

# Mirror stimulation in Eurasian jays (*Garrulus glandarius*)

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**Abstract**

Mirror exposure elicits a wide range of behavioural patterns: from social - indicating that an animal considers its own reflection as a conspecific - to mirror-guided and self-directed, as possible evidence of mirror self-recognition (MSR). MSR has only been found categorically in large-brained species, such as corvids, great apes and elephants. The evidence in corvids is currently debated, despite corvids being known for their remarkable socio-cognitive skills. In this study, we investigated the reaction of the Eurasian jays when performing three mirror-stimulation tasks. Combined evidence from the mirror-stimulation tasks suggests that jays perceived the image in the mirror as threatening and to be avoided. However, this alone does not indicate whether jays were afraid of a conspecific or of the mirror itself. We highlight how the high neophobia of corvids can hinder their likelihood to approach and explore a mirror, preventing the emergence of behaviours typically associated with MSR. Furthermore, we discuss how motivational factors and species differences must be taken into account when interpreting behavioural responses to the mirrors. In conclusion, after 50 years of intense MSR research, we believe it is necessary to develop new fruitful methods to test it, and change the way we approach MSR studies across species.

**Keywords:** avian cognition, consciousness, corvids, self-awareness

# Introduction

Self-recognition, also defined as the ability to become the object of one's own attention, has attracted attention in comparative psychology because of its direct link with self-awareness (Anderson & Gallup, 2011). The mark test (Gallup, 1970) has become the predominant method of systematically investigating mirror self-recognition in animals. When confronted with a mirror, many animals first respond to their reflection with social displays, suggesting they mistake their reflection for a conspecific. Over time, they might start exploring the mirror, performing contingent behaviours and, finally, their behaviour in front of the mirror becomes self-directed, opening up the possibility that they perceive the reflection as their own (Gallup, 1970). The typical assumption of this test is that self-recognition is demonstrated when an animal touches or attempts to remove a real mark on their body significantly more than a sham mark (or more frequently than comparable regions of the face without the mark), and more often in the presence of the mirror than not.

Mark-tests have been primarily applied to mammals, particularly primates (Anderson & Gallup, 2011, 2015; Gallup & Anderson, 2018 for studies on great apes passing the test), but three studies also claim evidence of MSR in corvids (Prior, Schwarz & Güntürkün, 2008; Clary & Kelly, 2016; Buniyaadi, Taufique & Kumar, 2020). However, the claims about MSR in birds, and some other non-human primates (see for a review, Gallup & Anderson, 2018, 2020, 2021) are highly debated, with later studies failing to replicate initial findings (Soler et al., 2020; Parishar, Mohapatra & Iyengar, 2021), and other studies reporting negative results (carrion and hooded crows, Vanhooland, Bugnyar & Massen, 2019; Brecht, Müller & Nieder, 2020; azure-winged magpies, Wang et al., 2020; grey tits, Kraft et al., 2017; keas and Goffin's cockatoos, van Buuren et al., 2018; ravens, Baciadonna et al., 2022). As such, the strength of evidence for mirror self-recognition in avian subjects is still open for debate (e.g. Gallup & Anderson, 2020).

The mark-test has been criticized for being ecologically invalid and ethologically restrictive, particularly when applied to animals different from chimpanzees (Heyes, 1995, 1996; de Waal, 2019; Vonk, 2019). For instance, the mark may not be salient to all species: animals might not note or be motivated to interact with the commonly-used colourful paint (Hauser et al., 1995); as happens for keas (van Buuren et al., 2018). Also, the iridescence of the feathers of many species, as well as the tactile properties of marks on sensitive, motile feathers, makes marking a difficult issue for birds (Soler, Pérez-Contreras & Peralta-Sánchez, 2014; Soler et al., 2020).

Likewise, motivational differences may affect whether a species is inclined to self-explore in front of a mirror or remove any mark (De Veer & Van Den Bos, 1999). A wide range of species-specific behaviours and ecological factors might explain negative findings. For example, the mark test has been applied to elephants using mirrors that were too small (Povinelli, 1989; Plotnik, De Waal & Reiss, 2006). Moreover elephants seem to rely predominately on olfaction for foraging and social interaction rather than vision (Plotnik et al., 2019; Ball et al., 2022). This suggests that findings on MSR based on vision, instead of the main sensory modality of a species, should be interpreted with caution. Gorillas, for example, do not usually explore objects by touching them and tend to avoid direct eye contact with others (however, some individuals did pass mark tests, see (Suarez & Gallup, 1981; Anderson & Gallup, 2015; Murray, Anderson & Gallup, 2022). Similarly, dolphins and birds do not possess hands to touch the mark, and many bird species inspect their body through the beak rather than their feet (Pepperberg et al., 1995; Reiss & Marino, 2001). Some of these concerns have occasionally been addressed, however when a task designed specifically for chimpanzees is applied to other species, it must be applied with caution, and appropriate adaptations, as well as careful interpretation of the results, must be employed when necessary (Vonk, 2019; Kohda et al., 2019). Finally, the mark-test has been criticized on principle for creating a “pass or fail” criterion, based on which species cannot demonstrate different gradients of self-recognition or self-awareness skills (Pepperberg et al., 1995; de Waal, 2019; Baciadonna et al., 2021b). As such, it is doubtful how much mirror mark-tests as currently designed can add to the body of knowledge regarding avian MSR – other tasks, such as mirror-use and mirror-stimulation, may therefore prove more fruitful.

Little is known about the MSR and mirror-use capacities of another caching corvid, the Eurasian jay (*Garrulus glandarius*), but they are excellent candidates for MSR tasks due to their complex social cognition abilities (Baciadonna et al., 2021a,b). Eurasian jays are territorial, highly specialized acorn cachers (Bossema, 1976; De Kort & Clayton, 2006). They depend on their caches in the winter, and routinely suffer pilfering of these caches (Goodwin, 1959; Bossema, 1976; Shaw & Clayton, 2012). As such, Eurasian jays engage in flexible cache-protection behaviours. For instance, jays recover more items when recent pilfering is high and, if paired with a subordinate observer, they then re-cache significantly more, as opposed to taking or eating those caches. When paired with a dominant observer, the jays suppress caching and cache further away (Shaw & Clayton, 2012). They also may take a potentially pilfering bird’s point of view into account,

preferentially caching in out-of-view trays when observed as compared to when caching in private (Legg & Clayton, 2014; Legg, Ostojić & Clayton, 2016).

Eurasian jays are also a species of interest for other studies of advanced cognitive abilities: they have been previously found to be able to understand some causal relationships between objects (Davidson et al., 2017); to have the capacity for some level of tool-use in captivity (Cheke, Bird & Clayton, 2011; Amodio et al., 2020); are able to attribute desire-states to conspecifics (Ostojić et al., 2013, 2014, 2016); and possess object permanence (Clayton & Krebs, 1994; Zucca, Milos & Vallortigara, 2007). Such potential abilities of complex social cognition, tool-use (in a laboratory setting), and complex physical cognition, as well as flexible cache-protection, make Eurasian jays a very interesting model for studies of MSR (Baciadonna et al., 2021b). As such, the present study presents a series of mirror-stimulation tasks to a new species of corvid, the Eurasian jay.

In the present study, we explored the responses of Eurasian jays towards three mirror tasks: a mirror preference task (Task 1), a mirror preference task with varying food quality (Task 2), and a vertical vs. horizontal mirror habituation task (Task 3). In Task 1, jays were presented with a choice of sitting on a perch and eating either in front of a mirror or in front of a medium-density fibreboard (MDF, a non-reflective surface), with only one food type and thus equal palatability. The purpose of Task 1 was to assess whether the birds displayed a preference for the mirrored surface compared to the non-reflective surface or vice-versa, and thus provide preliminary evidence as to how the birds may perceive their reflected image. The absence of a preference for one of the two conditions may indicate that both surfaces were not considered as threatening or particularly interesting, whereas a strong preference for eating the food in front of the wooden panel might indicate that the mirrored image was perceived as an unusual and fear-triggering stimulus. A preference for eating the food in front of the mirror may indicate an interest in its reflective surface and their image therein. Task 2 was similar to Task 1, but a bowl with a more-palatable food was placed in front of the mirror and the birds' normal daily food was placed in a bowl in front of the wooden panel. Task 2 was designed to investigate whether the presence of more-palatable food could increase exploratory behaviours towards the mirror panel by encouraging birds to overcome the lack of interest initially displayed towards the mirror in Task 1. In Task 3, we additionally assessed the birds' latency to approach and collect a food reward when it required the jays to land close to one of two different mirror configurations (vertical and

horizontal) comparing their latency to approach when presented with the same configurations, but of wooden boards rather than reflective surfaces. Task 3 was designed to provide the birds with further experience with a mirror, as well as to examine whether the physical configuration of a mirrored surface, compared to wooden controls, affected the birds' behaviour towards it.

## Materials and Methods:

### *Location, subjects, housing condition and animal ethics:*

Eight adult Eurasian jays housed at Comparative Cognition Laboratory at the Sub-Department of Animal Behaviour, University of Cambridge in Madingley, United Kingdom were tested. The jays were housed in two aviaries: Five from Aviary I (Caracas, Lisbon, and Lima, males; Wellington and Washington, females, 13 years old) and three from Aviary II (Romero and Hoy, males; Hunter, female, 14 years old). However, only seven jays were tested in Tasks 1 and 2: Lisbon was not included because he initially refused to come inside the testing compartment, but then started spontaneously entering for Task 3, and so was included. Outside of testing, jays lived in groups in two large outdoor aviaries ( $20 \times 6 \times 3$  m). Smaller indoor testing compartments ( $3 \times 1 \times 2$  m) connected to the aviary by hatch doors ( $0.5 \times 0.5$  m) were used for testing. Subjects participated voluntarily. In addition, the testing compartments contained two suspended platforms ( $1 \times 1$  m) approximately 1 m from the ground, where the birds could walk or land to rest. During testing sessions, which lasted 15 minutes per subject, each individual was physically and visually isolated from other jays. Birds were food deprived for an hour before testing (birds were never food deprived for more than 4 hours/day and were never water deprived). Individuals were tested once a day. Outside of testing, birds were fed a maintenance diet of soaked cat biscuits, vegetables, seeds, fruit and hard-boiled eggs. The jays were hand-raised by licensed breeders and had since lived in laboratory settings. Furthermore, these jays had previously participated in different experiments (e.g. Shaw & Clayton, 2014; Legg, Ostojić & Clayton, 2016; Ostojić et al., 2016; Amodio et al., 2021). They had also had exposure to mirrors during previous mirror-stimulation experiments: these included the placement of a mirror inside their aviary for two weeks and a mirror-guided string-pulling study (Baciadonna et al., 2021a). All experiments were approved by the University of Cambridge (ZOO63/19) and followed Home Office Regulations and the ASAB's Guidelines for the Treatment of Animals in Behavioural Research and Teaching. At the end of the study, jays were kept in the aviary in their respective social groups.

# *Experimental set-up and procedure*

## *Task 1: Mirror Preference Task*

In this task, each jay was moved into an indoor testing compartment and had the chance to approach and retrieve an identical reward (eight peanuts and eight macadamia nuts) from the front of either a wooden or mirror panel. On the longer side of the indoor testing compartment, a wooden (MDF) panel and a mirror panel of the same size (45 x 45 cm) were suspended vertically from the wire mesh using a metal hook; the sides on which the mirror or wood panels were placed were counterbalanced per subject. A small food container and a small resting perch (15 cm long and 20 cm distant from each panel) were fixed at the base of each panel. Each food container had eight half macadamia nuts and eight half peanuts. In total, the jays had 16 fifteen-minute sessions each (one session per day; total time 240 min).

## *Task 2: Mirror Preference Task with Varying Food Quality*

In this task, each jay was moved into an indoor testing compartment and had the chance to approach and retrieve either a more-desirable food (20 waxworms) from the front of a mirrored panel, or a less-desirable food (dried cat biscuits from their daily maintenance diet) from the front of a wooden panel (waxworms are used as experimental treats for the birds in most of our experiments). Furthermore, to reduce the speed of food consumption and increase the likelihood that the birds would explore the surfaces more, each food bowl was covered with cling-film that needed to be removed to retrieve the food. Before starting Task 2, a habituation phase (one session per day) was performed to allow the birds to learn how to remove a cling-film lid placed on top of a food bowl (placed in the centre of the wooden platforms, without corresponding boards) to retrieve a small portion of mealworms. To move on to Task 2, subjects had to successfully remove the cling-film from the bowl in four consecutive sessions. Once moved on to Task 2, the jays had eight fifteen-minute sessions each (one session per day; total time 120 min).

## *Task 3: Vertical vs. Horizontal Mirror Habituation Task*

In this task, each jay was moved into an indoor testing compartment and had the chance to approach and retrieve a food reward from the centre of a panel, either vertical or horizontal, and



either mirrored or wooden. This task was conducted to offer additional mirror experience to the jays, and to provide further information regarding their perception towards different configurations of mirrored surfaces when compared to wooden control surfaces. Subjects experienced first a vertical mirror (VM) and a horizontal mirror (HM) condition and, subsequently, a vertical wood (VW) and a horizontal wood (HW) condition. All subjects experienced each mirror condition before either of the wooden conditions. The placement of surfaces was randomized between subjects, so that half of the birds experienced the vertical conditions before the horizontal ones, and vice-versa. Mirrors and wooden surfaces were flat 30 x 30 cm squares. For the vertical condition, the surface hung from the compartment's mesh side using a metal hook and wire and rested on the wooden suspended platform so that a jay could walk directly up to it. For the horizontal condition, the surface was placed flat on the wooden platform inside the compartment, equidistant from both mesh sides. Glued at the centre of each surface was a small, transparent Plexiglas tube, approximately 1 cm in diameter and height, where a live waxworm would be baited at the beginning of each session. When a bird approached the surface and successfully retrieved the worm, the tube was then immediately re-baited, until a bird had successfully retrieved a worm 20 times (either within one 15 min. session, or over multiple sessions). If a bird did not pass a condition, testing on that condition ended after the bird had failed to retrieve any worm over five consecutive 15-minute sessions.

# *Video coding*

A digital video camera (GoPro Hero4) was used to record all test sessions. For Tasks 1 and 2, the videos were scored using Behavioural Observation Research Interactive Software (BORIS v. 7.7.3; Friard & Gamba, 2016). The ethogram used, largely based on the current literature (Prior, Schwarz & Güntürkün, 2008; Vanhooland, Bugnyar & Massen, 2019; Soler et al., 2020) included, at the initial stage, the following behavioural categories: exploration (food taken, duration and occurrences of looking), social behaviour, contingent behaviour and self-directed behaviour. However, considering jays' overall engagement with the mirror (0.10 occurrences per minute for Task 1 and 0.008 occurrences per minute for Task 2), only the most conspicuous behaviours displayed were investigated statistically (Table 1 and 2). For Tasks 1 and 2, the amount of food taken either from the mirror or the wooden panel conditions and the duration (sec) and occurrences of looking (body and head facing either the mirror or the wooden panel) were scored. LB coded

all the videos for Tasks 1 and 2. Twenty per cent of the videos randomly chosen were scored by a second independent observer (MM). The interclass correlation coefficient calculated for all the behaviours analysed statistically was: 0.98 for duration of looking, 0.91 for duration for occurrences of looking. For Task 3, the latency, i.e., the time elapsed between a bird successfully retrieving the worm from the surface and the moment in which the experimenter's arm was removed from the compartment after baiting the Plexiglas tube, was calculated. For Task 3, the latency was scored directly during testing: the stopwatch was controlled by a second experimenter (FMC), while the first experimenter (LB) was in charge of baiting the Plexiglas tube.

### *Statistical analyses*

Generalised linear mixed models were calculated using the lme4 package (Bates et al., 2015) in R 3.6.1 (R Development Core Team, 2020). For Task 1, a model was calculated for each of the following dependent variables: food taken and occurrences of looking. Condition (mirror, wood), Session (1-16), Aviary (group that each bird belonged to, with two levels), and Sex (female, male) were included as fixed factors for all models performed for Task 1. For Task 1, the GLMM TMD package (Brooks et al., 2017) was used because the dependent variables food taken (Poisson distribution) and occurrences of looking violated the normality assumption, as well as due to occurrences of a high frequency of zero-values. The dependent variable, duration of looking, was analysed using non-parametric methods for Task 1. Wilcoxon signed-rank tests were conducted to identify any significant differences between the duration of looking for each condition.

For Task 2, a model (GLMM) was calculated for each of the following dependent variables: food taken (binomial distribution), occurrences, and duration of looking. Condition (mirror, wooden panel), Session (1-8), Aviary (group that each bird belonged to, with two levels), and Sex (female, male), were included as fixed factors for all models performed for Task 2.

For Task 3, the latency to approach the food was analysed. The data obtained violated the normality assumption, and thus a non-parametric approach was employed for analysis. A Fisher's exact test was used to compare the number of birds that passed or failed each condition. A Friedman test was conducted to identify any significant differences between conditions in both latency to approach and the average number of sessions required to pass each condition.

For all GLMM models, the significance of the full model was established by comparing this model with the model that included only the random factor (null model) using a likelihood

ratio test. Model fit and over-dispersion were checked using the DHARMA 0.3.3.0 package (Harting, 2020). The p-value of each factor was derived using the “drop1” function (Barr et al., 2013). Also, the subjects’ identity was included as a random factor to control for repeated measurements of the same subject in all models performed.

## Results

### *Task 1: Mirror Preference Task*

When investigating which variables affected the food taken from either surface, it was found that the full model differed significantly from the null model (GLMM:  $\chi^2 = 21.54$ ,  $df = 4$ ,  $p < 0.0001$ ). The fixed factor Condition was significant (Table 3); jays took more food from in front of the wooden panel (Mean  $\pm$  SE =  $0.79 \pm 0.25$ ) compared to the mirror panel (Mean  $\pm$  SE =  $0.18 \pm 0.13$ ; Figure 1A). The Sex factor was also significant (Table 3), with male jays taking more food (Mean  $\pm$  SE =  $0.74 \pm 0.25$ ) than females (Mean  $\pm$  SE =  $0.15 \pm 0.06$ ), across conditions. The other fixed factors included in the model were not significant (Table 3). When investigating which variables affected the occurrences of looking, it was found that the full model differed significantly from the null model (GLMM:  $\chi^2 = 11.02$ ,  $df = 4$ ,  $p = 0.026$ ). The fixed Sex factor was significant (Table 4), with male jays looking more often (Mean  $\pm$  SE =  $2.57 \pm 0.95$ ) than females (Mean  $\pm$  SE =  $0.98 \pm 0.39$ ), across conditions. The factor Session was also significant (Table 4). Overall, across the sessions, jays looked either at the mirror or the wooden panel on average  $1.89 \pm 0.20$  times. In the last two sessions, the occurrences of looking increased (Session 15, Mean  $\pm$  SE =  $3.21 \pm 1.70$ ; Session 16, Mean  $\pm$  SE =  $2.78 \pm 1.80$ ). The other fixed factors included in the model were not significant (Table 4). A Wilcoxon signed-rank test showed that the duration of looking either at the mirror (Mean  $\pm$  SE =  $8.95 \pm 2.41$  s) or at the wooden panel (Mean  $\pm$  SE =  $11.10 \pm 3.37$  s) did not differ ( $V = 1381.5$ ,  $p = 0.67$ ).

### *Task 2: Mirror Preference Task with Varying Food Quality*

Six out of seven birds managed to remove the cling-film during the habituation phase (range 4-12 sessions). One subject was excluded (Wellington) because she never managed to remove the cling-film and retrieve the food in four consecutive sessions. When investigating which variables affected the food taken, it was found that the full model differed significantly from the null model (GLMM:  $\chi^2 = 53.01$ ,  $df = 4$ ,  $p < 0.001$ ). The fixed factor Condition was significant

(Table 5); jays took more food in front of the mirror panel (Mean  $\pm$  SE =  $0.66 \pm 0.21$ ) compared to the wooden panel (Mean  $\pm$  SE =  $0.16 \pm 0.10$ ; Figure 1B). The other fixed factors included in the model were not significant (Table 5). When investigating which variables affected the occurrences of looking, it was found that the full model differed significantly from the null model (GLMM:  $\chi^2 = 25.33$ ,  $df = 4$ ,  $p < 0.0001$ ). The fixed factor Condition was significant (Table 6), in that jays looked more often at the mirror panel (Mean  $\pm$  SE =  $3.12 \pm 1.13$ ) compared to the wooden panel (Mean  $\pm$  SE =  $1.41 \pm 0.26$ ; Figure 1C). The factor Session was also significant (Table 6). Overall, the amount of looks across sessions decreased (Session 1, Mean  $\pm$  SE =  $4.41 \pm 0.96$ ; Session 8, Mean  $\pm$  SE =  $2.16 \pm 1.07$ ). The other fixed factors included in the model were not significant (Table 6). When investigating which variables affected the duration of looking, it was found that the full model differed significantly from the null model (GLMM:  $\chi^2 = 54.31$ ,  $df = 4$ ,  $p < 0.0001$ ). The fixed factor Condition was significant (Table 7), with jays looking at the mirror panel for longer (Mean  $\pm$  SE =  $82.36 \pm 26.25$  s) than the wooden panel (Mean  $\pm$  SE =  $14.61 \pm 5.47$  s). The factor Session was also significant (Table 7). Overall, the duration of looking across sessions decreased (Session 1, Mean  $\pm$  SE =  $78.09 \pm 23.43$  s; Session 8, Mean  $\pm$  SE =  $45.01 \pm 15.33$  s). The other fixed factors included in the model were not significant (Table 7).

### *Task 3: Vertical vs. Horizontal Mirror Habituation Task*

The latencies to approach the food across the four conditions are represented in Figure 1D. Only one out of eight jays successfully retrieved the reward 20 times in the VM configuration (Romero; in two sessions). Two birds (Caracas and Wellington) did not complete any of the four conditions (Table 8). Five out of eight jays successfully obtained the reward 20 times (session range, 2-9) in the HM configuration (Mean  $\pm$  SE =  $75.50 \pm 36.07$ s; Romero, Hoy, Lima, Washington and Hunter). When tested in the VW configuration, five out of eight subjects (Mean  $\pm$  SE =  $54.02 \pm 13.36$  s; Romero, Lima, Washington, Hunter, Lisbon) successfully obtained the reward 20 times (session range, 1–5), whereas six (Romero, Lima, Washington, Hunter, Lisbon, Hunter) successfully retrieved the reward (session range, 1-8) in the HW configuration (Mean  $\pm$  SE =  $46.37 \pm 16.93$  s). However, there was not a significant association between the type of configuration and whether the jays succeeded (Fisher's exact test,  $p = 0.084$ ). The latency to approach the food was compared between three conditions (HM, and VW and HW). One condition, the VM, was excluded because of an insufficient number of observations (only one jay successfully completed the task). The latency to approach the food was not significantly different

between conditions (Friedman test:  $\chi^2 = 3.5$ ,  $df = 2$ ,  $p = 0.17$ ). The number of sessions required to complete Task 3 did not differ between conditions (Friedman test:  $\chi^2 = 4.30$ ,  $df = 2$ ,  $p = 0.11$ ).

## Discussion

Across the three tests, the Eurasian jays did not display the expected behavioural transition from social behaviours to exploration, contingency testing, mirror-guided self-exploration and self-directed behaviour that are typically observed in species in which mirror self-recognition has been reported. During Tasks 1 and 2, only three birds showed any contingent behaviours and none of the birds showed mirror guided self-exploration, which has been considered the main sign that needs to be observed before performing a classic mark-test (de Waal, 2019); as such, we did not proceed to designing or conducting a mark-test with these birds. The limited social behaviours displayed towards the reflected image throughout this study strongly suggest that the jays did not perceive the stimulus in the mirror as a conspecific worth interacting with or even confronting. Moreover, their strong preference for taking the food from in front of the wooden panel suggests, according to our initial prediction, that their reflected image was perceived as an unusual and fear-triggering stimulus which they avoided. The initial fear reaction towards the reflected image was attenuated by providing more palatable food placed near to the mirror. Although the jays took the more palatable food from the mirror panel more often as compared to a less-palatable food from the wooden panel, their general behaviour did not otherwise change from Task 1. Their overall lack of engagement and interest towards the mirror suggests that it was perceived as a threatening stimulus, and the results from Task 3 are consistent with this interpretation. Although there were no significant differences detected between conditions, only one jay passed the VM condition, whereas five passed each of the HM and VW conditions, and six passed the HW condition. The finding that fewer birds passed the vertical mirror condition compared with the horizontal mirror condition suggests that birds might interpret these two configurations differently. Grey parrots (*Psittacus erithacus*; Pepperberg et al., 1995), Goffin's cockatoos (*Cacatua goffiniana*; van Buuren et al., 2018), and jungle crows (*Corvus macrorhynchos*; Kusayama, Bischof & Watanabe, 2000) behaved more socially towards a vertical than a horizontal mirror. A vertical mirror seems more similar to a real-life bird, as birds are more often found upright, whereas they would only be standing on top of a bird (as reflected in a horizontal mirror) during agonistic or reproductive interactions. In our study, the horizontal mirror might have been perceived as less threatening than

the vertical one: while in the vertical position, the birds had to face the full view of their image in order to retrieve the food, in the horizontal configuration they could retrieve the food without stepping on the mirror and could only see a small portion of their face. During Tasks 1-3, it seems that the most consistent conclusion is that either the jays were afraid of the mirror as a stimulus, independent of the image reflected therein which may possibly not be considered a conspecific eliciting social interaction, or that the reflected image was perceived as a threatening conspecific, one thus not to be confronted but rather avoided. The expected behaviour of the subjects might largely depend on their relative dominance. However, they will never know the social status of the bird reflected in the mirror because it will either be unknown to them (if we assume lack of MSR) or known as themselves and so not likely to elicit social responses.

The behaviours displayed by the jays (absence of social behaviour) during the mirror stimulation are quite different from corvid species tested so far using a similar set-up (Prior, Schwarz & Güntürkün, 2008; Soler, Pérez-Contreras & Peralta-Sánchez, 2014; van Buuren et al., 2018; Vanhooland, Bugnyar & Massen, 2019; Brecht, Müller & Nieder, 2020; Soler et al., 2020; Buniyaadi, Taufique & Kumar, 2020). A possible explanation of what we observed in this study can be linked with the different levels of neophobia across the Corvidae family. Although corvids are well known for their remarkable cognitive skills (Taylor, 2014; Baciadonna et al., 2021b), they are also highly neophobic (Heinrich, 1995; O'Hara et al., 2017). The combination of behavioural flexibility with high levels of neophobia appears paradoxical, because neophobia tends to inhibit innovation and is associated with narrow ecological niches (Greggor, Thornton & Clayton, 2015). In a recent paper (Miller et al., 2022), investigating the socio-ecological drivers of neophobia in ten different corvids species, Eurasian jays were considered the most neophobic towards novel food, and to some extent towards a novel object, compared with the rest of species included in the study. From the latency to approach the novel object reported by Miller et al. (2022), it emerges that common ravens were more neophobic than azure-winged magpies, while azure-winged magpies, carrion crows, and Eurasian jays approached the novel objects with a similar, longer latency time than Clark's nutcrackers. This is quite interesting because these corvid species all failed to pass the classic mark-test and, more importantly, the proxy behaviours often considered crucial for passing the mark-test (exploratory behaviour, contingent behaviour and self-exploration) were limited both in the occurrences displayed, as well as in the number of individuals

displaying them (Vanhooland, Bugnyar & Massen, 2019; Brecht, Müller & Nieder, 2020; Wang et al., 2020).

Furthermore, an important driver of neophobia, at least in some species, is individual age. Empirical evidence from birds to mammals suggests that younger individuals are less neophobic and more prone to explore than adults (Greggor, Thornton & Clayton, 2015; Greggor et al., 2020). For example, Eurasian jays tested with a Piagetian object permanence paradigm 15 days post-hatching reached stage six with fewer sessions than individuals tested at 2-3 months of age (Zucca, Milos & Vallortigara, 2007). This result was unexpected from a general developmental standpoint but expected based on the behavioural developmental stages of corvids. During the first three weeks of age, they are extremely inquisitive and fearless, and supervised by their more expert parents. However, when left more alone by their parents, roughly at the age of two months, they become neophobic, limiting their willingness to approach new objects or food, as well as becoming more fearful of unfamiliar situations (Heinrich, 1995, 1999; Heinrich, Marzluff & Adams, 1995). In our study, the jays tested were all adults (13-14 years old) that had not been exposed to mirrors at a young age, and we cannot rule out that a different behavioural pattern may have emerged if they had been confronted with the mirror during their younger, more neophilic stage. Our results indicate that neophobia can posit a challenge for the jays, and most likely to other corvids as well, to approach and explore the mirror, appreciate its reflective property, and use it to explore parts of their body otherwise not visible. The difficulty of demonstrating mirror self-recognition in corvids might be the effect of such extraneous variables, such as their neophobia, that have nothing to do with cognitive abilities relating to an understanding of the self. These further challenge the methodological appropriateness of cross-administering methods developed for primates to more distantly-related species.

In the case of our study, firm conclusions cannot be drawn as to whether Eurasian jays saw their reflection as a conspecific or as themselves. In either case, it is appropriate to consider the unique morphology, as well as natural and behavioural constraints of birds, when attempting to administer mirror tasks to them, especially when they were originally conceived for apes. Limitations such as sensory preferences, physical constraints, neophobia, and more must be taken into account both when designing mirror tasks and when interpreting their results, and currently-existing MSR tasks may pose particularly steep challenges for avian subjects. Eventually, a more conclusive understanding of the presence and extent of MSR in non-human animals, and especially

417 in birds, is likely to only be attainable through continuous creativity and innovation in task design,  
418 rather than continuity of methodology.

419

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573 Table and Figure legends

574

575 **Table 1.** Individual Responses in the *Test 1*

576 **Table 2.** Individual Responses in the *Test 2*

577 **Table 3.** Results of the GLMM showing which variables affected the food taken in *Task 1*

578 **Table 4.** Results of the GLMM showing which variables affected the occurrences of looking in

579 *Task 1*

580 **Table 5.** Results of the GLMER showing which variables affected the food taken in *Task 2*

581 **Table 6.** Results of the GLMM showing which variables affected occurrences of looking in *Task*

582 *2*

583 **Table 7.** Results of the GLMER showing which variables affected the duration of looking in

584 *Task 2*

585 **Table 8.** Summary of the jays' performance to approach and retrieve the food during *Task 3*.

586 The green colour indicates the instances in which the tested subject approached and retrieved at

587 least once the waxworm during the 15 s allowed in each session. The yellow colour instead

588 indicates the instances in which the tested subject did not approach and retrieve at least once the

589 waxworm during the 15 s allowed in each session.

590

591 **Figure 1. A.** Mean of food taken in front of the mirror and the wooden panel during Task 1; **B.**

592 Mean of food taken in front of the mirror and the wooden panel during Task 2; **C.** Total duration

593 of looking time towards the mirror and the wooden panel-cached during the Task 2; **D.** Latency

594 time to approach and retrieve a waxworm across the four combinations presented to the jays in

595 Task 3 (Mirror: horizontal (MH) and vertical (MV); Wood: horizontal (WH) and vertical (WV)).

596 **E.** Proportion of food items cached across the three conditions (alone, mirror and observed)

597 during the caching sessions in Task 4; **F.** Proportion of food type taken by the jays during the

598 caching sessions in Task 4. **G.** Proportion of food items cached when the food was abundant (30

599 items for each food type, total 120 food items provided) and when scarce (15 items for each food

600 type, total 60 food items provided). Box plot: the horizontal line shows the median, the box

601 extends from the lower to the upper quartile and the whiskers to the interquartile range above the

602 upper quartile (max) or below the lower quartile (min); solid circles indicate each individual jay.

603

# **Table 1**(on next page)

Table 1.

Individual Responses in the *Test 1*



1 **Table 1.** Individual Responses in the *Test 1*

2

		Subject													
		Romero		Hoy		Lima		Washington		Caracas		Wellington		Hunter	
Behaviour	Condition	Mirror	Wood	Mirror	Wood	Mirror	Wood	Mirror	Wood	Mirror	Wood	Mirror	Wood	Mirror	Wood
	Food taken	16	32	0	13	0	21	3	4	1	12	0	1	1	6
	Duration of looking (s)	357.08	250.14	133.80	95.79	65.71	328.94	119.49	72.41	169.08	386.97	106.62	17.49	51.62	91.70
	Occurrence of looking	38	43	22	14	18	25	37	18	84	85	8	3	13	16
	Social behaviour	1	0	0	0	0	0	0	0	4	0	0	0	0	0
	Contingent	17	0	4	0	0	0	0	0	0	0	0	0	0	0
	Self-Directed	0	0	0	0	0	0	0	0	0	0	0	0	0	0

# **Table 2**(on next page)

Table 2.

Individual Responses in the *Test 2*

1

2 **Table 2.** Individual Responses in the *Test 2*

Condition	Subject													
	Romero		Hoy		Lima		Washington		Caracas		Wellington		Hunter	
	Mirror	Wood	Mirror	Wood	Mirror	Wood	Mirror	Wood	Mirror	Wood	Mirror	Wood	Mirror	Wood
Behaviour														
Food taken	142	4	160	17	160	0	158	1	0	0	0	0	0	0
Duration looking (s)	1155.02	246.02	619.25	257.77	1255.91	72.66	781.43	64.27	109.25	57.28	0	0	32.77	3.75
Occurrence of looking	39	15	16	14	14	11	64	13	10	14	0	0	7	1
Social behaviour	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Contingent	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Self-Directed	0	0	0	0	0	0	0	0	0	0	0	0	0	0

3

4

5

# **Table 3**(on next page)

Table 3.

Results of the GLMM showing which variables affected the food taken in *Task 1*

**Table 3.** Results of the GLMM showing which variables affected the food taken in *Task 1*

	Estimate	Standard Error	<i>z</i>	<i>p</i> - value
Intercept	-1.13	0.57	-1.96	
Condition	1.02	0.36	2.76	0.003
Session	-0.01	0.02	-0.64	0.51
Aviary	-0.35	0.32	-1.10	0.30
Sex	1.71	0.39	4.35	0.0011

# **Table 4**(on next page)

Table 4.

Results of the GLMM showing which variables affected the occurrences of looking in *Task 1*

**Table 4.** Results of the GLMM showing which variables affected the occurrences of looking in *Task 1*

	Estimate	Standard Error	<i>z</i>	<i>p</i> - <i>value</i>
Intercept	-0.06	0.38	-0.15	
Condition	0.11	0.10	1.25	0.26
Session	0.02	0.01	2.08	0.035
Aviary	0.33	0.36	0.93	0.38
Sex	0.85	0.37	2.25	0.042

# **Table 5**(on next page)

Table 5.

Results of the GLMER showing which variables affected the food taken in *Task 2*



1 **Table 5.** Results of the GLMER showing which variables affected the food taken in *Task 2*

	Estimate	Standard Error	<i>z</i>	<i>p</i> - value
Intercept	0.42	5.71	0.07	
Condition	-7.74	2.94	-2.62	< 0.0001
Session	-0.03	0.19	-0.19	0.84
Aviary	-1.60	4.86	-0.33	0.74
Sex	3.85	5.47	0.70	0.46

2

# **Table 6**(on next page)

Table 6.

Results of the GLMM showing which variables affected occurrences of looking in *Task 2*

**Table 6.** Results of the GLMM showing which variables affected occurrences of looking in *Task*

	Estimate	Standard Error	<i>z</i>	<i>p</i> - value
Intercept	1.31	0.58	2.24	
Condition	-0.56	0.17	-3.32	0.004
Session	-0.13	0.03	-4.17	0.007
Aviary	0.36	0.54	0.67	0.52
Sex	0.05	0.58	0.09	0.62

# **Table 7** (on next page)

Table 7.

Results of the GLMER showing which variables affected the duration of looking in *Task 2*

**Table 7.** Results of the GLMER showing which variables affected the duration of looking in  
*Task 2*

	Estimate	Standard Error	<i>t</i>	<i>p</i> – <i>value</i>
Intercept	77.85	25.36	3.06	
Condition	-67.74	8.22	-8.23	< 0.0001
.Session	-3.70	1.79	-2.06	0.041
Aviary	0.54	23.68	0.02	0.98
Sex	31.38	25.12	1.24	0.23

# Table 8 (on next page)

Table 8.

Summary of the jays' performance to approach and retrieve the food during *Task 3*. The green colour indicates the instances in which the tested subject approached and retrieved at least once the waxworm during the 15 s allowed in each session. The yellow colour instead indicates the instances in which the tested subject did not approach and retrieve at least once the waxworm during the 15 s allowed in each session.

**Table 8.** Summary of the jays' performance to approach and retrieve the food during *Task 3*. The green colour indicates the instances in which the tested subject approached and retrieved at least once the waxworm during the 15 s allowed in each session. The yellow colour instead indicates the instances in which the tested subject did not approach and retrieve at least once the waxworm during the 15 s allowed in each session.

ID	Position	Condition	Sessions													Tot
			1	2	3	4	5	6	7	8	9	10	11	12	13	
<b>Romero</b>	Vertical	Mirror	Green	Green												20/20
	Horizontal	Mirror	Yellow	Yellow	Green	Green										20/20
	Horizontal	Wooden	Green													20/20
	Vertical	Wooden	Green													20/20
<b>Hoy</b>	Horizontal	Mirror	Yellow	Yellow	Green	Green	Green									20/20
	Vertical	Mirror	Green	Yellow	Yellow	Yellow	Yellow	Yellow								1/20
	Vertical	Wooden	Yellow	Yellow	Yellow	Yellow	Yellow									0/20
	Horizontal	Wooden	Green	Green	Green											20/20
<b>Lima</b>	Vertical	Mirror	Yellow				Yellow									0/20
	Horizontal	Mirror	Yellow	Green												20/20
	Horizontal	Wooden	Green													20/20
	Vertical	Wooden	Yellow	Green												20/20
<b>Washington</b>	Horizontal	Mirror	Green													20/20
	Vertical	Mirror	Green	Green	Yellow	Green	Yellow	Yellow	Green	Green	Yellow	Yellow	Yellow	Yellow	Yellow	14/20
	Vertical	Wooden	Yellow	Green												20/20
	Horizontal	Wooden	Green													20/20
<b>Caracas</b>	Vertical	Mirror	Yellow	Yellow	Yellow	Yellow	Yellow									0/20
	Horizontal	Mirror	Yellow	Green				Yellow	Yellow							8/20
	Horizontal	Wooden	Green	Green				Yellow	Yellow							2/20
	Vertical	Wooden	Yellow	Yellow	Yellow	Yellow	Yellow									0/20
<b>Wellington</b>	Horizontal	Mirror	Yellow	Yellow	Yellow	Yellow	Yellow									0/20
	Vertical	Mirror	Yellow	Yellow	Yellow	Yellow	Yellow									0/20
	Vertical	Wooden	Yellow	Yellow	Yellow	Yellow	Yellow									0/20
	Horizontal	Wooden	Yellow	Yellow	Yellow	Yellow	Yellow									0/20
<b>Hunter</b>	Vertical	Mirror	Yellow	Yellow	Yellow	Yellow	Yellow									0/20
	Horizontal	Mirror	Green	Green	Yellow	Green	Green	Green	Green	Yellow	Green					20/20
	Horizontal	Wooden	Green	Green												20/20
	Vertical	Wooden	Yellow	Green	Green	Green										20/20
<b>Lisbon</b>	Horizontal	Mirror	Green	Green	Yellow	Yellow	Yellow	Yellow								7/20
	Vertical	Mirror	Yellow	Yellow	Yellow	Yellow	Yellow									0/20
	Vertical	Wooden	Yellow	Yellow	Green	Green	Green									20/20
	Horizontal	Wooden	Green	Green	Green	Yellow	Yellow	Green	Yellow	Green						20/20

# Figure 1

Figure 1.

A. Mean of food taken in front of the mirror and the wooden panel during Task 1; B. Mean of food taken in front of the mirror and the wooden panel during Task 2; C. Total duration of looking time towards the mirror and the wooden panel-cached during the Task 2; D. Latency time to approach and retrieve a waxworm across the four combinations presented to the jays in Task 3 (Mirror: horizontal (MH) and vertical (MV); Wood: horizontal (WH) and vertical (WV)). E. Proportion of food items cached across the three conditions (alone, mirror and observed) during the caching sessions in Task 4; F. Proportion of food type taken by the jays during the caching sessions in Task 4. G. Proportion of food items cached when the food was abundant (30 items for each food type, total 120 food items provided) and when scarce (15 items for each food type, total 60 food items provided). Box plot: the horizontal line shows the median, the box extends from the lower to the upper quartile and the whiskers to the interquartile range above the upper quartile (max) or below the lower quartile (min); solid circles indicate each individual jay



