

Explorative Innovators and Flexible Use of Social Information in Common Ravens (*Corvus corax*) and Carrion Crows (*Corvus corone*)

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Innovation and social information use are influenced by individual characteristics, and are important for the creation and transmission of novel behavioral patterns. Here, we investigated which individual factors predict innovation rates and social transmission of information in a comparative study with identically reared common ravens (*Corvus corax*) and carrion crows (*Corvus corone corone*; *Corvus corone cornix*). In the innovation experiment (1), we presented the birds with a novel problem-solving task while alone, to determine which individuals would quickly solve (“innovators”) or not solve (“noninnovators”) this task. We then related these findings to sex, object exploration (frequency of novel item manipulation), object neophobia (latency to novel item interaction), and social rank position. We found that innovators were more explorative than noninnovators, although they did not differ significantly in social rank, object neophobia or sex. In the social information use experiments (2 & 3), subjects first observed a model (Exp. 2: conspecific, heterospecific; Exp. 3: conspecific innovator & noninnovator) demonstrate a specific color selection in a 2-choice cup task, before being allowed to make their own cup selection. Innovator and noninnovator observers did not significantly differ in their tendency to use social information, that is, to select the demonstrated cup first, from a conspecific or heterospecific model. Furthermore, observers did not preferentially use social information from an innovator over a noninnovator model. We discuss our findings in relation to the likely benefits of flexible information use, and the role of other model characteristics, such as relationships, on the use of social information.

Keywords: innovation, social information use, corvids, object exploration, neophobia

Supplemental materials: <http://dx.doi.org/10.1037/com0000039.supp>

Individuals may differ significantly in their behavior when confronted with the same behavioral or environmental stimuli, even within captive environments (Gosling, 2001). Such behavioral variations apply to aggressiveness, activity, sociability, explorative tendencies, and neophobia (aversion to novelty; Herborn et al., 2010). Other individual traits that can influence behavior and

cognitive abilities include age, sex and social rank. Individual differences have important implications for ecology and evolution, as they influence learning, performance in cognitive tasks, and life history strategies affecting fitness and survival (Réale & Dingemanse, 2001; Sih & Del Giudice, 2012). Indeed, individual differences provide the “material for natural selection to act on” (Darwin, 1859).

Innovation—defined as solving a novel problem or finding a new solution to a familiar problem—is a key component of behavioral flexibility, and can lead to new behaviors that allow animals to more efficiently exploit their environments (Reader & Laland, 2003). Whereas innovative behaviors in general have received much attention, the differences between innovative and noninnovative individuals remain largely overlooked, although several studies have investigated this area (Reader & Laland, 2003; Thornton & Lukas, 2012). Innovative carib grackles (*Quiscalus lugubris*), for example, have been found to have higher exploration scores and lower neophobia scores than their noninnovator conspecifics (Overington, Cauchard, Côté, & Lefebvre, 2011). Highly urbanized Indian mynah birds (*Acridotheres tristis*) were less neophobic and quicker to solve an innovative technical foraging task than less urbanized individuals (Sol, Griffin, Bartomeus, & Boyce, 2011). There is support for the role of subordinates or juveniles as innovators in some species, such as meerkats (*Suricata*

This article was published Online First June 30, 2016.

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Rachael Miller was supported by the Vienna Science and Technology Fund (WWTF) through project CS11-008 to Christine Schwab and the Austrian Science Fund (FWF) through project Y366-B17 to Thomas Bugnyar. Many thanks to Jorg Massen and Caroline Ritter for providing access to the social rank data, and to Martina Schiestl for running the color preference control task.

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suricatta; Thornton & Samson, 2012), great tits (*Parus major*), and blue tits (*Cyanistes caeruleus*; Morand-Ferron, Cole, Rawles, & Quinn, 2011). These latter findings may indicate that innovation in these species is driven by competition, where subordinates or juveniles explore new foraging opportunities due to dominant or older animals monopolizing familiar resources (Reader & Laland, 2003). However, this pattern does not hold across all species, as the more socially dominant starlings (*Sturnus vulgaris*) are innovators (Boogert, Reader, Hoppitt, & Laland, 2008), and adult callitrichid monkeys are more innovative than juveniles (Kendal, Coe, & Laland, 2005).

Social learning, which may be defined as learning from observing the behavior of others, is vital for the spread of novel behavior patterns, such as those created through innovation (Lefebvre, 2000; Zentall, 2004). Social information use relates closely to social learning, and refers to information made available by others (Danchin, Giraldeau, Valone, & Wagner, 2004). Social information use affects several important aspects of an individual's ecology, including foraging and dispersal (Kурvers et al., 2010). The likelihood of social learning occurring may be influenced by context, such as copying when uncertain or copying the majority (Laland, 2004). Furthermore, as with innovation, the likelihood of social learning occurring may be influenced by the identity of individuals—both that of the observers and the “models” (Laland, 2004). For example, with regard to model identity, vervet monkeys (*Chlorocebus pygerythrus*) are more likely to copy a female than a male model, which may be related to female philopatry in this species (van de Waal, Renevey, Favre, & Bshary, 2010).

Human children tend to identify with and imitate an adult model with “rewarding power” (i.e., controlling and dispersing rewarding resources) over an adult that is a competitor for the rewards (Bandura, 1963). In nonhuman animals, innovative individuals may be regarded in a similar manner to these human models with “rewarding power” in Bandura's (1963) child study—as “producers” of resources or information, such as providing access to a novel food source (Reader & Laland, 2003). We may therefore expect observers—and in particular noninnovative individuals as “scroungers” of this information/resource—to be more likely to pay attention to the behavior of innovative individuals—or producers—over noninnovative individuals. However, few studies have empirically linked innovation and social information use through focusing on the role of a model's characteristics of being an innovator in a social learning related task. One study that did address the effectiveness of innovators as models, however, found that, in canaries (*Serinus canaria*), observers did not preferentially copy male over female models, despite males being more innovative than females (Cadieu, Fruchard, & Cadieu, 2010).

Furthermore, the identity of the observer is likely to be as important as that of the model. In large-billed crows (*Corvus macrorhynchos*), dominant observers continue to copy the technique used by a subordinate model over subsequent trials, whereas subordinate observers (after observing a dominant model) learn alternative techniques (Izawa & Watanabe, 2011). In barnacle geese (*Branta leucopsis*), using social information in a feeding context decreased with an individual's increasing “boldness” score—the latter being determined by consistent individual differences in approach latency and minimal distance to a novel object (Kурvers et al., 2010). In chacma baboons (*Papio ursinus*), “bolder” (in response to novel food) and more “anxious” (in

response to a predator) individuals showed greater improvement in solving tasks related to foraging after observing a model, than did “shyer” or less anxious individuals (Carter, Marshall, Heinsohn, & Cowlshaw, 2014). Therefore, as an observer, being an innovator or noninnovator may also influence the propensity to use socially rather than individually acquired information, although so far this question has received little focus on the intraspecific level, making it difficult to predict the outcome.

Here, we took a comparative approach to investigate the link between individual differences, innovation, and social information use in two closely related corvid species: common ravens (*Corvus corax*) and carrion x hooded crows (*Corvus corone corone*; *Corvus corone cornix*). Reflecting the hybridization belt in Europe, the crows were primarily hybrids of carrion crow and hooded crow as determined by appearance, that is, varying degrees of black to gray plumage. As carrion and hooded crows have highly similar life histories and are usually considered to be subspecies (De Knijff, 2014; Glutz von Blotzheim, Bauer, & Haffer, 1993; Lack, 2011), we will refer to both subspecies as “carrion” crows hereafter. Common ravens and carrion crows are large brained birds and are opportunistic generalists in both diet and habitat use, although only the crows tend to utilize highly urbanized environments (Emery & Clayton, 2004; Goodwin, 1986). Both species have high fission–fusion dynamics across days and months, being highly social in the nonbreeding stage, when they form large foraging and roosting flocks, and territorial in the breeding stage (Braun, Walsdorff, Fraser, & Bugnyar, 2012; Goodwin, 1986). Both species are highly neophobic as adults, although relatively neophilic (attracted to novelty) as juveniles (Heinrich, 1995).

The corvid family has the most diverse innovation repertoire among passerines (Overington, Morand-Ferron, Boogert & Lefebvre, 2009). Examples of innovative behavior in corvid species include tool use and manufacture in New Caledonian crows (*Corvus moneduloides*; Hunt, 1996) and tool use in American crows (*Corvus brachyrhynchos*; Powell & Kelly, 1977). Several species were able to use spontaneous string-pulling as an innovative problem-solving solution to access hanging food (wild carrion crows; Glutz von Blotzheim et al., 1993; captive ravens: Heinrich & Bugnyar, 2005), but see findings from New Caledonian crows indicating use of perceptual feedback as opposed to insight (Taylor, Knaebe, & Gray, 2012). In relation to social cognition, ravens have been shown to possess advanced social skills, such as social learning preferences (Schwab, Bugnyar, Schloegl, & Kotrschal, 2008), use of tactical deception (Bugnyar & Kotrschal, 2002), and understanding of third-party relations (Massen, Pašukonis, Schmidt, & Bugnyar, 2014). There is considerably less work on social influences and learning in carrion crows, although social context has recently been found to influence exploration (frequency of interaction) with novel food and objects (Chiarati, Canestrari, Vera, & Baglione, 2012; Miller, Bugnyar, Pölzl, & Schwab, 2015). Common ravens and carrion crows therefore make promising model species for this innovation and social information use study, particularly for a directly comparative study, which is still lacking in this field (although see Griffin & Diquelou, 2015; Tebbich, Sterelny, & Teschke, 2010).

In the present study, we first investigated whether innovation ability, that is, being a quick problem solver in an extractive foraging task, was explained by individual traits such as sex, object exploration (frequency of novel item manipulation), ob-

ject neophobia (latency to novel item interaction), or social rank (dominance hierarchy) position (Experiment 1). We predicted innovators to be more exploratory, less neophobic, and more subordinate (low in social rank) than noninnovators, as found in other social species, like spotted hyenas (*Crocuta crocuta*: Benson-Amram & Holekamp, 2012), carib grackles (Overington et al., 2011) and meerkats (Thornton & Samson, 2012).

We then utilized these findings to investigate the propensity of observing individuals to use social information, that is, select the same colored cup as demonstrated by a model in a two-choice cup task, provided by either a conspecific or a heterospecific innovator model (Experiment 2), and a conspecific innovator or a conspecific noninnovator model (Experiment 3). Here, we asked whether individuals' innovation ability predicts individuals' propensity to use social information. We expected innovating and noninnovating observers to differ in their propensity to use social information, that is, to select the demonstrated cup first, although the direction of this prediction could potentially favor either innovator "category."

Innovator observers may be more likely to use social information. The performance of pigeons (*Columba livia*) in an innovation task and a social learning task was positively correlated; individuals that were quicker problem-solvers were also better at learning from a model (Bouchard, Goodyer, & Lefebvre, 2007). Indeed, across various species, a positive correlation between social learning and innovation has been found (Reader & Laland, 2002). Alternatively, noninnovator observers may be more prone to using social information than individual trial-and-error learning, as suggested in a previous raven study (Range, Bugnyar, Schögl, & Kotrschal, 2006). In the Range et al. (2006) study, individuals that were better and faster learners in simple discrimination tasks, including a color discrimination task, while alone, paid less attention to physical and social manipulations (motor task and scrounging) than individuals that took longer and made more mistakes. In addition, a negative correlation between individual innovativeness and social learning was found in marmosets (*Callithrix jacchus*), suggesting occurrence of a trade-off between these two processes (Burkart, Strasser, & Foglia, 2009). Clearly the link between innovation and the use of social information requires further focus.

We expected innovators and noninnovators to differ more generally in their use of social information, with respect to the use of information from a known conspecific model, as well as in their tendency to utilize *any* type of social information, regardless of their relationship or familiarity with the model. We therefore expected not only to find differences between innovator and noninnovator observers in their use of information provided by a conspecific model, but also from an unknown, heterospecific model.

Finally, we asked whether individuals' innovation ability affects the transmission of social information, that is, if social information provided by innovator and noninnovator models similarly affect observers' behavior. We expected that observers would preferentially use social information provided by an innovator over a noninnovator model. Specifically, we expected that either (a) all observers in general or (b) all noninnovative individuals would utilize information provided by the innovator model.

The comparative approach incorporated in this study enabled us to investigate whether our findings were likely to be raven-specific—the species that has received more focus in these re-

search areas—or also applicable to another social corvid species: carrion crows. We did not expect to find species differences in any of the 3 experiments with these two closely related species with similar life histories—particularly as a recent study comparing ravens and crows found similar influences of social context on group-level exploration behavior (Miller et al., 2015). Behavioral similarities between these species may be driven by phylogenetic relatedness and/or life history similarities. However, if we did find any significant species differences, this species comparison would further allow us to ascertain whether these behavioral differences were more likely to be related to minor differences in lifestyle aspects, like habitat use, rather than phylogenetically inherited traits.

General Method

Study Animals

Subjects were kept in species groups of 9 captive common ravens (*Corvus corax*; 6 males, 3 females), and 9 captive carrion crows (*Corvus corone corone*; *Corvus corone cornix*; 4 males, 5 females). The crows were obtained at pre fledging age from wild nests in parks within Vienna, Austria. The ravens were collected at pre fledging age from several European zoos: 4 ravens were second generation in captivity (i.e., their grandparents were wild-born), and 5 ravens were first generation in captivity (i.e., their parents were wild-born). All ravens and crows were hand-reared in 2012 under the same conditions and were subadult (approximately 1.5 years old) at the time of testing. They were housed at Haidlhof research station (University of Vienna & University of Veterinary Medicine) in large, outside aviaries (total size ~680 m²) with large, connecting test compartments (~20 m²), under license number BMWFV-66.006/0011-WF/II3b/2014 from 22 May, 2014. Sex was determined via DNA sexing from blood samples. Subjects were individually identifiable via colored leg rings. To control for any potential individual differences in motivation due to hunger, all subjects were satiated prior to testing through provision of 50% of their daily maintenance diet (mix of meat, fruit, vegetables, yogurt, and bread) 30 min before testing began. Subjects were never food-deprived in general and had constant access to water.

Data Collection and Analysis

All experimental trials were videotaped (Canon HD camera Legria HF510), with test trials coded using *Solomon Coder* version 14.01.14 as well as being coded live by the experimenter (RM). RM and CS both coded a selection of videos from all 3 experiments (12% of all videos), and interobserver reliability was excellent (Cohen's kappa $k = 0.969$, $p < .001$).

Data were analyzed using SPSS version 19. As most variables had a non-normal distribution, nonparametric statistics were used. All tests were exact and two-tailed, and α was set to 0.05. Figures were prepared using SPSS and Adobe Illustrator CS5.

Ethical Note

We adhered to animal welfare guidelines and conducted our research in accordance with Austrian law and American Psychological Association ethical standards. The study was noninvasive

and observational, and therefore not classified as an animal experiment according to Austrian law (§2. Federal Law Gazette No.501/1989). The study was approved by the Internal Animal Welfare Board at the Faculty of Life Sciences, University of Vienna (2014.012).

Experiment 1: Innovation

Method

Subjects and apparatus. Eight of the 9 available ravens (5 males, 3 females) and 8 of the 9 available crows (3 males, 5 females) participated in the innovation experiment (see Table S1 in online supplementary materials).

The apparatus consisted of a “foraging tube” (17 cm height $\times$ 6 cm diameter) pet toy originally designed for parrots (sourced via www.parrotshop.de; see Figure 1). The task required repeatedly turning a horizontal wheel to cause the food to drop down consecutive levels until it eventually dropped out of the tube. Food rewards were eight small, shelled sunflower seeds—a reward highly valued by the birds.

Procedure. In early July 2013, prior to beginning the experiment, all subjects were exposed to the apparatus as a group for approximately 1.5 months to habituate, with the wheel locked and the apparatus mounted on the outside wall of the enclosure so that only minor contact from the birds was possible. Furthermore,

immediately prior to starting the innovation test trials, we ran three 20-min habituation trials in the group over 3 consecutive days, where the apparatus was mounted inside the enclosure on the mesh close to the ground. A familiar concrete block was placed beside it to allow the birds to choose whether to approach the apparatus from the ground or from the top of the block. During these habituation trials, the apparatus’s wheel remained securely locked, but food was presented nearby and the birds had free access to explore the apparatus. For the habituation trials, we recorded whether each subject in the group setting came down to the ground, approached, and touched the apparatus.

The innovation experiment test took place in mid/late August, 2013. For the test, the apparatus was presented as in the habituation trials, except that it was placed within a large test compartment where the birds could be individually and visually separated from the group for testing, and baited with the reward out of sight of the birds. Subjects received four test trials of 10 min each, with one trial run per day. At each test trial, the measures recorded were whether the subject approached the apparatus (within 0.5 m), touched the apparatus, and solved the task, that is, accessed the food. Birds that solved the task within the four test trials were considered to be “innovators,” whereas birds that did not solve the task within these trials were considered to be “noninnovators.” We also recorded which and how many area(s) of the apparatus were touched, and assigned a number from 1 to 4 by counting the following areas separately: 1. Wheel (functional part), 2. Side of tube, 3. Board behind tube, 4. Other part. We then obtained a sum across the four trials of apparatus areas touched per individual.

In a separate experiment during separate testing sessions from the innovation experiment, object exploration and neophobia measures were taken per individual while temporarily separated from the group in September 2013. Subjects were presented with 4 novel item conditions: food, object (small, movable item), person, and structure (large, nonmovable item), during separate 10-min test trials with one condition run per day. The conditions were presented in a set order. The object exploration measure was the mean frequency of manipulation of novel items. The object neophobia measure was the mean latency to interact (approach and touch) with novel items.

Social rank data were collected via three food monopolization experiments (pooled data available for general use at the field station) run one day per month in December 2013 and January and February 2014 for both species. Here, the birds were presented with a large piece of meat, which could be monopolized by one or more individuals, and all unidirectional displacements were recorded (Gwinner, 1964). Hierarchy position was determined via the frequency of directed and received displacements across all individuals, by calculating Landau’s linearity indices (h') using MatMan 1.1, reordered to best fit a linear hierarchy (de Vries, Netto, & Hanegraaf, 1993).

For object exploration, object neophobia, and social rank, subjects were ranked in relation to their conspecifics for each of these measures separately from lowest to highest frequency of manipulation, latency to interact, and social rank position. A binary score was then assigned to each individual (0 = low; 1 = high) for these three measures, where subjects with a score below the group median were assigned a “0,” whereas those with a score above the group median were assigned a “1.”



Figure 1. Innovation Experiment 1 apparatus (sourced via www.parrotshop.de). Subjects were required to repeatedly turn the horizontal wheel in either direction to cause the reward (8 shelled sunflower seeds) to drop down each level within the tube and be released at the bottom of the tube.

Data analysis. A Generalized Linear Mixed Model (GLMM) was used to assess which factors may affect innovation ability in the birds, which was a binary variable of whether the subject solved the trials (1) or not (0), and entered as a dependent variable into the model. Subject (nested within species) was entered as a random effect to control for repeated measures. We included five fixed effects to the model: sex, species, social rank position, object neophobia, and object exploration. Data were fitted using a binomial distribution with a logit link function. A stepwise backward elimination analysis was used removing the least significant variable in each step until the final model was obtained. Each dropped variable was then re-added separately to the final model to check that it remained nonsignificant, as determined by p values ($p > .05$).

Fisher's exact tests and Mann-Whitney U test were run for Experiment 1. The comparisons were: innovator versus noninnovator proportions and number of trials solved between species, as well as interaction (approach and touch) with apparatus and mean number of apparatus areas touched by noninnovators and innovators.

Results

In Experiment 1, 50% of ravens and 50% of crows solved the task; that is, they accessed the food at least once (see Table 1).

Between species, there was no significant difference in the number of innovators per species or in the total number of trials solved (see Table 1). In relation to social rank, a significant linear hierarchy was found for the ravens ($h' = 0.86$, $n = 8$, $p < .001$), based on 524 interactions with 5.6% unknown relationships, and for the crows ($h' = 0.89$, $n = 8$, $p < .001$) based on 427 interactions with 8.3% unknown relationships. Five of 8 innovators (3 crows, 2 ravens) were found to be subordinate (low in social rank). Likewise, 5 of 8 innovators (3 crows, 2 ravens) had a low latency to interact with novel items and were considered to show a low neophobic tendency. In relation to object exploration, 6 of 8 innovators (3 per species) showed high frequencies of novel item manipulation and were considered to be highly explorative.

Innovation ability was significantly affected by object exploration (frequency of novel item manipulation). Specifically, subjects that solved test trials, which were referred to as innovators, were significantly more likely to have a high exploration tendency, whereas subjects that did not solve trials, referred to as noninnovators, had a low exploration tendency (GLMM innovation ability, object exploration: $F = 6.106$, $df_1 = 1$, $df_2 = 62$, $p = .016$; Table 2). No significant effects of sex, species, social rank, or object neophobia on innovation ability were found.

The noninnovators solved no trials, although they approached the apparatus within 0.5m in 94% of trials and touched it in 66%

Table 1

Experiment 1 Results: Innovation Task. 16 Subjects Participated in the Experiment. P-Values Represent Fisher's Exact Test Results Unless Stated Otherwise, and are Exact and Two-Tailed

Measure	Proportion of individuals		p-value (if applicable)
Number of subjects to solve task at least 1 × = "innovator"	Overall: 8 of 16 Ravens: 4 of 8 (2 males, 2 females) Ravens: 4 of 8 (2 males, 2 females)		Species comparison—no. of innovators per species: $p > .999$
Trial number each innovator subject first solved task (trial length = 10 minutes)	Trial 1: 4 ravens, 1 crow Trial 2: 2 crows Trial 4: 1 crow		/
Number of trials solved per innovator subject	Ravens: 12 trials (Laggie: 4 George: 4 Nobel: 2 Adele: 2)	Crows: 12 trials (Corbie: 3 Daisy: 3 Peppi: 4 Juno: 2)	Species comparison—total number of trials solved: $p > .999$
	Number of non-innovator subjects to interact with apparatus (all 8 innovator subjects interacted with apparatus in all trials)		Innovator vs. non-innovator interaction with apparatus per trial
Approach apparatus (within .5 m)	Trial 1: 7 of 8 Trial 2: 8 of 8 Trial 3: 8 of 8 Trial 4: 8 of 8		Trial 1: $p > .999$ Trial 2: no p-value as constant Trial 3: no p-value as constant Trial 4: no p-value as constant No effect of trial number: $p > .999$
Touch apparatus	Trial 1: 3 of 8 Trial 2: 6 of 8 Trial 3: 5 of 8 Trial 4: 7 of 8		Trial 1: $p = .026$ Trial 2: $p = .467$ Trial 3: $p = .2$ Trial 4: $p > .999$ No effect of trial number: $p = .528$
Mean frequency of areas touched across 4 trials per subject (wheel, side of tube, board behind tube, other parts)	Innovators: Ravens: 3.25, 3.25, 2.75, 2.5 Crows: 3.25, 2.5, 1.75	Non-innovators: Ravens: 1.75, .75, .5, .5 Crows: 1.75, 1.25, .75, .75	Mann-Whitney U-test: $U = 1$, $n_1 = 8$, $n_2 = 8$, $p < .01$

Table 2
Generalized Linear Mixed Model on Factors Affecting
Innovation Ability (Whether Subject Solved Test Trials or Not).
The Analysis Used Data From 16 Subjects Over 64 Trials, With
Subject (Nested Within Species) as a Random Effect

Fixed term	Full model			Final model		
	F	df1, df2	p	F	df1, df2	p
Object exploration	4.767	1, 56	.033	6.106	1, 62	.016
Species	.004	1, 56	.947	.004	1, 61	.951
Sex	.000	1, 56	.996	.002	1, 61	.961
Social Rank	.001	1, 56	.975	.002	1, 61	.961
Object neophobia	.002	1, 56	.967	.002	1, 61	.963

of trials, with each subject touching the apparatus in at least 2 of 4 trials. In comparing trials for the noninnovators, there was no significant effect of trial number on approaching or touching the apparatus, which indicated that subjects continued to interact with the apparatus throughout the test (see Table 1). There was no significant difference in the likelihood to *approach* the apparatus between the innovators and noninnovators in any of the four trials, although innovators were significantly more likely to *touch* the apparatus than noninnovators in the first trial only ($p = .026$; Table 1). Additionally, we found that innovators touched significantly more areas of the problem-solving apparatus than noninnovators ($p < .01$; Table 1). Interestingly, all subjects did primarily touch the wheel (in 53 of 64 trials), which was the functional part of the apparatus, as turning it resulted in the reward.

Experiment 2: Social Information Use From (a) Conspecific and (b) Heterospecific Models

Method

Subjects and apparatus. All birds participated in Experiment 2, that is, 9 birds per species with 8 observers and 1 model per species. Specifically, 8 ravens (5 males, 3 females) and 8 crows (3 males, 5 females) acted as observers, and one male raven and one male crow acted as models (see Table S1 in online supplementary materials).

For this experiment, two small round cups (6 cm diameter) of different colors were presented on a small, moveable wooden board (50 cm $\times$ 15 cm) on the ground (Figure 2; see Table S2 in online supplementary materials). The cups were secured to the board using a metal stick and bolts 30 cm apart, so that they could be lifted upward to reveal a hidden reward, but the cups could not be removed entirely from the board. Two small pieces of *Frolic* dog biscuit (1 biscuit cut into 4 pieces)—another highly valued reward—were used to bait both of the cups out of sight of the subjects.

Procedure. Experiment 2 was run from mid-September to mid-October 2013. Subjects were presented with two model types: first, a conspecific innovator model (Experiment 2a), and then a heterospecific innovator model (Experiment 2b). For each species, we used the same conspecific model and heterospecific model, which were both male and socially high ranking individuals. In Experiment 2a, the conspecific model was assigned a rewarded cup color (blue) and a nonrewarded cup color (yellow) for both

species. In Experiment 2b, the heterospecific model was assigned a rewarded cup color (pink) and a nonrewarded cup color (light green) for both species (see Table S2 in online supplementary materials).

Before the test, the model received three 10-min training sessions of 10 trials per session in visual isolation from the group on separate days in order to establish the rewarded color. During training sessions, both cups were present but only one colored cup was consistently baited with food underneath it. To aid the model bird learning the correct colored cup association, the nonrewarded cup was also securely closed using the bolt so that the model could not lift it. Within 1–2 sessions, the models learned to touch and lift the rewarded color immediately and did not touch the nonrewarded cup, despite being able to do so.

The test subjects then received multiple demonstrations, with the rewarded cup location (left, right) counterbalanced across demonstrations. During the demonstrations, the model demonstrated the rewarded color to all observers in a group at once, which could observe the model from an adjacent test compartment, by lifting the relevant colored cup and collecting the food. Both cups were present and baited although the model would only touch and access food from the designated colored cup. The model demonstrations took place on the ground approximately 2 m from the dividing mesh between the two compartments, which was visible from all locations in the adjacent observer compartment. The conspecific model demonstrated to its conspecifics, whereas the heterospecific model demonstrated to the subjects of the other species, that is, the crow model to the ravens and vice versa. We ran four sessions of five demonstration trials each, with each session lasting 5 min, and one session run per day across 4 consecutive days.

For the test, each subject received 1 test trial while alone directly following the final demonstration trial using the same two-cup choice apparatus as in the model demonstration sessions (see Figure 2). Each test lasted 3 min, although subjects generally accessed the food within the first minute (mean latency to access food: Experiment 2a: 46 seconds; Experiment 2b: 47 seconds). Within this time, subjects were allowed to make a choice between the two cups by touching and accessing food from underneath the cup(s) – both of which were baited. The position (left, right) of the demonstration cup, that is, the cup color previously demonstrated by the model, was randomized for subjects across experiments, as well as within each experiment. The maximum amount of time between observers watching the final demonstration session and



Figure 2. Social information use Experiments 2 and 3: two-choice cup apparatus. Subjects first observed a model (Exp.2: conspecific, heterospecific; Exp.3: conspecific innovator & noninnovator) demonstrate its choice of one of two colored cups by lifting the cup upward to access the reward underneath (2 pieces of *Frolic*), before being allowed to make their own cup selection.

being tested was 28 min (3 min per test plus ~1 min preparation time = 4 min per subject; last subject per group waited for maximum of 7 subjects' tests = 28 min). It was recorded whether the subject touched and accessed the food from the demonstrated cup first, which was taken to indicate social information use.

Data analysis. Binomial tests and Fisher's exact tests were run for Experiment 2. These comparisons were as follows: proportion of observers selecting the demonstrated cup first; innovators' and noninnovators' propensity to select the demonstrated cup first from a conspecific and heterospecific model; and species' propensity to select the demonstrated cup first.

Results

In Experiment 2 (a) with a conspecific model and (b) with a heterospecific model, all observers except 1 male raven accessed the food from underneath a cup(s), although this bird did touch the cup(s) and therefore is included in the analyses, resulting in a total of 16 subjects per subexperiment (8 ravens, 8 crows; see Table S1 in online supplementary materials). For the conspecific model (Experiment 2a), 100% of observers across both species selected the demonstrated cup first. Additionally, we ran a simple color preference test with a control group of 8 ravens and 3 crows that did not participate in the original study, using the same color cup combination from Experiment 2a, where the demonstrated cup was blue and the nondemonstrated cup was yellow. Control subjects received no demonstration or reward. In this control group, 5 of 11 subjects (4 ravens, 1 crow) touched the blue cup first, and 6 of 11 subjects (4 ravens, 2 crows) touched the yellow cup first (see Table S3 in online supplementary materials).

For the heterospecific model (Experiment 2b), 87% of ravens and 50% of crows selected the demonstrated cup first, which was a trend for the ravens ($p = .07$) and not significant for the crows ($p > .999$, Table 3). The subjects that did not select the demonstrated cup first in Experiment 2b were not the last subjects to be tested, that is, they were not the subjects with the longest delay

between final demonstration session and test. In total, 3 of 8 ravens and 0 of 8 crows chose the cup on the same side as they had chosen in Experiment 2a (see Table S4 in online supplementary materials). Furthermore, for 4 of 5 subjects (1 raven, 4 crows) that did not choose the demonstrator cup in Experiment 2b, the demonstrator cup was on the same side that was previously rewarded in Experiment 2a (see Table S4 in online supplementary materials).

There were no significant differences between innovators and noninnovators in selecting the demonstrated cup first from either the conspecific or the heterospecific model (see Figure 3). There was no significant species difference in selecting the demonstrated cup first when the model was (a) conspecific or (b) heterospecific (see Table 3).

Experiment 3: Social Information Use From Innovator and Noninnovator Models

Method

Subjects and apparatus. All birds participated in Experiment 3, that is, 9 birds per species, with 7 observers and 2 models per species. Specifically, 7 ravens (6 males, 1 female) and 7 crows (4 males, 3 females) acted as observers, and 2 female ravens and 2 female crows acted as models (see Table S1 in online supplementary materials).

The set-up was the same two-choice cup used in Experiment 2 (see Figure 2), although differently colored and shaped cups were used (see Table S2 in online supplementary materials).

Procedure. Experiment 3 was run from late October to early November 2013. In Experiment 3, the procedure was similar to Experiment 2. Models were trained on one demonstration color in visual isolation of observers, as in Experiment 2. In Experiment 3, we used two models: a conspecific innovator and a conspecific noninnovator, as determined by the previous innovation experiment (Experiment 1). The models selected were female and of

Table 3

Experiment 2 Results: Social Information Use With (A) Conspecific and (B) Heterospecific Innovator Models. 1 Crow and 1 Raven Did Not Participate in Innovation Experiment 1 and Therefore Their Innovation Status was unknown. P-Values are Exact and Two-Tailed

Subjects	Conspecific model		Heterospecific model	
	Proportion of individuals	<i>p</i> -value (if applicable)	Proportion of individuals	<i>p</i> -value (if applicable)
Selected demonstrated cup first				
All Subjects	16 of 16	Binomial test: <i>p</i> < .0001	11 of 16	Binomial test: <i>p</i> = .2
Ravens	8 of 8	Binomial test: <i>p</i> = .008	7 of 8	Binomial test: <i>p</i> = .07
Crows	8 of 8	Binomial test: <i>p</i> = .008	4 of 8	Binomial test: <i>p</i> > .999
- Species comparison	Fisher's Exact test: <i>no p-value as variable constant as all subjects selected demonstrated cup first</i>		Fisher's Exact test: <i>p</i> = .282	
Influence of observer status on cup selection: Observer status—innovator (IN), non-innovator (NI), unknown (U)				
All Subjects	6 IN: 8 NI: 2 U	Fisher's Exact test: <i>no p-value as variable constant as all subjects selected demonstrated cup first</i>	4 IN: 6 NI: 1 U	Fisher's Exact test: <i>p</i> > .999
Ravens	3 IN: 4 NI: 1 U	/	3 IN: 3 NI: 1 U	/
Crows	3 IN: 4 NI: 1 U	/	1 IN: 3 NI	/

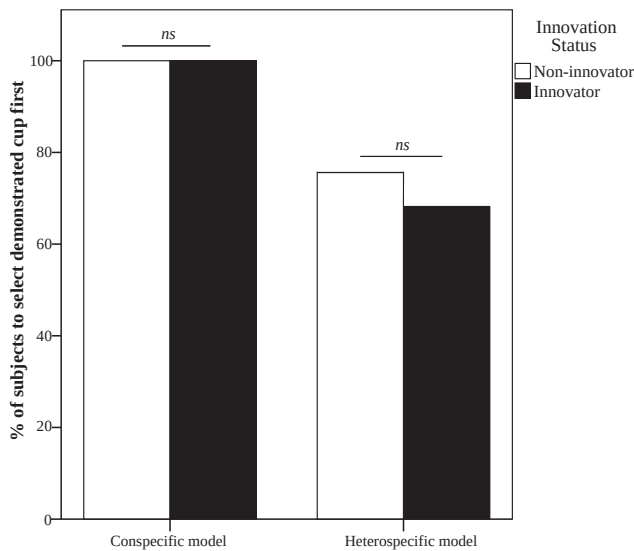


Figure 3. Social information use Experiment 2: (a) conspecific and (b) heterospecific model. There was no significant difference between innovators and noninnovators in selecting the demonstrated cup first from either the conspecific or heterospecific model.

similar mid social rank position for both species. In contrast to Experiment 2, the observer group was split into 2 subgroups of 3 or 4 birds—each subgroup consisting of both innovator and non-innovator observers (see Table S4 in online supplementary materials). Each subgroup watched both model demonstration sessions from an adjacent compartment along with their conspecifics in this subgroup, while the other subgroup was visually isolated. Model order was counterbalanced so that each subject observed the innovator model prior to the noninnovator model in 2 of 4 demonstration sessions. In Trial 4, directly prior to the test, one subgroup observed the innovator model first whereas the other subgroup observed the noninnovator model first.

The star-shaped cups used were dark green or white. For the ravens, the innovator was trained to select dark green and the noninnovator to select white. For the crows, the innovator was trained to select white and the noninnovator to select dark green. Subjects received multiple demonstrations, with the rewarded cup location (left, right) counterbalanced across demonstrations. There were four demonstration sessions, with each consisting of 5 demonstration trials per model, that is, 5 demonstration trials from the innovator and 5 demonstration trials from the noninnovator model. Before demonstrating its cup choice (part 2), each model was first presented with the apparatus from the innovation Experiment 1 (see Figure 1) to demonstrate its role as an innovator or noninnovator by either solving (accessing food) or not solving (not accessing food) the apparatus (part 1). The aim of this additional part (1) was to inform the observers about the role of each model as an innovator or noninnovator using a problem-solving task that was familiar to all birds. The noninnovators generally approached and only briefly touched but did not access any food from the innovation experiment apparatus, whereas the innovators immediately approached and solved the task in all cases. Demonstration sessions lasted 20 min in total with 10 min per model—5 min for part

1 and 5 min for part 2 of the demonstration. One demonstration session was run per day, across 4 consecutive days.

As in Experiment 2, the one test trial in Experiment 3 was conducted while subjects were alone and lasted 3 min. Within this time, subjects were allowed to make a choice between the two cups by touching and accessing food from underneath the cup(s) – both of which were baited. The position (left, right) of the demonstrated cup was counterbalanced between subjects for the test trials. The maximum amount of time between observers watching the final demonstration session and being tested was 12 min (3 min per test plus ~1 min preparation time = 4 min per subject; last subject per subgroup waited for maximum of three subjects' tests = 12 min). It was recorded whether the subject selected and accessed the food from the cup(s), with regard to the model (innovator or noninnovator) that had previously demonstrated this cup.

Data analysis. Binomial tests were run for Experiment 3. We tested for preference to select the demonstrated cup first from an innovator compared with a noninnovator model overall, as well as whether the status of the observers as an innovator or noninnovator significantly influenced their model choice.

Results

Directly after observing a demonstration from (a) an innovator model and (b) a noninnovator model, 6 of 14 subjects (4 ravens, 2 crows) selected the “innovator” cup first—the cup color demonstrated by the innovator model. The other 8 subjects (3 ravens, 5 crows) selected the “noninnovator” cup first—the cup demonstrated by the noninnovator model. Three of 7 ravens and 3 of 7 crows chose the cup on the same side as they had chosen in Experiment 2b, although this was not the same side that they chose in Experiment 2a for 1 of these 3 ravens and all 3 of these crows (see Table S4 in online supplementary materials). Three of 7 ravens and 2 of 7 crows chose the cup that they had seen demonstrated most recently, that is, demonstrated immediately before the test (see Table S4 in online supplementary materials). There was no significant preference for an innovator over a noninnovator model for each species separately, or with both species combined (Table 4; Figure 4). Furthermore, there was no significant effect of observer status as an innovator or noninnovator observer on choosing a model of either innovator or noninnovator status (Table 4; Figure 4).

General Discussion

Who Are the innovators?

Our comparative study with group-living, identically reared and tested individuals provided the first indication of innovation rates in common ravens and carrion crows. As expected, because of relatedness and similarities in species' life histories, we found highly similar proportions of innovators to noninnovators and innovation ability, as determined by the number of trials solved, in the two species. In relating innovation to individual characteristics, we found a significant effect of individual object exploration on innovation ability in both species. However, there was no such significant effect of individual social rank, object neophobia, or sex on innovation ability, although the relatively small sample size utilized in the study should be noted. These findings do however

Table 4

Experiment 3 Results: Social Information Use With Conspecific Innovator and Non-Innovator Models. 14 Observer Subjects Accessed Food From Underneath A Cup(S). 1 Crow and 1 Raven Did Not Participate in Innovation Experiment 1 and Therefore Their Innovation Status was Unknown. P-Values Represent Binomial Test Results and are Exact and Two-Tailed

Subjects	Proportion of individuals	p-value (if applicable)
Selected cup demonstrated by innovator model first		
All Subjects	6 of 14	$p = .79$
Ravens	4 of 7	$p > .999$
Crows	2 of 7	$p = .453$
Influence of observer status on cup selection: Number of observers that were innovator, non-innovator or unknown and their selection of cup demonstrated by innovator model “innovator cup” or non-innovator model “non-innovator cup” first		
All Subjects	Selected innovator cup first	Selected non-innovator cup first
Innovator observer	3	3
Non-innovator observer	2	4
Unknown innovation status	1	1
p-value	$p > .999$	$p > .999$
Ravens		
Innovator observer	2	1
Non-innovator observer	1	2
Unknown innovation status	1	0
Crows		
Innovator observer	1	2
Non-innovator observer	1	2
Unknown innovation status	0	1

correspond with those found in some other species, such as spotted hyenas and pigeons, where no significant effect of social rank or sex on problem-solving performance was found (Benson-Amram & Holekamp, 2012; Bouchard et al., 2007). As in the present study, innovative hyenas and carib grackles were found to be more

exploratory than their noninnovative conspecifics (Benson-Amram & Holekamp, 2012; Overington et al., 2011).

It is interesting to note that we found that 50% of individuals in both species in our captive colony innovated despite not being food deprived—which has been proposed to drive innovation in some species, such as innovative “bin-opening” during winter in wild kea (*Nestor notabilis*; Gajdon, Fijn, & Huber, 2006). We did not find a significant influence of social rank on innovation ability, which may be related to testing individuals while alone. Testing for innovation in a group setting may reveal a stronger influence of social rank position. However, in a group context, it is difficult to control for potential influences of social learning on individual behavior.

The innovation problem-solving task was selected with the aim of being a novel task that required a novel problem-solving solution (repeatedly turning a horizontal wheel to obtain food). Problem solving of extractive foraging tasks has been found to be a valid experimental test for investigating innovation (Griffin & Guez, 2014). Both innovators and noninnovators approached the problem-solving apparatus during test trials, and innovators were only more likely than noninnovators to touch the apparatus in the first of the four trials. All subjects were equally well habituated to the apparatus, and were satiated prior to testing. Therefore, not solving the task did not appear to reflect an individual’s general lack of interest, lower food-driven motivation, or a stronger neophobic response to the apparatus. Rather, our findings appear to reflect differences between innovator and noninnovator individuals in their tendency to solve the novel problem.

Innovators were, however, more likely to touch more areas (i.e., wheel, side of tube, board behind tube, other parts) of the problem-

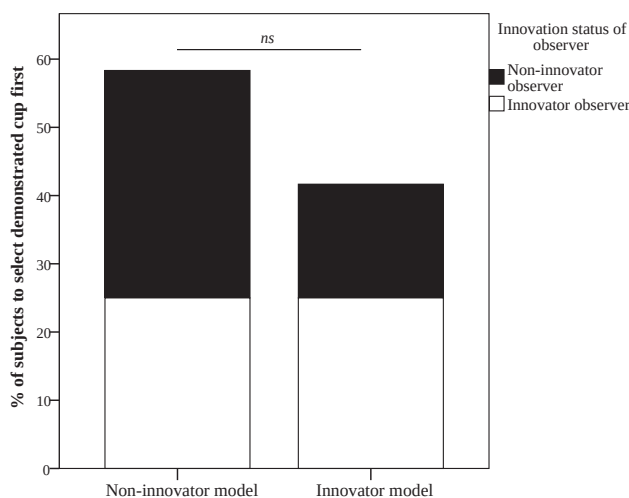


Figure 4. Social information use Experiment 3: conspecific innovator versus conspecific noninnovator model. There was no significant preference to select the cup demonstrated by the innovator over the noninnovator model. Furthermore, there was no significant effect of observer status as an innovator or noninnovator observer on model choice of an innovator or noninnovator model.

solving apparatus than noninnovators. It is possible that more explorative individuals that also touched more areas of the problem-solving apparatus were more likely to solve the task because of this increased interaction, which may lead to releasing the food and then learning what to do, compared with less explorative individuals. However, although explorative behavior is likely to be a precursor to innovation (Reader & Laland, 2003), exploration alone does not suffice for innovations to emerge (Thornton & Samson, 2012). Furthermore, all subjects generally touched the “functional” part of the apparatus—the wheel—so touching more areas of the apparatus does not necessarily increase the likelihood of solving the task. In further support of potential differences between innovators and noninnovators—not only with regard to exploration but also potentially to persistence—we note that despite being given additional opportunities to solve the task while acting as noninnovator models in Experiment 3, these two noninnovator individuals still did not solve the task. Rather, instead of continuing to attempt to solve it, they appeared to gradually lose interest in the apparatus as they only briefly touched it and therefore demonstrated “nonsolving” of the task.

Differences in the Use of Social Information?

In social information use Experiment 2, contrary to our predictions, we did not find differences between innovators and noninnovators in their propensity to use social information, suggesting that, in general, these birds can and will utilize social information, regardless of their own innovation ability. Hoppitt, Samson, Laland, and Thornton (2012) demonstrated that wild meerkats—a highly social species—were able to flexibly utilize a range of social and asocial learning mechanisms. These mechanisms included three types of operant conditioning and three forms of social learning, including enhancement, where the observers’ attention is drawn toward a specific location or item where the model acts (Hoppitt et al., 2012). Both ravens and crows are also highly social, as well as being generalists that utilize a range of food and habitat options. Our findings may therefore be related to an ability to be able to flexibly use any available information, social as well as individual trial-and-error learning, which would be expected to be highly adaptive, particularly for species living in variable physical and social environments. To further assess whether high sociality and generalist living promotes higher problem solving and social learning abilities, future studies may compare species with different social/ecological lifestyles.

Similar to the present study, Burkart et al. (2009) did not find a relationship between individual innovativeness and social learning in marmosets when the innovation task was “goal-directed,” that is, involved finding a solution to a novel problem, as in our innovation task. They did, however, find a negative correlation between innovation and social learning in a “flexibility” innovation task involving registering and switching to a novel though easier solution after learning a previous solution (Burkart et al., 2009). Other factors, including mode of innovation, may therefore play a role on the link between innovation and social learning. Furthermore, all observers selected the demonstrated cup from the conspecific model, resulting in a ceiling effect. It is therefore possible that with a more challenging task, innovators and noninnovators may show differences in use of social information.

In Experiment 2, in line with our prediction, we did not find species differences in propensity to use social information from a conspecific or heterospecific model. Although the primary aim of including the heterospecific model condition was to further explore whether innovators and noninnovators differed in propensity to utilize any type of available social information, exploring interspecific social information use is interesting in its own right. Social learning between species appears to be fairly widespread, such as in relation to predator recognition and food source location (Avarguès-Weber, Dawson, & Chittka, 2013). However, the degree to which species with similar life histories and habitat requirements may learn from one another may depend on the natural relationship between the two species, like overlapping ranges and the type of feeding interactions. For example, group-foraging zenaida doves (*Zenaida aurita*) learn novel foraging tasks more readily from conspecific models, whereas territorial doves learn more readily from a species with which they form mixed flocks: carib grackles (Dolman, Templeton, & Lefebvre, 1996).

Although ravens and crows do encounter one another and occupy similar environments, they rarely form mixed-species flocks. Hence, it is interesting to note that both species utilized social information from the conspecific but not from the heterospecific model in our study. Specifically, 100% of observers showed a significant preference for the cup demonstrated by the conspecific model. Eighty-seven percent of ravens and only 50% of crows showed a preference for the cup demonstrated by the heterospecific model, which was a trend for the ravens and not significant for the crows. It is therefore still possible that, particularly in the ravens, some individuals may have used the information from the heterospecific model, although other individuals clearly did not. It would be worthwhile to investigate interspecific learning in corvids further by including species that regularly form mixed-species flocks, such as jackdaws (*Corvus monedula*) and rooks (*Corvus frugilegus*).

Differentiated Social Information Use From Innovators?

In social information use Experiment 3, when provided with a choice of conspecific models, observers did not show a preference for the innovator over the noninnovator model. This finding indicated that, although both species are capable of using social information provided by a conspecific in the same type of simple task as in Experiment 2, the innovation status of the model does not appear to enhance the likelihood of using social information. Additionally, as an observer, being an innovator or noninnovator did not significantly influence the preference for either model. The inclusion of the demonstration of innovative ability by the models in Experiment 3 aimed to give the observers information about the innovation status of the model within the experiment. It is possible that the birds did not make an association between observing the model demonstrating its “innovative ability” in the separate problem-solving task and demonstrating its cup selection, despite observing several demonstration sessions for both models. As innovators were self-selected, rather than arbitrarily chosen and trained, the subjects may have been familiar with the individual’s innovation status from previous observations/interactions. Furthermore, previous studies with these and other corvid species

showed these birds to possess advanced cognitive abilities in both the social and physical domains (Emery & Clayton, 2004), and could therefore reasonably be expected to be able to make such an association. However, in house sparrows (*Passer domesticus*), model identity as an “innovator” following a demonstration of successful problem-solving performance to observers had no effect on their subsequent social interactions with the group (Preisner, Papp, Vincze, Bókony, & Liker, 2015). The authors suggested that observers may use other more subtle cues to determine the innovation abilities of their group-mates, rather than direct observation of their performance in an experimental setting (Preisner et al., 2015).

Alternatively, it may be the case that other model individual characteristics, such as age, sex, or their kinship or affiliative relations with the observer—although we did aim to control for relationship—are more important for these birds than the model’s innovation ability. For instance, in ravens, presence of siblings facilitates novel object exploration (Stöwe et al., 2006), and sibling models enhance social learning (Schwab et al., 2008), and in crows, presence of fathers facilitates offspring access to novel food (Chiarati et al., 2012). This key role of relationship with the model may have also resulted in neither species significantly using social information provided by the heterospecific model, although the ravens did show a trend in this direction. The heterospecific model was visually and acoustically familiar to the observers, as both species were housed in adjacent aviaries, although they never had physical access to one another, so were highly unlikely to have established a relationship with this model.

Potential Confounds

We used differently colored and shaped cups between experiments (see Table S2 in online supplementary materials) with the aim of reducing any confounding influence of experience between experiments and increasing the salience of demonstrated information in each experiment. Corvids are capable of making feature discriminations, including color discriminations (Range et al., 2006), and so should perceive the cups as novel in each experiment. It could be suggested that the social information use task was so simple and the information so relevant and straightforward, that observers should always copy the model regardless of their identity. However, our findings suggested otherwise, as all subjects copied the conspecific model, but not the heterospecific model, despite using the same type of two-choice cup task with each model. We did not counterbalance the demonstrated color in Experiment 2 in order to ensure the demonstrator characteristics were the same for all observers. It is unlikely that the birds displayed spontaneous group-level color preferences, as they did not all select one color over another in Experiment 2b or 3. In Experiment 2a, all subjects did select the same color (blue, the color demonstrated by the model). We ran a color preference test with a control group of 8 ravens and 3 crows that did not participate in the original study, using the same color cup combination from Experiment 2a (blue vs. yellow) but with no demonstration or reward. We found no evidence for spontaneous group-level color preferences for blue over yellow colored cups in this control group (5 subjects selected blue: 6 subjects selected yellow; see Table S3 in online supplementary materials). Furthermore, we found no evidence for an influence of previously rewarded cup location

(left/right), that is, cup choice, in Experiment 2a on future cup choice; cup choice (left/right) in Experiment 2b and 3; or cup last seen demonstrated by observers immediately prior to the test in Experiment 3 (see Table S4 in online supplementary materials).

Although the crows were primarily carrion and hooded crow hybrids, these are typically considered to be subspecies; indeed, hooded crows are not currently recognized as a separate species by BirdLife International (2015). We therefore referred to the crows as “carrion” and expected our sample to be representative of this species. Because of logistic limitations related to the use of captive, same age individuals, our study was conducted with a relatively small sample size of 7–8 individuals per species, although this increased to 14–16 subjects with species combined, which was possible given there were no significant species differences. The use of this sample allowed us to make a comparison across species of individuals reared in identical conditions, with the same developmental background and general captive environment. Using few individuals limits the chances of finding interindividual variation and the conclusions that can be drawn from our results. Despite this sample size, we did find results that are comparable with studies in other social species with larger sample sizes (62 hyenas: Benson-Amram & Holekamp, 2012; 42 pigeons: Bouchard et al., 2007).

Conclusion

Overall, our findings highlighted that individuals in both species will readily utilize socially acquired information, regardless of their own innovation status. Also, innovators and noninnovators do not seem to be rated as differently valued information sources by their conspecifics, although it is possible that other factors, like relationship with the model, may have overshadowed the influence of innovator status. This flexible information use likely enables individuals to respond adaptively to differing conditions and environments (Laland, 2004). Furthermore, the ability to behave flexibly, alongside a tendency for explorative behavior, is likely to contribute to the occurrence of innovations (Benson-Amram & Holekamp, 2012). As we found behavioral similarities between common ravens and carrion crows, our findings may be related to life history similarities and/or phylogenetic relatedness. Flexibility in the use of social information may also be an adaptive trait in other social and habitat generalist avian species, which requires further comparative captive and field studies.

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Received February 7, 2015

Revision received May 14, 2016

Accepted May 18, 2016 ■