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Crows (*Corvus corone ssp.*) Check Contingency in a Mirror yet Fail the Mirror-Mark Test

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Mirror reflections can elicit various behavioral responses ranging from social behavior, which suggests that an animal treats its own reflection as a conspecific, to mirror-guided self-directed behaviors, which appears to be an indication for mirror self-recognition (MSR). MSR is scarcely spread in the animal kingdom. Until recently, only great apes, dolphins, and elephants had successfully passed this test. The range of convergence was, however, expanded by an avian species, the Eurasian magpie (*Pica pica*). Efforts to find MSR in other corvid species have so far failed, and with only a few studies conducted, the cause of these discrepancies is difficult to identify. In the present study, we examined the responses to mirrors and the ability of MSR in hitherto untested species: the carrion and hooded crows (*Corvus corone ssp.*). These crows showed a pronounced and lasting interest in the mirror; unlike many species, they did not exhibit social behaviors on their first encounters but immediately started investigating the mirror. Some crows showed contingent behaviors in front of the mirror, but none of the crows showed significant mirror-guided self-directed behaviors nor mark-directed behavior during the subsequent mark test. This lack of mark-directed behavior could not be explained by a lack of interest in the mirror nor in the mark. These findings could indicate that crows lack a concept of self, or the need for other means of investigating self-recognition and self-awareness in avian species.

Keywords: mark test, mirror self-recognition, self-awareness, corvids, avian cognition

Supplemental materials: <http://dx.doi.org/10.1037/com0000195.supp>

Providing evidence for self-awareness in animals has been of interest to researchers because of its implications for the conception of animals' "mental life." Being aware of one's self implies the ability to reflect upon one's own actions, thoughts, and emo-

tions. It therefore implies the ability to monitor one's mental states through introspection but also to ascribe similar mental states to others, an ability reflected by behaviors like the expression of sympathy, empathy, intentional deception, or reciprocal altruism (Gallup, 1982). The most wide-spread paradigm to explore self-awareness is to test whether individuals recognize themselves in mirrors. Originally designed to prove the ability of mirror self-recognition (MSR) in chimpanzees (*Pan troglodyte*; Gallup, 1970) and human infants (*Homo sapiens*; Amsterdam, 1972), the mark or rouge test consists of applying a colored mark on a part of an animal's body, which it would not be able to see without the aid of a mirror. Attempts to remove the mark after perceiving its reflection are considered evidence for the animal's ability to recognize itself in the mirror. Although the test and its interpretation have met some controversy (Heyes, 1994, 1995; Suddendorf & Butler, 2013, 2014; Swartz, 1997), the ability of MSR is generally seen as an indication of an individual's concept of its own body image (Nielsen, Suddendorf, & Slaughter, 2006), and has further been interpreted as an index for the possession of a concept of self and self-awareness (Gallup, 1982; Gallup, Anderson, & Shillito, 2002).

The confrontation with a mirror, that is, mirror image stimulation, elicits a very similar string of behaviors in different species. When first exposed to mirrors most animals, similarly to children in their first months, exhibit social behaviors, whether positive or negative, toward their own reflections, suggesting that they treat their reflection as a conspecific. However, with increased exposure

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to the mirror, these behaviors can fade to more investigative, and sometimes contingent, behavior, behavioral steps reached by toddlers by the ages of 9–12 months. Finally, children will start exhibiting self-directed behaviors, suggesting that they understand that the mirror portrays a reflection of themselves, between the ages of 15–22 months, whereas only a few nonhuman species reach this stage of mirror understanding (Reiss & Marino, 2001; Rochat, 2003).

Extensive investigations of primates' performances in this paradigm disclosed a divergent evolution between great apes and the remaining primate species in their ability to recognize themselves in mirrors (Anderson & Gallup, 2015; Inoue-Nakamura, 1997; *but see* Chang, Fang, Zhang, Poo, & Gong, 2015; Rajala, Reininger, Lancaster, & Populin, 2010). Only great apes were found to perform spontaneous self-directed behaviors when facing the mirror, and some individuals of these species successfully passed the mirror-mark test (Lethmate & Dücker, 1973; Povinelli, Rulf, Landau, & Bierschwale, 1993; Suarez & Gallup, 1981). Attempts to find MSR in other species rendered disparate results in several taxonomic groups. Some nonprimate mammals passed the mark test (such as bottlenose dolphins [*Tursiops truncatus*]: Reiss & Marino, 2001; and Asian elephants [*Elephas maximus*]: Plotnik, de Waal, & Reiss, 2006), whereas others failed, for example, panda (*Ailuropoda melanoleuca*; Ma et al., 2015), or results were inconclusive, for example, orca (*Orcinus orca*; Delfour & Marten, 2001). It should further be noted that among all the species that showed positive results on the mirror-mark test, generally only a quarter to a third of the tested individuals actually passed the mark test (Plotnik et al., 2006; Povinelli et al., 1993; Prior, Schwarz, & Güntürkün, 2008; Reiss & Marino, 2001). These high interspecies and interindividual disparities call into question the relation between the performances in the mark test and the possession of self-awareness. In addition, recent findings in insects and fish showed that ants (*Myrmica sabuleti*, *Myrmica rubra*, and *Myrmica ruginodis*; Cammaerts & Cammaerts, 2015) and cleaner wrasses (*Labroides dimidiatus*; Kohda et al., 2019) display behaviors indicative of self-recognition and that giant manta rays (*Manta birostris*) exhibit contingency checking and self-directed behaviors in front of mirrors (Ari & D'Agostino, 2016). These results indicate that the ability of self-recognition might be more widespread than initially assumed. However, the evidence of successful self-recognition in many of the aforementioned primate and all of the nonprimate animals are still being disputed (Anderson & Gallup, 2011, 2015; Gallup & Anderson, 2018). Alternatively, these findings may hint at a more gradualist view on animal self-awareness rather than it being a yes or no concept (de Waal, 2019).

Traditionally, birds, like fish, were assumed to only express social behaviors in front of mirrors and to not be able to pass the mark test (Gallup & Capper, 1970; Kraft, Forštová, Utku Urhan, Exnerová, & Brodin, 2017; Ryan, 1978; Stout, Wilcox, & Creitz, 1969). With the success of Eurasian magpies (*Pica pica*) equaling the performances of great apes in the mark test (Prior et al., 2008), interest has recently shifted back toward birds' understanding of mirrors. Renowned for their high encephalization index (Emery, 2006; Iwaniuk, Dean, & Nelson, 2005), large forebrain neuron numbers (Olkowicz et al., 2016), complex social structures, and advanced social and physical cognitive abilities, often found to equal the ones of apes (Emery, 2004; Emery & Clayton, 2004; Güntürkün & Bugnyar, 2016), corvids, like the Eurasian magpies,

harbor the potential of performing well in self-recognition tasks. However, although some corvid species perform well in mirror use tasks (Dally, Emery, & Clayton, 2010; Medina, Taylor, Hunt, & Gray, 2011), out of five species tested for MSR, three (i.e., New Caledonian crows [*Corvus moneduloides*; Medina et al., 2011], jungle crows [*Corvus macrorhynchos*; Kusayama, Bischof, & Watanabe, 2000], and jackdaws [*Coloeus monedula*; Soler, Pérez-Contreras, & Peralta-Sánchez, 2014]) failed to show significant self-directed behavior when presented with a mirror. Only two out of five Eurasian magpies and one out of 17 Clark's nutcracker (*Nucifraga columbiana*) showed evidence for self-recognition in the mark test (Clary & Kelly, 2016; Prior et al., 2008). The Clark's nutcracker, however, seemed to perform better in a blurred mirror condition (Clary & Kelly, 2016) than in a normal mirror condition, making the interpretation of these results even more difficult. Although the origin of the observed interindividual and interspecies variations remains largely unexplored, investigating MSR in further corvid species might allow us to triangulate the causes of these substantial differences.

Therefore, the present study examined the reaction to mirror image stimulation of carrion and hooded crows (from this point forth referred to as crows) which are food-caching birds (de Kort & Clayton, 2006; Goodwin, 1986), capable of individual recognition (Braun, 2013), and which live in complex fission–fusion societies (Deventer et al., 2016). As members of the corvid family they possess a high encephalization index (Emery, 2006) and perform well in various cognitive tasks (Balakhonov & Rose, 2017; Hoffmann, Rüttler, & Nieder, 2011; Smirnova, Lazareva, & Zorina, 2003; Smirnova, Zorina, Obozova, & Wasserman, 2015). They, thus, combine all characteristics formerly associated with MSR, making them ideal candidates for this type of investigations.

Based on the behavioral responses to reflective surfaces of other avian species (Andrews, 1966; Diamond & Bond, 1989; Gallup & Capper, 1970; Kraft et al., 2017; Kusayama et al., 2000; Medina et al., 2011; Pepperberg, Garcia, Jackson, & Marconi, 1995; Prior et al., 2008; Soler et al., 2014; Stout et al., 1969; van Buuren, Auersperg, Gajdon, & Tebbich, 2018; Watanabe, 2002), we predicted the crows in this study to overcome their neophobia toward the mirror, and to manifest a preference for the reflective surface (Gallup & Capper, 1970). We further anticipated the crows to initially exhibit social behaviors toward their reflection, but for these behaviors to fade with increased mirror experience and for behaviors of an investigative, contingent, and possibly self-directed nature to increase. In the second part of the study, we explored the crows' ability to pass the mirror-mark test. Successfully passing the mark test presupposes an interest on the animal's part in its mirrored reflection as well as a motivation to remove a colored mark applied to its body. It further presumes that the individual should only react to the applied mark as a response to the visual feedback given by a mirror and not as a consequence of tactile perception to be said self-recognizing. In this respect, the results of the jackdaws in Soler and colleagues' study have questioned the lately employed methods using stickers to mark the birds in the mark test. Although the magpies (Prior et al., 2008) that were marked using this method did not seem to exhibit signs of somatosensory cuing by the applied stickers, the jackdaws (Soler et al., 2014) that were marked using the same method, tried to remove the stickers from their throats as much in the mirror as in the nonreflective control condition, hinting toward a somato-

sensory perception of the stickers on the feathers. Therefore, in the present study, the crows were marked with a paint substitute. Should the crows meet the earlier cited conditions and manifest interest for their reflections as well as prove to be motivated to remove visible colored marks from their bodies, then crows could be expected to pass the mark test and should try to remove the marks on their bodies placed outside of their visual field only when allowed access to mirror.

Method

Subjects

Our captive crow colony consists of wild-caught and then hand-raised carrion crows (*Corvus corone corone*), hooded crows (*Corvus corone cornix*), and hybrids of these two subspecies ($n = 8$; three males and five females; age: 2–4 years), native to Europe's hybridization belt reflecting the composition of Austria's natural population. The crows were group- or pair-housed at the Haidlhof research facility in Bad Vöslau, Austria. Once in captivity, none of the crows had experience with mirrors prior to this experiment. Five of these subjects (three females and two males) were group living with two more crows that did not take part in this study and were housed in a large outdoor aviary ($9.6 \times 10 \times 5$ m). Out of the three other subjects, two were paired and kept in a separate outdoor aviary ($2 \times 10 \times 5$ m later $3 \times 6 \times 3$ m) and one was group-living during the first part of the experiment and pair-living for the second ($3 \times 6 \times 3$ m). The changes in group constellation and living arrangement were due to the formation of pair bonds within the group requiring the pairs to be transferred into new aviaries (see Table 1). The usual daily feeding protocols were kept up throughout the study, and all birds had ad libitum access to water in all compartments.

Apparatus

The apparatus consisted of a wooden frame with interchangeable plates (dimensions 50 cm \times 50 cm) that could hold either a plate covered with a silver foil (for habituation), a mirror, or a wooden board (for exposure and test sessions) and was permanently installed in the birds' home range compartments (see Figure 1). For the group-living subjects, the apparatus was suspended at 1 m 50 cm off the ground. For the paired subjects, the frame was placed on a table (surface: 70 \times 80 cm), 1 m off the ground. Both settings allowed the

birds to easily access all sides (including the back) of the apparatus and comfortably sit in front of it.

Ethical Statement

All birds participated voluntarily in the study. A bird was only tested when it came on its own into the compartment where the test was conducted. In case the bird exhibited signs of distress due to separation from the group or to external events, the session was aborted, and the bird was released back into the group. The tests, including the marking procedure described in the following text, were noninvasive and in adherence with the Austrian Animal Experimentation Act as well as the ethical guidelines of the Association for the Study of Animal Behaviour and were approved by the ethical board of the University of Vienna (number 2017–013).

Experimental Procedures

All birds were habituated to the apparatus holding a plate with nonreflective silver foil for 1 month prior to mirror image stimulation, to minimize neophobic reactions to the mirror during trials, while avoiding habituation to the mirror itself. The apparatus continued to display the silver foil to the birds outside of experimental sessions. The experiment comprised two parts, first a mirror image stimulation phase, which allowed the birds to gain experience with the mirror followed up by a mark test for seven out of the eight subjects (see Table 1).

Mirror image stimulation. The mirror image stimulation part of the experiment was two phased and consisted of group exposure and individual exposure. Group exposure sessions consisted of periods of free exploration of the apparatus in a group setting with ad libitum access to the compartment where the mirror was, intended to habituate the birds to the apparatus, to dampen neophobic reactions, and to quicken the individuals' approach to the apparatus, as subadult crows are known to increase the frequency of interactions with objects when conspecifics are present (Miller, Bugnyar, Pölzl, & Schwab, 2015). The six group-living as well as the two pair-bonded subjects received three sessions (two with a mirror in the apparatus and one with a wooden board in the frame) for a total of 190 min in the mirror condition and 130 min in the wood condition.

The subsequent individual exposure sessions consisted of 20-min sessions in which the tested subject was alone in the compartment where the mirror was. Birds were free to move around the

Table 1

Subject Characteristics: Name, Sex, Year of Birth (YoB), Living Arrangements, Types of Exposure to Mirrors, and Whether It Participated in the Mark Test (Y/N)

Subject	Sex	YoB	Living arrangements	Types of exposure	Mark test
Daisy	F	2012	Group living	Group ($n = 8$) + Individual	6 (out of 8) sessions
Saul	M	2012	Group living	Group ($n = 8$) + Individual	Y
Peppi	F	2012	Group living	Group ($n = 8$) + Individual	Y
Paula	M	2014	Group living	Group ($n = 8$) + Individual	N
Caruso	F	2013	Group living	Group ($n = 8$) + Individual	Y
Juno	M	2012	Group living (later pair living)	Group ($n = 8$) + Individual	Y
Corbie	F	2012	Pair living	Pair + Individual	Y
Rainer	M	2012	Pair living	Pair + Individual	Y

Note. F = female; M = male; Y = yes; N = no.

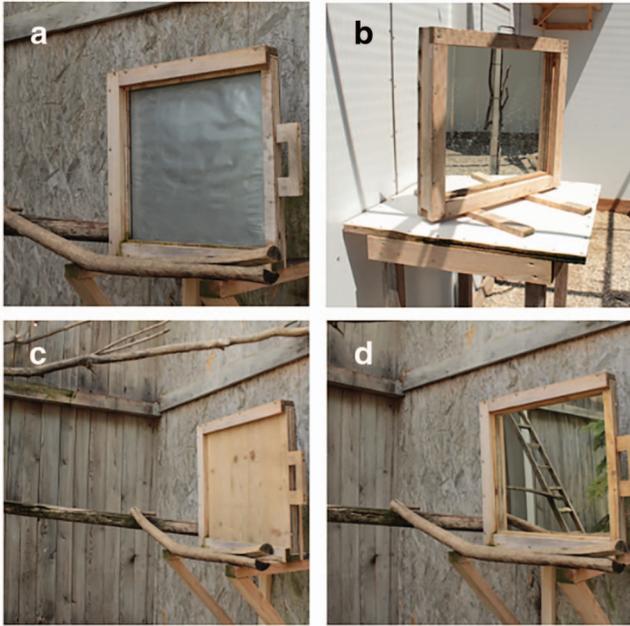


Figure 1. Experimental setup for the group-living (d) and paired (b) crows in the three conditions: silver foil, outside of testing sessions (a), mirror (b, d), and wooden control (c).

compartment (dimensions of the test compartment when kept in the group: 3.8 m \times 7 m \times 5 m; individuals paired during testing received their exposure in the 2-m \times 10-m \times 5-m compartment and were subsequently tested in a 3-m \times 6-m \times 3-m compartment) and to approach the apparatus at will. The birds were given at least five sets of sessions, one set consisting of two sessions in the mirror condition and one session in the control (wood) condition in a randomized order. In the first two sets of individual exposure, the apparatus got baited twice: at the start and 10 min into the session. In the second stage (three sets) the apparatus was only baited once at the beginning of the session. Each baiting event consisted of depositing seven small cubes of cheese in front of the apparatus that the test subjects could take within one visit to the apparatus. Two criteria had to be met by each bird before entering the mark test: complete 10 mirror sessions and five control sessions (corresponding to a total of 200 min of individual exposure to the mirror) and spend at least a cumulative time of 10 min in front of the mirror. Note that some birds received additional sessions of mirror exposure until they met the second criterion. Due to the transfer into another aviary, three of the birds (Juno, Corbie, and Rainer) received a supplementary four mirror- and four control-sessions after meeting criterion, as to habituate them to the mirror in the new aviary and to the slightly different setup (see Table 1).

Mark test. During the individual sessions, the birds were trained on being touched by a pencil, as to habituate them to the marking procedure used. Consequently, in the mark test the crows engaged in the marking procedure voluntarily, and we thus avoided stress related to catching and restraint (see Video S6 in the online supplemental materials). During the training procedure the crows were trained to approach the experimenter (Lisa-Claire Vanhooland) at the fence or come on the experimenter's arm,

while she presented a food reward, and to stay in this spot while being touched on the throat with a dry dyed brush (consequently, the tip of the brush was always colored, whether it was dry or applying the sham and colored mark). As in previous studies, we decided to mark the crows on their throats (see Figure 2), as this is a body part that birds should not be able to see without the help of a mirror (Prior et al., 2008).

The mark test consisted of two rounds of 20-min sessions per individual in each of the following four conditions: mirror-mark, mirror-sham, wood-mark, and wood-sham. In one round, we applied a blue mark to the birds, whereas we used red markings in the other round. The order of exposure to the different colors was randomized over the two rounds over the subjects. The order of condition within each round was randomized over the subjects. Some of the test sessions were aborted due to major disturbances in the environment (e.g., flocks of wild crows flying over the aviary) or unsatisfactory markings (e.g., mark positioned too low on the throat), and consequently were excluded from the analysis, and repeated at a later stage. Further, in case a bird's first visit to the apparatus was toward the end of the session and it subsequently sat still in front of the apparatus when the session ended, we analyzed the duration of that entire visit; that is, surpassing the 20-min cutoff.

Seven of the birds participated in the mark test in which a colored or transparent (sham) mark was applied to the subject's



Figure 2. Depiction of a colored mark on a crow's throat.

body before being given access to a reflective (mirror) or nonreflective (wooden plate) surface. The crows were marked on their throats using glycerin in its pure form (sham mark) or mixed with blue or red food coloring (mark; Figure 2). The sham mark controlled for the somatosensory cueing of the location of the mark. Glycerin is water soluble, odorless, and colorless in its pure form. Both glycerin in its pure form and food coloring are nontoxic and nonirritating and should therefore not be noticeable on the crow's plumage, easily washed off, and less conspicuous than a sticker.

Motivation control. An additional control session was conducted to test the crow's inclination to remove marks placed on their bodies only after completing all test sessions to minimize possible habituation to the markings on their body. The use of directly visible body marks allowed us to assess the crows' propensity to remove marks from their bodies, which allowed us to address the issue of a possible lack of motivation (i.e., the animal does not care about the marking), and to exclude this reason from the explanations for possible nonresponsiveness to the marks in front of the mirror (Gallup, Wallnau, & Suarez, 1980; Suarez & Gallup, 1981). For this motivational control, the crows were marked on directly visible parts of their body (i.e., belly, wings, or feet) with colored and sham marks and observed for 2 min after each marking.

Data Analysis

Each experimental session was recorded from the outside of the testing compartment by two cameras (Canon Legria HFG25 CMOS Pro). Video recordings were coded (by Lisa-Claire Vanhooland) for study-relevant behaviors (listed in the following text) with Solomon Coder Version beta (Péter, 2017) using continuous sampling. In all, 10% of all videos were also coded by a research assistant to measure interrater reliability. The measures we coded included the position of the birds in relation to the apparatus (in front, on top, behind and next to the apparatus) and their behavior when they were near it (Table S1 in the online supplemental materials). These behaviors were pooled into four categories: (a) social behaviors, that is, agonistic displays, aggressive behaviors toward the apparatus (e.g., tufted leg feathers [display of dominance], tufted ear feathers, thick head display due to erected head feathers or attacking the mirror by jumping against [see Video S1 in the online supplemental materials] it), and vocalizations (Video S1 in the online supplemental materials); (b) investigative behaviors, that is, pecking the apparatus's surface and frame (see Video S2 in the online supplemental materials), looking behind (Video S2 in the online supplemental materials) or under the apparatus; (c) contingent behavior, that is, stretching and "peekaboos" (the bird moves out and back in sight of the mirror within 3 s—see Video S3 in the online supplemental materials); and (d) self-directed behaviors, that is, autopreening and scratching (see Video S4 in the online supplemental materials). As the number of sessions differed per condition and across individuals, we calculated the individuals' mean values per variable, and subsequently analyzed these using two-tailed Wilcoxon's Signed-Rank and Friedman Tests in IBM SPSS Statistics 23 as well as a Change Point Analyzer (Taylor, 2007). Interrater reliability (two-way random effects model of intraclass correlation coefficient [ICC]) was evaluated using SPSS (v.24.0). The median ICC value was 0.999 (interquartile range 0.945 to 1; range: 0.352–1). This large range in ICC is caused by

one behavior that is, "looking behind" which rendered a very low interrater correlation; however, this was an exception (see Table S2 in the online supplemental materials). The interrater reliability was otherwise satisfactory.

Results

Individual Mirror Image Stimulation

During the individual exposure sessions, the crows ($n = 8$) visited the apparatus significantly more often in the mirror condition (Mirror: 2.12 ± 0.49 s, Wood: 1.54 ± 0.47 s, $T^+ = 33$, $N = 8$, $p = .036$, $r = -0.525$) and spent significantly more time close to the apparatus when it contained a mirror than when it contained the control board (Mirror: 54.05 ± 11.87 s, Wood: 30.64 ± 12.45 s, $T^+ = 36$, $N = 8$, $p = .012$, $r = -0.630$). They further spent significantly more time directly in front of the apparatus when it contained the mirror than when it contained the wooden control plate (Mirror: 36.04 ± 13.90 s, Wood: 18.15 ± 14.99 s, $T^+ = 36$, $N = 8$, $p = .012$, $r = -0.630$; see Figure 3) but did not spend more

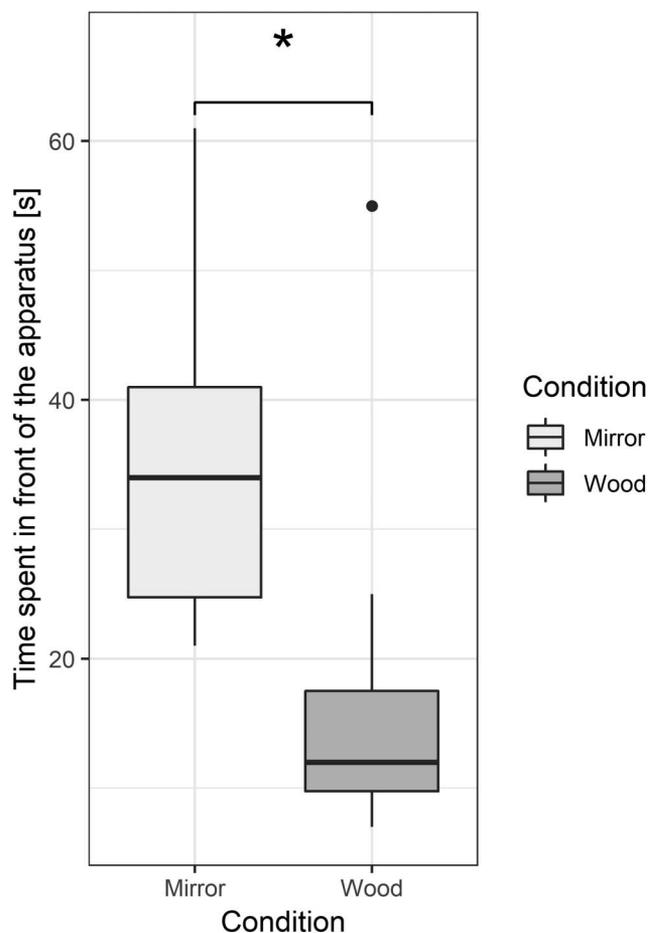


Figure 3. Amount of time spent in front of the apparatus per session at the group level in the mirror and wood condition during individual exposure sessions. Box plots represent medians (line), upper- and lower quartile range (box) ± 1.5 and the respective interquartile range (whiskers); * $p < .05$.

time behind (Mirror: 1.02 ± 1.65 s, Wood: 0.29 ± 0.55 s, $T^+ = 8$, $N = 8$, $p = .273$, $r = -0.274$), on top of (Mirror: 5.05 ± 2.69 s, Wood: 2.28 ± 1.79 s, $T^+ = 31$, $N = 8$, $p = .069$, $r = -0.455$), or next to (Mirror: 12.08 ± 6.54 s, Wood: 9.91 ± 4.93 s, $T^+ = 22$, $N = 8$, $p = .575$, $r = -0.14$) the apparatus. They also spent significantly more time performing close inspection in front of the mirror (Mirror: 7.06 ± 5.88 s, Wood: 0.15 ± 0.32 s, $T^+ = 36$, $N = 8$; $p = .012$, $r = -0.630$).

Social behaviors, generally exhibited first in response to a mirror, tended to be performed more often in front of the mirror than in front of wood ($T^+ = 24$, $N = 8$, $p = .091$, $r = -0.393$). Most of the social behaviors observed were vocalizations not specifically addressing the mirror image. Only three instances of other social behaviors were observed during the experiment.

Further, not all investigative behaviors were exhibited more frequently in front of the mirror than in front of the control (Figure 4a), but some behaviors of this category showed a significant difference between the two conditions: For example, with regard to investigative behaviors, pecking the surface of the apparatus (mirror or wood) happened significantly more often toward the mirror than toward the wooden plate ($T^+ = 28$, $N = 8$, $p = .018$, $r = -0.596$; Figure 4b), while looking under ($T^+ = 1.5$, $N = 8$, $p = .655$, $r = -0.447$) and looking behind ($T^+ = 7$, $N = 8$, $p = .463$, $r = -0.184$) did not. Note, however, that results regarding looking behind should be treated with care due the low interrater reliability.

Like investigative behaviors, not all behaviors from the behavioral category of contingency checking were exhibited more frequently in front of the mirror than in front of the wooden plate ($T^+ = 18$, $N = 8$, $p = .116$, $r = -0.506$), as none of the crows stretched in front of either the mirror nor the wood, and object manipulations rarely occurred (Figure 4a). The crows, however, performed significantly more “peekaboo” behaviors (i.e., staring at mirror image and then quickly moving their heads in and out of view within 3 s) in the mirror than in the control condition ($T^+ = 15$, $N = 8$, $p = .043$, $r = -2.023$; Figure 4b).

Finally, we did not find a difference in amount of self-directed behaviors displayed in front of the apparatus between both conditions ($T^+ = 3$, $N = 8$, $p = .180$, $r = -0.336$), as only two events of autopreening and four events of scratching were recorded in two subjects while each was perched in front of the apparatus (however, all were performed in front of the mirror).

The behaviors performed by the crows in front of the mirror appeared to supersede each other in the expected order on a group level (see Figure 5). Most social behaviors occurred between the first and ninth individual mirror session. Investigative behaviors were mostly exhibited between the fifth and 12th individual mirror session, with a significant drop in investigative behaviors on Session 13 (Taylor’s change point analysis: Level 1, 96%). Contingency checking behaviors mostly occurred between the sixth and the 15th individual mirror session and were never observed in the first five sessions. Finally, we found a significant rise in self-directed behaviors in Session 16 (Taylor’s change point analysis, Level 1, 91%) that did not appear in the control condition. Not all fluctuations were significant, but this may be due to the low occurrence of some behaviors, making the changes difficult to detect in the analysis. Further, such changes rarely occurred on an individual level, and the string of behaviors patterns did not follow

the expected pattern in all individuals (Figure S1 in the online supplemental materials).

Mark Test

In the *Motivation Control*, when the applied mark was directly visible to the individual, each subject reacted to the colored mark shortly after being marked and tried to remove the mark by preening the area until cleaned. None of the subjects had a similar reaction to the sham mark. Thus, these types of marks are suited for the controlled conduct of the classical mark test.

Although all subjects met the set criteria, only six of the eight mirror-experienced crows completed all the sessions of the mark test. One of the birds (Paula) never habituated to the marking procedure and was therefore excluded from the test and the motivational control, and a second bird (Daisy) completed six out of the eight test sessions as she refused to be marked again in the last two test sessions. The results beneath are presented in exclusion and inclusion of this individual ($n = 6$ and $n = 7$). Neither the number of visits to the apparatus ($\chi^2 = 3.911$, $N = 6$, $p = .271$, $W = 0.217$; $\chi^2 = 3.609$, $N = 7$, $p = .307$, $W = 0.172$) nor the time spent close to the apparatus ($\chi^2 = 5.4$, $N = 6$, $p = .145$, $W = 0.300$; $\chi^2 = 5.571$, $N = 7$, $p = .134$, $W = 0.265$) differed between the four conditions. There was, however, a significant difference in the time spent in front of the apparatus ($\chi^2 = 15.2$, $N = 6$, $p = .002$, $W = 0.844$; $\chi^2 = 13.114$, $N = 7$, $p = .004$, $W = 0.624$) between the mirror-mark and the wood-mark conditions (see Figure 6; post hoc test; $T^+ = 0$, $N = 7$, $p = .018$, $r = -0.632$; $T^+ = 0$, $N = 6$, $p = .028$, $r = -0.635$). But, no significant difference was found between the mirror-mark and mirror-sham conditions (post hoc test: $T^+ = 12$, $N = 7$, $p = .735$, $r = -0.090$; $T^+ = 12$, $N = 6$, $p = .753$, $r = -0.091$), nor between the wood-mark and wood-sham condition (post hoc test: $T^+ = 15$, $N = 7$, $p = .866$, $r = -0.045$; $T^+ = 15$, $N = 6$, $p = .345$, $r = -0.272$; see Figure 6). Importantly, no difference in the crows’ self-directed behaviors was found between the conditions ($\chi^2 = 2.0$, $N = 6$, $p = .572$, $W = 0.111$; $\chi^2 = 2.0$, $N = 7$, $p = .572$, $W = 0.095$). Only one event of mark-directed behavior was recorded in front of the apparatus throughout the experiment, in which the bird (Rainer) attempted to remove the red mark on its throat with its beak while standing in front of the mirror (see Video S5 in the online supplemental materials). This behavior was, however, not repeated in a later session of the same condition. The behavior of the birds in the four experimental conditions did not differ significantly with regard to the amount of investigative behaviors ($\chi^2 = 3.8$, $N = 6$, $p = .284$, $W = 0.211$; $\chi^2 = 3.8$, $N = 7$, $p = .284$; $W = 0.181$), but the crows showed a tendency to still exhibit more contingency checking behaviors in the mirror conditions ($\chi^2 = 7.2$, $N = 6$, $p = .066$, $W = 0.400$; $\chi^2 = 9.923$, $N = 7$, $p = .019$, $W = 0.209$). Further, there was no effect of the color of the mark on the crow’s behavior. When facing the mirror with a blue or red mark on their throat, the crows did not show differences in self-directed behavior ($T^+ = 1$, $N = 6$, $p = .317$, $r = -0.289$) nor in the amount of time they spent close to ($T^+ = 18$, $N = 6$, $p = .116$, $r = -0.454$) and in front of ($T^+ = 14$, $N = 6$, $p = .463$, $r = -0.211$) the mirror.

Discussion

The present investigation of crows’ responses to reflective surfaces through mirror image stimulation showed that crows

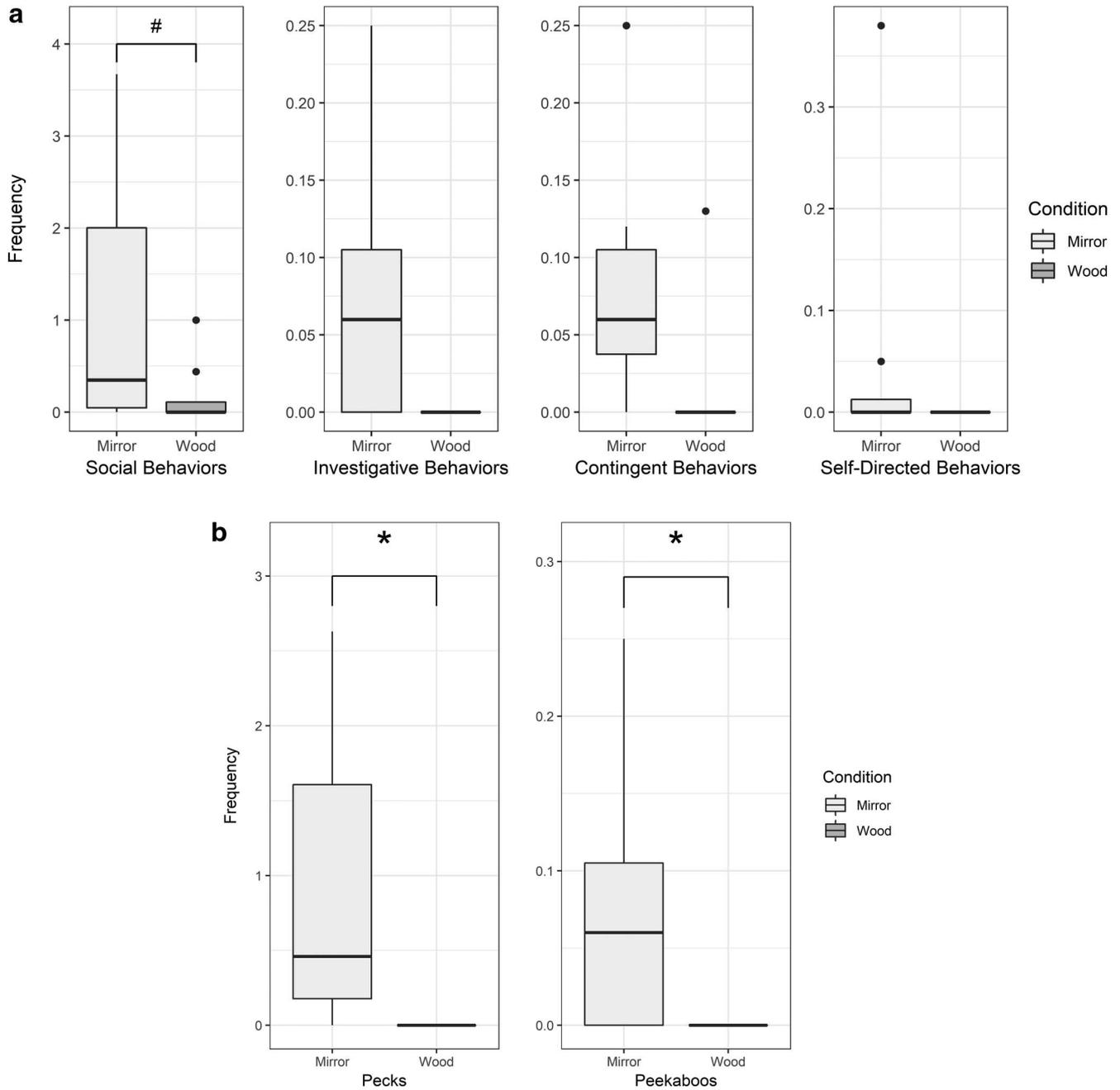


Figure 4. (a) Frequency of the four behavioral categories in the mirror and wood condition during individual exposure. Box plots represent medians (line), upper- and lower quartile range (box) ± 1.5 and the respective interquartile range (whiskers); * $p < .05$ and # indicates $0.1 > p > .05$. (b) Frequency of pecking and “peekaboo” behaviors per session in the mirror and wood condition. Box plots represent medians (line), upper- and lower quartile range (box) ± 1.5 and the respective interquartile range (whiskers); * $p < .05$.

were willing to explore the apparatus once they overcame their neophobia and were particularly keen to do so when it contained a mirror. Although the crows did not exhibit any aggressive or self-directed behaviors toward their reflection, some of the crows did show indications of contingency testing (e.g., “peekaboo”) that may be considered a precursor

of self-recognition (Rochat, 2003). In the subsequent mark test, however, the crows (with one exception) did not exhibit any mark-directed behaviors, whereas they did remove colored marks placed on directly visible body parts, suggesting that they did not demonstrate an ability of mirror-self-recognition.

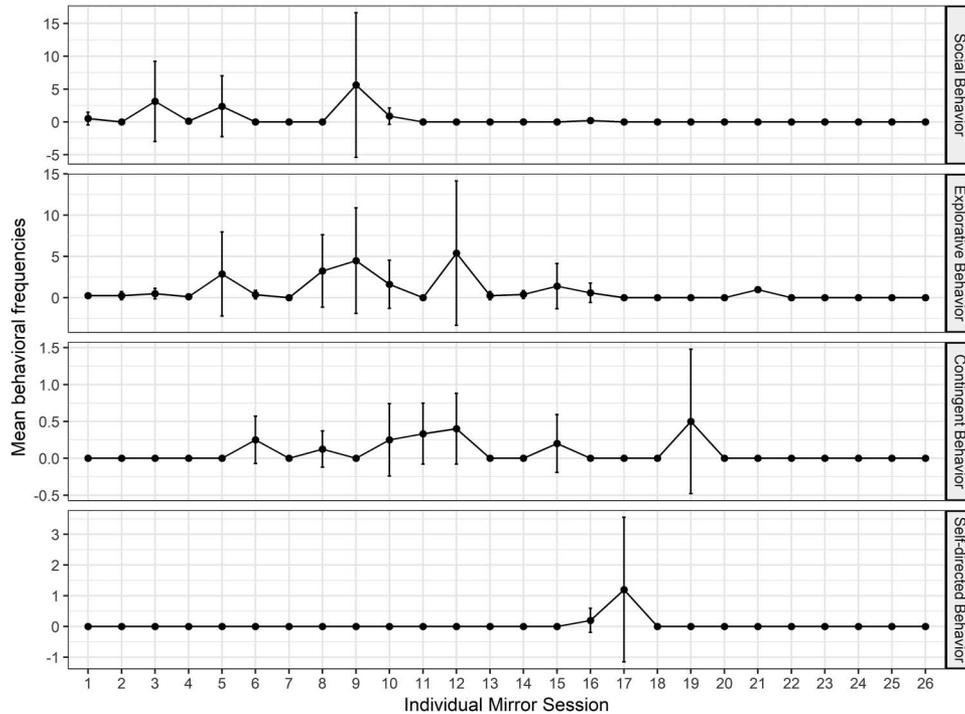


Figure 5. Group averages (and 95% confidence interval) of the number of social, investigative, contingent, and self-directed behaviors exhibited by the crows during the individual mirror sessions (excluding habituation sessions).

Behavioral Response in Front of Mirrors

Crows showed interest in the mirror throughout the study and exhibited behaviors that can be ascribed to the behavioral categories previously described in mammals, which are subsequently related to different levels of mirror understanding. The crows manifested a clear preference for the mirror's reflective surface, which is commonly found in many avian species (e.g., finches: Ryan, 1978; budgerigars: Gallup & Capper, 1970; sparrows: Watanabe, 2002; magpies: Prior et al., 2008; jackdaws: Soler et al., 2014) and primate species (e.g., chimpanzee: Povinelli et al., 1993). Yet, contrarily to those species, the crows in the present study hardly engaged in any aggressive or submissive behaviors when facing their reflection. Instead, they already started displaying investigative behaviors during the group habituation phase of the experiment, which generally occurred only after an animal had shown social behavior toward its mirror reflection. Although it is conceivable that the crows overcame the stage of social behaviors during the group sessions of the habituation process, the data do not support this hypothesis, as we did not find significant differences in social behavior exhibited in front of the mirror or the nonreflective control during these sessions. In two out of three instances of coded *aggressive behaviors*, the crows, like many other birds, jumped or flew against the mirror resembling an attack. However, these behaviors were neither preceded nor followed by any form of social display nor repeated at any point, unlike the behavior they would exhibit toward conspecifics in an aggressive context and unlike the repeated social behavior exhibited in front of mirrors by other avian species (Gallup & Capper,

1970; Ryan, 1978; Stout et al., 1969). It is therefore probable that these occurrences were misjudgments of the virtual space of the mirror and part of the learning process of the mirror's physical properties for some of the birds.

The crows manifested their interest in the mirror through extensive explorations. They investigated the apparatus mostly through the pecking of its frame and surface, a commonplace behavior in crows, that they exhibited more in response to the mirror. However, against our expectation they did not explore the space behind the apparatus ("looking behind" behavior) more in the mirror condition. Despite being commonly interpreted as a searching behavior for the conspecific observed in the mirror and assumed to be the second level of mirror interaction, it is possible that in this case the behavior rather conveyed the crows' curiosity to investigate the space behind the visual barrier, irrespective of what kind of surface it contained.

Nonetheless, behaviors like *peekaboos* were performed significantly more in the mirror condition and do indicate a form of contingency checking. These behaviors attest to a certain understanding of the physical properties of a mirror learned by the prolonged exposure to the mirror and are comparable with the performances of New Caledonian crows (Medina et al., 2011) and African gray parrots (Pepperberg et al., 1995). Additional testing would, however, be required to prove that the crows in the present study, like the New Caledonian crows and African gray parrots are also able to use mirrors in a food location task. The fact that contingent behaviors only started arising in the fifth individual session is a further indication for the exposure-dependent nature of

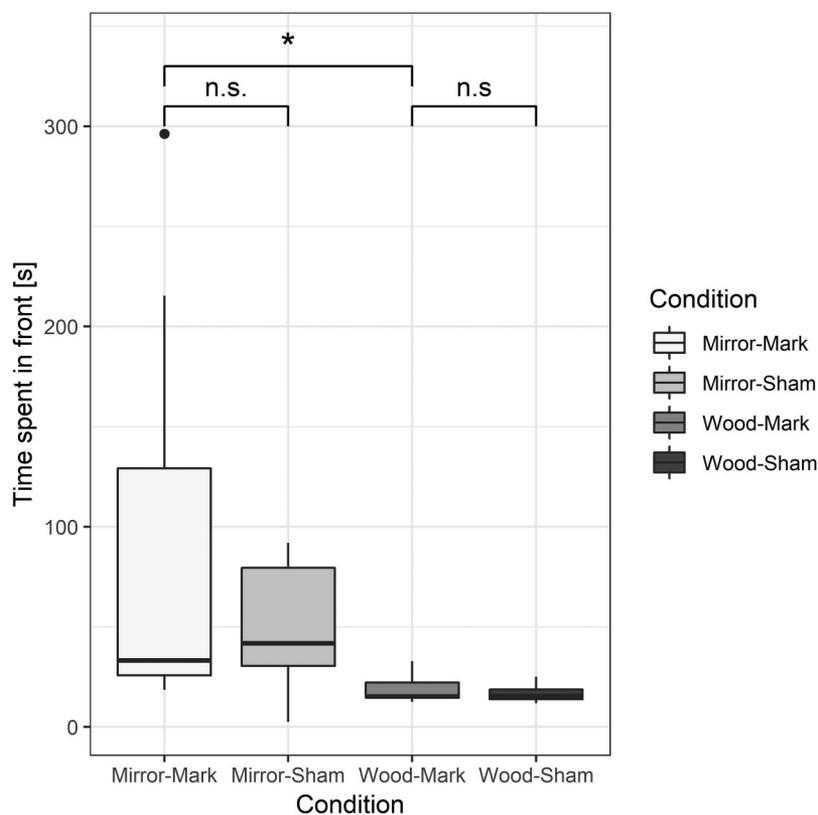


Figure 6. Amount of time spent in front of the apparatus in the four conditions of the mirror-mark test. Box plot represent medians (line), upper- and lower quartile range (box) ± 1.5 and the respective interquartile range (whiskers); * $p < .05$. n.s. $p > .05$.

this behavior and the development of a better mirror-understanding over the course of the sessions by the crows. It is open to question how much time a species or an individual may need to reach the different stages of mirror understanding. For example, in chimpanzees reports of the time required to reach the stage of self-exploration vary from just a couple of minutes to several days (Povinelli et al., 1993). The crows in this study (with one exception) needed a total of 260 min of mirror exposure before starting to exhibit contingent behaviors, which stands in contrast to magpies (Prior et al., 2008) that started exhibiting contingency checking behaviors already after 150 min of exposure. These differences, however, could originate from methodological discrepancies between the two studies. Although the total exposure time (i.e., time of access to the mirror) of the two species was comparable, the sizes of the crows' testing compartments largely exceeded the ones used for testing the magpies (Prior et al., 2008) and jackdaws (Soler et al., 2014), offering the crows many locations to perch out of sight of the mirror, whereas the magpies and jackdaws were forced to stay on the ground at the level of the mirror (Prior et al., 2008; Soler et al., 2014). The crows, therefore, had all in all less time in direct view of the mirror than, for example, the two magpies that passed the mark test, as none of the crows spent as much time in front of the mirror in one session as these individuals. It is therefore conceivable that the crows might have required more testing sessions to equal the amount of time

spent in front of the mirror by the magpies. This assertion is substantiated by the fact that contingency checking behaviors only occurred in later sessions, and that the few birds that did show self-directed behaviors only did so in the final sessions.

Although crows should be expected to attend to their plumage as diligently as magpies and jackdaws, the exhibition of self-directed behavior by the crows in this study was rare during the exposure sessions. This pattern continued in the mark test where we only recorded one other event of self-directed behavior in front of the apparatus. It should be noted, however, that the crows in our experiment were not restricted to stay on ground level and could move to a higher perch out of sight of the mirror, which is where they usually choose to preen.

Methodological Issues

Somatosensory cuing by the marks on the subject's body has always been a methodological concern in the mark test (Bard, Todd, Bernier, Love, & Leavens, 2006; Soler et al., 2014). All three previous mark test studies on corvids (Clary & Kelly, 2016; Prior et al., 2008; Soler et al., 2014) made use of stickers to mark their subjects. After several jackdaws reacted to the sticker on their throat to an equal amount in the mirror and control condition, Soler and colleagues (2014) suggested this type of marking procedure to cause the birds to feel the mark on their plumage and react to this

sensation by preening or scratching the area rather than reacting to their mirrored body image. Whereas they also used black marks as a control, something the birds did not react to when confronted with a mirror, these authors further questioned the efficiency of such black stickers as controls for the colored stickers when placed on the birds' black yet iridescent feathers. Unfortunately, none of these studies report the birds' reaction to these markings when directly visible on their plumage as to ensure that the black stickers are indeed not noticed by the birds. In contrast, the crows' attempts to remove the colored mark when applied on a visible body part and the lack thereof when marked with the sham mark, as well as the lack of mark-directed behavior in the two wood-control conditions of the mark test indicate that the method employed to mark the animals in the present study proves effective and does not elicit self-directed behaviors caused by somatosensory cuing of the marks location. At the same time, our marking procedure possesses the advantage of not requiring any catching nor fixation of the bird to apply the mark, therefore, making it a nonstressful event for the bird. We were thus able to show that the crows were motivated to remove colored marks from their body and that the colored marks were salient enough to be perceived and to incite a response (i.e., preening behavior). Yet importantly, apart from one subject, the crows ultimately did not exhibit such behaviors in the mark test.

Comparison Across Species

The findings of corvids' reactions to mirrors raise the same issues about interspecies and interindividual differences in visual self-recognition as previously observed in primates. In both taxa, only a restricted number of species seem to be able to recognize themselves in mirrors and within these species only about one third of the experimental subjects also pass the mark test (e.g., chimpanzees: Povinelli et al., 1993; magpies [two out of five]: Prior et al., 2008; elephants [one out of three]: Plotnik et al., 2006). Most species, like the crows in our study, seem to fail this test despite sharing the common characteristics of self-recognizing species. Moreover, the possible origins of these discrepancies in nonhuman species, aside from cognitive capacities (e.g., a species' ecology, neuroanatomy, personality, ontogeny, or genetics) have rarely been addressed (Hecht, Mahovetz, Preuss, & Hopkins, 2017; Lin, Bard, & Anderson, 1992; Mahovetz, Young, & Hopkins, 2016). We therefore need more in-depth investigations of the proximate mechanisms of interspecific and interindividual variation in visual self-recognition, as (for example) culture, experience, and neuropsychiatric states are known to affect MSR in humans (Brosch, Callaghan, Henrich, Murphy, & Rochat, 2011; Platek & Gallup, 2002) resulting sometimes in documented cases where even humans fail the mark test (Gallup, 1997).

Finally, the inspection of body parts that individuals would usually not have visual access to (e.g., facial features or genital regions), is a common indication for MSR in mammals. We did not record any indubitable event of mirror-guided inspections of otherwise not visible body parts by the crows in this study. However, the observation of this type of self-directed behavior poses difficulties in avian species, as birds are known to be able to see most of their body without requiring the help of a mirror (Jahnke, 1984). The few out of sight body areas (i.e., inside of the beak, throat, and top of the head) are also for good parts out of the

reach of the beak, making the definition of behavior indicating MSR prior to the mirror-mark test challenging for birds. The crows' failure in the mark test unfortunately also only provides uncertain conclusions about their ability of visual self-recognition and capacity of self-awareness. Whereas passing the mark test can prove MSR, failing cannot be construed as a lack of MSR, and even less as a lack of self-awareness (Gallup, 1993). A more gradualist view of animal self-awareness (de Waal, 2019) may aid in our interpretation of these results, yet so far has not led to conclusive and testable hypotheses. Therefore, further investigations into these questions are indispensable to draw definitive conclusions about the level of understanding crows have of reflective surfaces and of themselves.

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