugnyar, T., Loretto, M.-C., Schlögl, C., Range, F., & Kotrschal, K. (2006). Novel object exploration in ravens (*Corvus corax*): Effects of social relationships. *Behavioural Processes*, *73*, 68–75.
- Templeton, J. J., & Giraldeau, L.-A. (1996). Vicarious sampling: The use of personal and public information by starlings foraging in a simple patchy environment. *Behavioural Ecology and Sociobiology*, *38*, 105–113.
- Valsecchi, P., Choleris, E., Moles, A., Guo, C., & Mainardi, M. (1996). Kinship and familiarity as factors affecting social transfer of food preferences in adult Mongolian gerbils (*Meriones unguiculatus*). *Journal of Comparative Psychology*, *110*, 243–251.
- Wechsler, B. (1988). The spread of food producing techniques in a captive flock of jackdaws. *Behaviour*, *107*, 39–58.
- Zajonc, R. B. (1965). Social facilitation. *Science*, *149*, 269–274.

Received December 1, 2006

Revision received March 23, 2007

Accepted May 24, 2007 ■