

Carrion Crows (*Corvus corone corone*) Fail the Mirror Mark Test Yet Again

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The mirror mark test is generally considered to be an indicator of an animal's ability to recognize itself in the mirror. For this test, an animal is confronted with a mirror and has a mark placed where it can see the mark only with the help of the mirror. When the animal extensively touches or interacts with the mark, compared with control conditions, the mirror mark test is passed. Many nonhuman animal species have been tested, but few have succeeded. After magpies and Indian house crows passed, there has been a sustained interest to find out whether other corvids would pass the mirror mark test. Here, we presented 12 carrion crows (*Corvus corone corone*) with the mirror mark test. There was no significant increase of mark-directed behavior in the mirror mark test, compared with control conditions. We find very few occasions of mark-directed behaviors and have to interpret them in the context of self-directed behavior more generally. In addition, we show that our crows were motivated to interact with a mark when it was visible to them without the aid of a mirror. We conclude that our crows fail the test, and thereby replicate previous studies showing a similar failure in corvids, and crows in particular. Because our study adds to the growing literature of corvids failing the mirror mark test, the issue of mirror self-recognition in these birds remains controversial.

Keywords: carrion crow, self-recognition, mirror mark task, corvid cognition

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Fifty years ago, Gallup (1970) devised the so-called mirror mark test to study the question whether nonhuman animals can recognize themselves in a mirror. In this mirror mark test, a mark is placed on the body where it is impossible for the animal to detect visually. Then, the animal is confronted with its own mirror reflection. When the animal touches this mark (i.e., exhibits mark-directed behaviors) in the presence of the mirror, it is assumed to pass the test and recognize its mirror reflection as itself. The mirror mark test relies on important controls to rule out explanations related to sensory cues or handling during the marking: Subjects should not show mark-directed behavior when a sham marking is applied, or when no mirror is present. Importantly, the mirror mark test is preceded by a familiarization period where the animals can learn about the properties of the mirror. Animals often spontaneously respond with social

behaviors toward their mirror image, such as by threatening or attacking their reflection (Gallup, 1970), or “shadow boxing” (Roerig, 2013). Interestingly, individuals who pass the mirror mark test will typically show less of these behaviors over time and congruently start to explore the mirror and their reflection in the mirror (contingency checking, i.e., unusual repetitive body movements; Povinelli, Rulf, Landau, & Bierschwale, 1993). In a last stage, the animals proceed to inspect their body with help of the mirror (Gallup, 1970; Kohda et al., 2019; Plotnik, de Waal, & Reiss, 2006; Reiss & Marino, 2001).

The ability to recognize oneself in a mirror is considered to be a marker of self-recognition or even self-awareness (Bard, Todd, Bernier, Love, & Leavens, 2006; Gallup, 1970), an interpretation criticized by others (Heyes, 1994), and other tests have been proposed (Dale & Plotnik, 2017). Still, mirror self-recognition is associated with, and is at times even considered to be a prerequisite of, higher cognitive abilities, especially in the social domain (Lewis & Brooks-Gunn, 1979). Chimpanzees and orangutans reliably pass this test of self-recognition (Gallup, 1970; Lethmate & Dücker, 1973; Suarez & Gallup, 1981). In addition, magpies, dolphins, and elephants are routinely cited as passing the mark test (Plotnik et al., 2006; Prior, Schwarz, & Güntürkün, 2008; Reiss & Marino, 2001). However, reports of nonprimate self-recognizers have been heavily debated (Soler, Pérez-Contreras, & Peralta-Sánchez, 2014), for example, due to the small number of animals passing the mirror mark test (Gallup & Anderson, 2018) or due to

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difficulties defining which behavior constitutes “mark-directed” behavior in animals outside the primate order (Kohda et al., 2019).

It has been a longstanding question whether birds of the crow family, such as ravens, crows, jays, and magpies, can recognize themselves in the mirror. Corvids are known for their cognitive sophistication (Brecht, Hage, Gavrilov, & Nieder, 2019; Clayton & Emery, 2015; Ditz & Nieder, 2016; Moll & Nieder, 2015; Nieder, 2017), and their social–cognitive abilities specifically. For example, Eurasian jays have been reported to flexibly respond to the desires of their partner (Ostojčić et al., 2016; Ostojčić, Shaw, Cheke, & Clayton, 2013), and ravens and California scrub-jays seem to be sensitive to the perspective and knowledge of their conspecifics (Bugnyar, Reber, & Buckner, 2016; Dally, Emery, & Clayton, 2006). This behavior has earned corvids the title of “feathered apes” (Emery, 2004)—but do they share the capacity for self-recognition with some of the great apes, too?

Previous studies have yielded mixed results of mirror mark tests in corvids: Magpies and Indian house crows are the only species that spontaneously showed increased mark-directed behavior when presented with a mirror, as opposed to when no mirror is present (Buniyaadi, Taufique, & Kumar, 2019; Prior et al., 2008). However, other corvid species such as California scrub-jays (Clary, Stow, Vernouillet, & Kelly, 2020), jackdaws (Soler et al., 2014), and carrion crows (Vanhooiland, Bugnyar, & Massen, 2019) have previously failed the mirror mark test.

Studies investigating mirror use and recognition in other contexts have reported similarly mixed results. For example, scrub-jays do not seem to treat their mirror reflection as an (unknown) conspecific: When confronted with a mirror during caching, scrub-jays did not protect their caches later on. They recached a similar amount of caches when they had been caching alone as when in front of mirror, and in both conditions less than when observed by a conspecific (Clary et al., 2020; Dally, Emery, & Clayton, 2010). This result suggests that they might have recognized their mirror reflection. By contrast, Clark’s nutcrackers suppressed caching both when they were observed by a conspecific and when confronted with a clear mirror reflection of themselves. Only when confronted with a blurred mirror did they increase caching to similar levels as when they were alone, and some of the nutcrackers showed an increase of mark-directed behaviors in the blurred mirror condition. However, when confronted with a standard mirror, they did not pass the test (Clary & Kelly, 2016). Lastly, New Caledonian crows have been able to use a mirror to locate hidden food, suggesting that they understand the relationship between the

mirror reflection and reality (Medina, Taylor, Hunt, & Gray, 2011).

In sum, whether or not corvids recognize themselves in the mirror mark test is still debated. We here tested 12 carrion crows with the mirror mark test. We closely mirrored the testing conditions of Prior et al. (2008) in that our crows were tested in a compartment that ensured that they were exposed to their mirror image during testing, that is, that they could not get out of reach of the mirror. However, we marked them not with a sticker, as in the original study, but with a liquid chalk marker. Before the mirror mark test, our crows were given 8 days of all-day familiarization with the mirror. Their behavior during this time was recorded and analyzed.

Method

Subjects and Housing

We tested 12 male carrion crows (*Corvus corone corone*) in this study. The crows were housed at the Animal Physiology Unit at the Institute of Neurobiology of the University of Tübingen in accordance with German and European law and the Guidelines for the Care and Use of Laboratory Animals of the National Institutes of Health. All crows were hand-raised and lived in large aviaries in groups of two to four individuals. All crows were mirror-naïve at the beginning of the experiment and participated in other daily experiments where they were each in the care of one experimenter. All experimental procedures were approved by the local ethical committee and authorized by the national authorities (Regierungspräsidium Tübingen).

Materials

The crows were tested in a separate testing compartment, measuring 105 cm × 105 cm × 140 cm (see Figure 1A) where they were visually and auditorily isolated from their conspecifics. The mirror (80 cm × 80 cm) was a standard, silver-coated, rear-surfaced mirror, placed on the far end of the compartment.

We marked the crows using a yellow liquid chalk marker (Schneider Maxx 265) that used a combination of water and chalk and is removable with water. In the sham condition, we used the same pen but without color. Consequently, in both the “real” marking and the sham marking, the crows should have had the

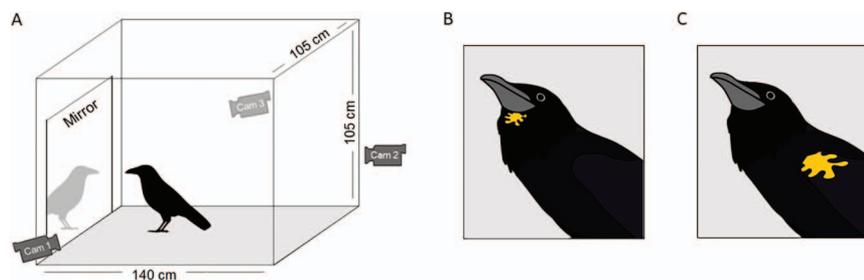


Figure 1. Mirror mark test setup. (A) Illustration of the testing compartment. (B) Location of the mark in the mirror mark test (in yellow). (C) Location of the mark in the visible mark test (in yellow/gray). See the online article for the color version of this figure.

same sensation where the mark was applied, but only in the mark condition the mark was colored.

Procedure Mirror Mark Test

Four conditions were conducted in a randomized order: no mirror present and sham marking (*no-mirror sham*), no mirror present and marked (*no-mirror mark*), mirror present and sham marking (*mirror sham*), and mirror present and marked (*mirror mark* condition). In the trials where no mirror was present, the mirror was covered with a nonreflective gray plastic plate. We introduced the controls to ensure that any behavior in the mirror mark test was not simply due to the marking process the crows underwent (both sham conditions), or any tactile perception of the mark (no-mirror mark condition). The sham-mark no-mirror condition served to assess baseline self- and mark-directed behaviors.

The crows were fed before testing, either in the context of their daily experiments, or in their housing aviary. One condition was conducted per day, with a duration of 20 min, which is the usual duration for the mirror mark test (Gallup, 1970; Prior et al., 2008). We ran each condition twice to account for daily fluctuations in activity or alertness. Consequently, each crow participated in eight sessions on 8 consecutive days. They were brought into the compartment by their experimenter. Then, the mark was applied on the throat area, under the beak (see Figure 1B), ensuring that the bird could not see the mark without the use of a mirror. During the process, the crows were handled by their experimenter and held in such a way that they would not see the marking. Jan Müller then applied the mark. In addition, four different regions on the body were gently pressed to avoid drawing attention to the marked region.

Familiarization and Mirror Exploration

Because corvids are neophobic, we introduced the mirror in their aviaries gradually. First, a mirror (120 cm × 80 cm, 2.5 cm from the floor) was left covered with nonreflective opaque plastic in the aviary for 5 days. After these 5 days, the mirror was uncovered and left in the aviary for 8 consecutive days, giving the crows a chance to explore the mirror and learn about its properties. After this familiarization period, they participated in the mirror mark test. The crows typically spend a minimum of 20 hr in their housing aviary each day, and around 40% of that time on the floor, giving them a total of ~64-hr exposure to the uncovered mirror in the aviary.

Subsequently, the crows were gradually introduced to the testing facility over the course of 3 days. On the first day, the crows spent up to 30 min in the compartment with no mirror present. During that time, the crows had access to 10 to 20 mealworms in a bowl, placed in the middle of the compartment. After they approached the food, we considered them familiarized, and moved on to present them with a mirror in this setup. Here, they had 2 days and 30 min each day to approach the food. Once they approached the food with the mirror present, they moved on to the mirror mark test. Notably, all crows fed from the mealworms on the first day the mirror was present.

Visible Mark Test

One difficulty with the mark test is the possibility that the tested animals are not motivated to remove the mark even if they would be able to see it. For example, because keas were not motivated to remove a painted mark, they were marked with food (van Buuren, Auersperg, Gajdon, Tebbich, & von Bayern, 2018). To assess how many crows would, assuming they pass the mirror mark test, remove the mark once they notice it in their reflection, we conducted a visible mark test 6 months after the mirror mark test. All crows that participated in mirror mark test were tested. The procedure was the same as in the mirror mark test; however, now, the mark was placed on their wings, clearly visible to them (Figure 1C). As a control, the birds were marked with a sham mark on the same spot. The two conditions were conducted on two separate days, and the crows were presented with both conditions twice, to mirror the procedure from the mirror mark test. The order of trials was counterbalanced.

Behavioral Recording

We used Panasonic HC-V160 camcorders to record the crows' behavior during the familiarization period and the test. Additionally, the crows' behavior during test trials was monitored via a video system from an adjacent room. Self-directed behavior (preening, cleaning of the feet) and mark-directed behavior (touching the mark with the beak or foot) were assessed during the mirror and the visible mark test trials.

To investigate the crows' behavior during the familiarization period with the open mirror, the crows' behaviors were video recorded for 8 consecutive days from 6:00 to 21:00 each day. On each day, the behavior of our adult crows ($n = 8$: Buddy, Callimero, Edgar, Jello, Ozzy, Vince, Walt, and Yoshi) was scored during three time slots of 1.5 hr each: 6:30–8:00, 12:00–13:30, and 16:00–17:30. This was to ensure that the crows' behavior would not be disturbed by other activities in the aviaries, such as cleaning. Note that we only coded the data of our adult crows because subadult crows (Freddy, Quinn, Nero, and Uri) show different behavioral patterns (e.g., they are less neophobic, and they usually do not show any dominance displays but do show more begging behavior). This makes their behavior during the familiarization period more difficult to interpret.

Only behaviors that occurred in view of the mirror were considered for the subsequent analysis. Three parameters were investigated: (a) the frequency of social behaviors (e.g., aggression, shadow boxing), (b) the frequency of self-directed behaviors (e.g., preening), and (c) the frequency of explorative behaviors (e.g., standing in proximity of the mirror, looking behind the mirror).

All behaviors were coded offline by Jan Müller using BORIS (Friard & Gamba, 2016). The coding of the videos was performed according to established standards (Kusayama, Bischof, & Watanabe, 2000; Medina et al., 2011; Prior et al., 2008; Soler et al., 2014). After familiarization with the range of behaviors the crows showed during the 5 days in front of the covered mirror (e.g., preening, caching etc.), this coding expertise was used to rate the crows' behaviors in front of an open mirror. Coding consistency was evaluated and confirmed by Katharina F. Brecht for a fraction of the videos.

Analysis

Data were analyzed using R. To investigate how social, explorative, and self-directed behavior developed over the familiarization with the mirror, a linear mixed-effects model was fitted using the R-package nlme (Pinheiro, Bates, DebRoy, & R Core Team, 2020) for each behavioral category (explorative, social, and self-directed). Note that the crows were less active in the beginning of the familiarization period, and we consequently used the proportion of behaviors of interest in relation to other behaviors exhibited in the aviary (such as eating or bathing). The behavior of eight adult crows was analyzed for this phase of the study.

In the mirror mark and the visible mark test, the data for all crows were analyzed. We scored the number of mark-directed behaviors as well as all other self-directed behaviors. Data were pooled from two trials for each condition in the mirror mark test. To pass the mirror mark test, the percentage of mark-directed actions should be higher in the mirror mark condition than in the control conditions. A one-tailed Fisher's exact test was used to compare the number of mark-directed behaviors in relation to the total number of self-directed behaviors between conditions for each individual.

To assess whether a similar number of crows showed mark directed behavior in the visible and the mirror mark test, we compared the number of animals passing and failing in both tests with a McNemar's test for paired data (McNemar, 1947). In the visible mark test, passing was defined as showing relatively more mark-directed behaviors in the mark condition than in the sham condition. We applied an α level of .05 throughout.

Results

A linear mixed-effects model was used to analyze the crows' behavior. The frequencies of behaviors (explorative, social, and self-directed) were modeled with fixed effects of familiarization time (across days) and random error to account for the within-subjects design. There was a significant effect of familiarization time on the proportion of observed explorative behavior (Estimate = 0.026, $SE = 0.010$, $p = .015$, $n = 8$). However, neither the observation of social behavior or self-directed behavior varied with familiarization time (social behaviors: Estimate = -0.007 , $SE = 0.010$, $p = .417$, $n = 8$; self-directed behaviors: Estimate = -0.001 , $SE = 0.004$, $p = .78$, $n = 8$). Figure 2 shows the proportion of behavior from the three categories across the 8 familiarization days.

Figure 3 shows how certain exemplary behaviors of interest develop over time: looking behind the mirror, walking past the mirror, preening, bristling, attacking the mirror, and "shadow boxing." For example, attacks against the mirror did not decrease over time. Notably, none of our crows showed self-contingent behavior as defined by previous studies (Prior et al., 2008).

Results of the mirror mark test can be found in Table 1. In total, seven mark-directed actions were found in three individuals: Buddy, Calimero, and Walt showed instances of mark-directed behaviors. In Buddy's case, the mark-directed action occurred in the no mirror mark condition. Both Calimero and Walt exhibited mark-directed behaviors during the mirror mark condition. Compared with the no-mirror sham condition, there was no significant increase in mark-directed behavior (Fisher exact: Calimero $p = .625$, odds ratio [OR] = 0; Walt $p = .6$, OR = 0). All of Walt's

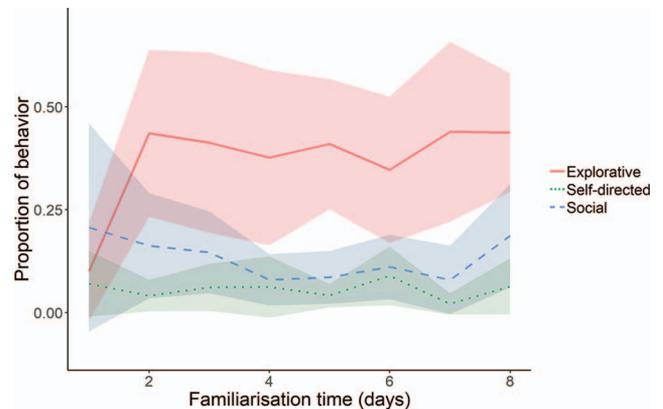


Figure 2. The average frequency of explorative (red, solid), self-directed (green, dotted), and social behaviors (blue, dashed) observed across the 8 familiarization days. Shaded areas denote the 95% confidence interval. See the online article for the color version of this figure.

mark-directed behaviors in the mirror mark condition occurred in the first test session and were accompanied by several self-directed behaviors toward other regions of the body. No mark-directed behaviors occurred in this individual's second session.

Comparing the pooled data of all crows, no significant increase in the number of mark-directed behaviors during the mirror mark condition was found compared with the no-mirror sham condition (Fisher exact: $p = .391$, OR = 0.292). Because we did not find a significant difference in mark-directed behaviors in this comparison, we did not test any other comparisons. There was further no effect of condition on the amount of self-directed behavior shown (Fisher exact: $p = 1$, OR = 0.998).

Seven out of 12 crows passed the visible mark test in that they showed comparatively more mark-directed behavior when the mark was colored compared with the sham mark. This outcome is significantly different from the mirror mark test (0 of 12 crows, McNemar's $X^2 = 10.321$, $p = .0013$).

Discussion

Whether or not corvids can recognize themselves in a mirror is debated. So far, there are two positive report of corvids passing the mirror mark test: When presented with a mirror, both magpies (Prior et al., 2008) and Indian house crows (Buniyaadi et al., 2019) showed mark-directed behavior.

We here present another study failing to demonstrate mirror self-recognition in a corvid species. Testing 12 carrion crows, we could not find a single crow that passed the mirror mark test, thereby replicating a recent study suggesting that carrion crows cannot recognize themselves in the mirror (Vanhooland et al., 2019). Notably, we also did not observe any instances of contingency checking as defined by Prior et al. (2008) in the familiarization phase, and found neither a decrease in social behavior toward the mirror nor an increase in self-directed behaviors. We did find an increase of explorative behaviors, such as looking behind the mirror, walking in front of it, or pecking it. This increase is to be expected as the crows became more and more familiar with the mirror, and less scared of it.

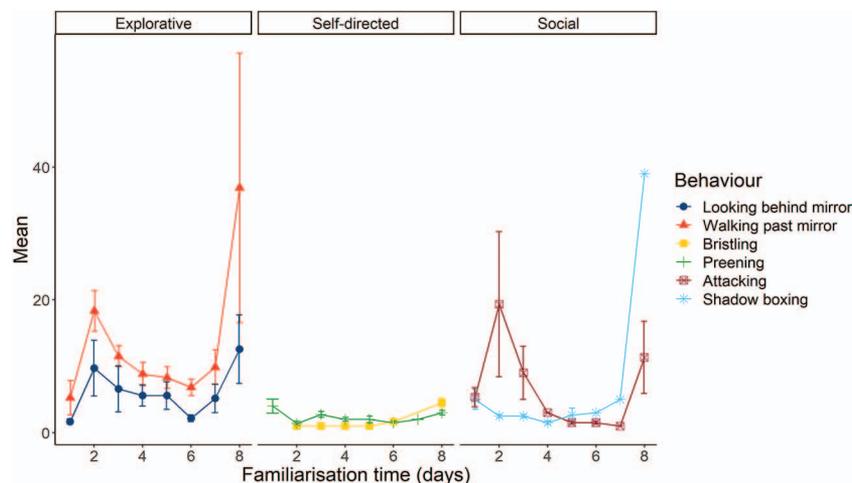


Figure 3. The mean (\pm SE) of a range of selected behaviors observed across the 8 days of the familiarization period. Note that some behaviors were only shown by one bird on certain days (e.g., shadow boxing on Days 7 and 8). See the online article for the color version of this figure.

Absence of evidence is not evidence of absence, especially in the mirror mark test (cf., Farrar & Ostojic, 2019). First, a failure to interact with the mark could have motivational reasons. For example, chimpanzees quickly cease to interact with the mark once they have found it to be nonconsequential (Anderson & Gallup, 2015). Similarly, as keas were not motivated to remove a painted mark, they were marked with food (van Buuren et al., 2018). However, as we show earlier, our crows pass the mark test when the mark is visible to them. In addition, our crows showed other self-directed behaviors, such as preening.

Moreover, the mirror we and others have used likely does not reflect ultraviolet light well. Their mirror image might thus have looked impoverished to the crows. However, although many pas-

serine bird species have four cone types, suggesting tetrachromatic vision including ultraviolet vision (Burkhardt, 1996; Finger & Burkhardt, 1994), corvids seem to be the exception from this rule in that they have a bias toward violet light rather than ultraviolet light (Odeen & Hastad, 2003). In addition, the potential lack of ultraviolet light reflection of standard mirrors did not prevent magpies (Prior et al., 2008) or Indian house crows (Buniyaadi et al., 2019) to pass the mirror mark test. It also did not prevent social behavior toward their mirror image in our crows.

Another alternative explanation might be that the crows did not have enough time to learn about the properties of the mirror. We familiarized our crows for 8 days with the mirror before testing. During testing, we also ensured that the crows would see themselves in the mirror due to its size and positioning in the testing compartment. Moreover, in previous attempts with macaques, more time did not seem to change their behavior toward their mirror image (Anderson, 1994).

Interestingly, however, macaques and pigeons can be trained to touch a mark on their face when trained that the mark was behaviorally meaningful (Chang, Fang, Zhang, Poo, & Gong, 2015; Chang, Zhang, Poo, & Gong, 2017; Epstein, Lanza, & Skinner, 1981; Uchino & Watanabe, 2014). Training helps animals to associate visual and sensorimotor input related to images in a mirror, as is required for passing the mirror mark test. Such studies suggest that the ability to recognize one's own body in a mirror might be widespread in the animal kingdom, but that this capability cannot surface without proper sensorimotor feedback experience. If so, self-recognition might be regarded as a graded or subliminal mental capacity (de Waal, 2019; Toda & Platt, 2015). According to this interpretation, training has the potential to unveil a latent capability for self-recognition. It is possible that carrion crows would also pass the mirror mark test after such sensorimotor training.

Other attempts to assess corvids' use and understanding of mirrors have produced varied results. For example, scrub-jays do not exhibit cache protection strategies when confronted with a mirror (Clary et al., 2020; Dally et al., 2010). However, there are

Table 1

Instances of Mark and Self-Directed Behaviors During the Mark Test

Crow	No mirror sham mark	No mirror mark	Mirror sham mark	Mirror mark
Buddy	0 4	1 5	0 0	0 1
Calimero	0 3	0 2	0 5	1 4
Edgar	0 0	0 1	0 2	0 1
Freddy ^a	0 1	0 0	0 0	0 5
Jello	0 6	0 9	0 9	0 6
Nero ^b	0 1	0 3	0 0	0 8
Ozzy	0 0	0 0	0 6	0 3
Quinn ^a	0 0	0 2	0 0	0 0
Uri ^b	0 0	0 1	0 0	0 0
Vince	0 0	0 0	0 0	0 0
Walt	0 1	0 0	1 1	4 5
Yoshi	0 0	0 0	0 0	0 0
Total	0 16	1 23	1 23	5 33

Note. The entries show pooled data from both trials of each condition. The first value indicates the number of mark-directed behaviors during each condition, and the second value indicates the number of all other self-directed behaviors.

^a Juveniles at the time of testing (3 months posthatching). ^b Subadult at the time of testing (15 months posthatching).

alternative explanations for this finding. They might simply consider their mirror reflection as a nonthreatening observer (e.g., a subordinate conspecific or their partner). Relatedly, the “behavior” of this “mirror-observer” is likely not how a real-live conspecific observes the caching event and because scrub-jays respond to the behavioral cues of conspecifics (Ostojic et al., 2017), the mirror-observer’s behavior might not be perceived as a threat to their caches. From the perspective of the caching scrub-jay, the “observer” is not very concerned with stealing its food, but is rather caching itself. Consequently, the scrub-jays might not display cache-protection strategies in its presence. Furthermore, although it was reported that New Caledonia crows can use mirrors to locate hidden food, here again alternative explanations for this performance should be considered (Medina et al., 2011). In the study’s Experiment 2, the crows had access to four containers underneath a perch, one of which was baited with food. A mirror was placed flat on the floor below the perch, which provided the only possibility to the crows to see which container was baited. The crows learned to retrieve the food by bending down and searching the food in the baited container by using its mirror image. However, over the course of the training, the crows might have simply learned that when they see the food in the mirror, say in the left-most container, a search here will be rewarded. They could thus have solved the task without realizing that the mirrored image is just that—a mirror representation of the food.

How, then, do we explain that only two corvid species studies have so far passed the mirror mark test? First, it should be noted that previous positive findings require direct replications to corroborate these conclusions, especially in light of our and others’ negative results (Soler et al., 2014). In addition, Prior et al.’s (2008) interpretation of their result has been contested. Specifically, it has been argued that their mark (a yellow sticker applied to the throat area) might have been noticed by the magpies (Soler et al., 2014)—unlike chimpanzees, the magpies did not lose interest in the mark across the two trials (Anderson & Gallup, 2015). An equivalent argument can be made for the Indian house crows, which were marked with similar stickers (Buniyaadi et al., 2019). Thus, we suggest that the recent sobering reports of corvids’ failure in the mirror mark test might outweigh the evidence supporting mirror self-recognition in the crow family.

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