



RESEARCH PAPER

Mirror-mediated responses of California scrub jays (*Aphelocoma californica*) during a caching task and the mark test

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Abstract

Mirror self-recognition, as an index of self-awareness, has been proposed as a precursor for more complex social cognitive abilities, such as prosocial reasoning and cooperative decision-making. Indeed, evidence for mirror self-recognition has been shown for animals possessing complex social cognitive abilities such as great apes, dolphins, elephants and corvids. California scrub jays (*Aphelocoma californica*) have provided strong evidence that non-human animals are capable of mental state attribution. For instance, scrub jays are reported to use their experience stealing the food of others to infer that other birds may similarly intend to steal from them. If a concept of “self” is required for such complex social cognitive abilities, then scrub jays might be expected to show mirror self-recognition. Thus, we examined whether California scrub jays are capable of mirror self-recognition using two experimental contexts: a caching task and the mark test. During the caching task, we compared the extent to which scrub jays protected their food after caching alone, in the presence of a conspecific and in the presence of a mirror. The birds did not engage in more cache protection behaviours with a mirror present than when caching alone, suggesting scrub jays may have recognized their reflection and so did not expect cache theft. Alternative explanations for this behaviour are also discussed. During the mark test, the scrub jays were surreptitiously marked with a red or plumage-coloured control sticker. The scrub jays showed no evidence of mirror self-recognition during the mark test, as the birds did not preferentially attempt to remove the red mark in the presence of a mirror. Together, the results provide mixed evidence of the mirror self-recognition abilities of California scrub jays. We highlight the need to develop alternative approaches for evaluating mirror self-recognition in non-human animals to better understand its relationship with complex social cognition.

KEYWORDS*Aphelocoma californica*, cache protection, corvid, self-awareness, self-recognition, social cognition

1 | INTRODUCTION

Recently, there has been renewed interest in whether non-human animals are capable of mirror self-recognition. Historically,

investigations of mirror self-recognition by non-human animals have focused on primates, especially our closest living evolutionary relatives, the great apes (Gallup, 1970; Gallup et al., 1995). Importantly, this renewed interest has led to a diversity of new species being

investigated (e.g., giant pandas [*Ailuropoda melanoleuca*]: Ma et al., 2015; horses [*Equus caballus*]: Baragli, Demuru, Scopa, & Palagi, 2017; killer whales [*Orcinus orca*] and sea lions [*Zalophus californianus*]: Delfour & Marten, 2001; cleaner wrasses [*Labroides dimidiatus*]: Takeyama et al., 2019; manta rays [*Manta birostris*]: Ari & D'Agostino, 2016; and cichlids [*Neolamprologus pulcher*]: Hotta, Komiyama, & Kohda, 2018). These studies illustrate a nascent comparative approach aimed at identifying the evolutionary origins of the cognitive abilities underlying mirror self-recognition.

Although many additional species are now being investigated, most of these studies have not provided convincing evidence of mirror self-recognition (Gallup & Anderson, 2018). Thus far, the current consensus suggests that among non-human animals, only great apes show strong evidence of mirror self-recognition (Anderson & Gallup, 2015; Gallup & Anderson, 2018). Multiple studies have found that some individuals within each species of great ape pass the "mark test" developed by Gallup (1970). During this test, an animal is surreptitiously marked on a location on their body that can only be seen using a mirror's reflection. Attempts to inspect or remove the mark when in the presence of a mirror, compared to a control condition without a mirror, are considered evidence the animal recognizes the image as its own reflection (i.e., *passing* the mark test). Developed originally for use with primates, the mark test has since been adapted for use with a variety of other species (e.g., Asian elephants [*Elephas maximus*]: Plotnik, de Waal, & Reiss, 2006; Clark's nutcrackers [*Nucifraga columbiana*]: Clary & Kelly, 2016b; Eurasian magpies [*Pica pica*]: Prior, Schwarz, & Güntürkün, 2008; and jackdaws [*Coloeus monedula*]: Soler, Pérez-Contreras, & Peralta-Sánchez, 2014). With these modifications and the development of new tasks, moderate evidence now suggests other mammals, such as Asian elephants (Dale & Plotnik, 2017; Plotnik et al., 2006) and dolphins (*Tursiops truncatus*: Morrison & Reiss, 2018; Reiss & Marino, 2001), may also possess a representational understanding of the "self."

Subsequent research has provided preliminary evidence that mirror self-recognition may not be limited to mammals. Prior et al. (2008) reported that two Eurasian magpies, a species belonging to the large-brained Corvidae family, passed the mark test. This finding was particularly controversial as it suggested the mammalian neocortex may not be required for the cognitive abilities underlying mirror self-recognition. This initial finding has since been supported by research on another corvid, the Clark's nutcracker, which provided evidence of mirror self-recognition using the mark test as well as a more ecologically relevant food-caching task (Clary & Kelly, 2016b). However, other corvids show no evidence of mirror self-recognition during either the mark test (carrion crows/hooded crows [*Corvus corone* spp.]: Vanhooland, Bugnyar, & Massen, in press; jackdaws: Soler et al., 2014) or by measuring social behaviours and/or contingency checking behaviours when exposed to mirrors (jungle crows [*Corvus macrorhynchos*]: Kusayama, Bischof, & Watanabe, 2000; New Caledonian crows [*Corvus moneduloides*]: Medina, Taylor, Hunt, & Gray, 2011). Outside of the Corvidae family, no evidence of mirror self-recognition has been found in other avian families, even among those with relatively large brain-to-body size, such as parids (Branch,

Kozlovsky, & Pravosudov, 2015; Kraft, Forštová, Utku Urhan, Exnerová, & Brodin, 2017) and parrots (van Buuren, Auersperg, Gajdon, Tebbich, & von Bayern, 2018; Pepperberg, Garcia, Jackson, & Marconi, 1995). More recently, a study on cleaner wrasses has provided the first preliminary evidence for mirror self-recognition in fish (Takeyama et al., 2019). However, this conclusion is contentious, as the self-directed behaviours observed (i.e., self-scraping against a substrate) have been argued to be a stereotypical response to being parasitized (de Waal, 2019). That is, irritating tactile cues from the implanted mark combined with the possibility the marked individual in the reflection was considered a parasitized conspecific may have prompted the wrasses to behave (i.e., self-scrape) as if they were also parasitized (de Waal, 2019).

With more species being studied, and with some species showing evidence of mirror self-recognition, the evolutionary origins of this ability can begin to be investigated. Researchers have proposed mirror self-recognition is a necessary precursor for more complex social cognition (Byrne, 1995; Gallup, 1982; Plotnik et al., 2006; Whiten, 1996), as an individual first needs to have an understanding or recognition of self, before being able to differentiate its sense of self from others. This idea fits with the developmental trajectory of mirror self-recognition (18–24 months, Amsterdam, 1972) and social cognitive abilities like theory of mind (36–48 months, Gergely, 1994; Gopnik & Meltzoff, 1994) in children. Likewise, the emerging comparative literature also supports this idea, as species showing evidence for mirror self-recognition also tend to be capable of complex social cognitive abilities. For example, chimpanzees (*Pan troglodytes*) may infer the mental states of other individuals (Byrne & Whiten, 1992; Hare, Call, & Tomasello, 2001; Kaminski, Call, & Tomasello, 2008; Krupenye, Kano, Hirata, Call, & Tomasello, 2016), dolphins require close coordination during cooperative hunting and foraging behaviours (Acevedo-Gutierrez, 1999; Connor, Wells, Mann, & Read, 2000; Reynolds, Wells, & Eide, 2000), and elephants form close social bonds that may persist even after the death of a group member (Douglas-Hamilton & Douglas-Hamilton, 1975; McComb, Baker, & Moss, 2006; Moss, 1988; Spinage, 1994). Furthermore, Eurasian magpies and Clark's nutcrackers adjust where and how much they cache to mitigate the risk of cache theft (i.e., theft of hidden food stores) and depending on the social context (Clarkson, Eden, Sutherland, & Houston, 1986; Clary & Kelly, 2011, 2016a; Tornick, Rushia, & Gibson, 2016), thereby supporting their ability for aspects of complex social cognition. In the case of cleaner wrasses, foraging demands may also select for social cognitive skills. Cleaner wrasses service other client reef fish by removing ectoparasites from their skin, but occasionally eat the client's mucus (a preferred food source), which risks irritating the client. To ensure continued "patronage" to their territory, cleaner wrasse must adjust their cleaning behaviour over repeated interactions with a particular client and when in the presence of other bystander clients (Bshary, 2002; Bshary & Bronstein, 2011; Bshary & Grutter, 2002, 2005, 2006). Therefore, other species that also exhibit complex social cognitive abilities during their natural behaviours may be good candidates for the study of mirror self-recognition.

California scrub jays (*Aphelocoma californica*) provide an interesting case for evaluating the link between mirror self-recognition and complex social cognitive abilities. Some of the strongest evidence that non-human animals might be capable of mental state attribution has been shown through studies with scrub jays. California scrub jays are sensitive to the social conditions of the environment in which they cache food (Emery, Dally, & Clayton, 2004), preferring to cache in locations visually obscured from other individuals (Dally, Emery, & Clayton, 2004, 2005). Indeed, if another bird witnesses the caches being made, the caching bird may move the compromised caches to new locations when the other bird has left (Emery & Clayton, 2001). Other research has found scrub jays adjust their re-caching strategies depending on which specific individual observed a caching event (Dally, Emery, & Clayton, 2006). California scrub jays may also “project” from their own experiences of stealing others' caches to infer that other birds may have similar intentions to steal their caches (Emery & Clayton, 2001)—an ability argued to resemble theory of mind. Therefore, if the capacity for mirror self-recognition is a precursor for complex social cognitive capabilities, then California scrub jays would be expected to show this ability. Indeed, preliminary evidence in a caching context suggests scrub jays may not respond to their reflection as if it were another individual (Dally, Emery, & Clayton, 2010), although it is not clear whether they show mirror self-recognition.

Here, we further examined mirror self-recognition abilities of California scrub jays using two contexts: a caching task (similar to that used by Clary & Kelly, 2016b and Dally et al., 2010) and the traditional mark test (Gallup, 1970). During the caching task, we measured the extent to which scrub jays protected their caches after caching alone, after caching in the presence of a conspecific and after caching in the presence of either a regular or blurry mirror. These two mirror conditions allowed us to parse the sources of information important for mirror self-recognition: identity information (i.e., the discernable visual features of an individual) and the contingency of motion between the individual and the reflection. In a natural environment, self-generated images to which an animal would be exposed rarely contain clear identity information, whereas contingent motion is much more abundant (e.g., shadows or distorted reflections in water). Therefore, these two sources of information may contribute differently towards fostering mirror self-recognition, depending on an animal's learning history and exposure to the information. The results of Clary and Kelly (2016b) suggest using a blurry mirror, which provides only contingent motion information, might facilitate mirror self-recognition for Clark's nutcrackers. By including the blurry mirror in the present study, we evaluated whether scrub jays responded similarly towards their blurred reflection, with mirror self-recognition facilitated by contingent motion. The caching task was followed by the mark test, during which a sticker (either red or matched [to the human eye] with the colour of scrub jay plumage) was placed on the birds' throat feathers. While marked, the birds were subsequently exposed to a regular and blurry mirror, as well as a non-reflective control

barrier. By including the mark test in addition to the caching task, we evaluated whether the two mirror procedures produced similar results. Taken together, these tests aim to build a more comprehensive profile of the mirror self-recognition abilities of California scrub jays.

2 | METHODS

2.1 | Subjects

Seven adult wild-caught California scrub jays (*A. californica*) participated in the experiment. The caching task was completed by six focal birds (3 female, 3 male), with an additional female used as the observer. As such, half the birds had a same-sex observer and the other half had an opposite-sex observer. All seven birds completed the mark test. The birds had been in captivity for 8–12 years and had no previous experimental experience with mirrors or caching. The birds were housed in individual cages (73 × 48 × 48 cm; H × L × W) within a larger colony room at the University of Manitoba. As such, the birds were familiar with one another visually, but had not interacted with one another within a caching context. Males were housed in adjacent cages a few metres away from the females, so pair bonds were unlikely to have formed between any male and the female observer. The scrub jays were fed a daily ration of turkey starter, cockatiel pellets, sunflower seeds, mealworms and a vitamin supplement to maintain their weight at 90%–95% of their free feeding weight. All birds had ad libitum access to grit and water. The colony room was maintained on a 12:12 hr light:dark cycle. Procedures were approved by the local Animal Care Committee at the University of Manitoba (Protocol #F10-029) in accordance with the guidelines of the Canadian Council on Animal Care.

2.2 | Caching task

2.2.1 | Apparatus

Trials were conducted by placing a focal bird into one half of a two-compartment cage (123 × 63.5 × 66.5 cm), with a clear acrylic barrier or a mirror (both 65 × 62 cm) separating the compartments. The mirror used was a “second surface” mirror (thin metal film affixed to the back of a pane of glass). White curtains enclosed the testing area to provide a uniform view, devoid of distracting stimuli. All trials were video-recorded using an Allied Vision® Guppy PRO 1/3” digital camera, with the lens slightly protruding through a small hole in the curtains such that it was not visually obtrusive.

2.2.2 | General procedures

Procedures were modelled after those described by Clary and Kelly (2016b). During the morning of a trial, any food remaining in the cage from the previous day's ration was removed to ensure the birds were motivated to eat and cache during the experiment.

Each trial was comprised of a *Caching Phase* and, approximately 2 hr later, a *Retrieving Phase*. During a *Caching Phase*, birds were provided a dish containing 30 pine nuts and were allowed 15 min to eat or cache the pine nuts in a sand-filled plastic ice-cube tray (26 wells; 13 × 2 matrix; herein referred to as the “caching tray”). The caching tray was placed parallel to the acrylic barrier separating the two compartments. Each bird was provided the same caching tray for every *Caching Phase*, and the caching trays were made visually distinct by a combination of coloured Mega Building Blocks™ affixed to its base. A second tray (herein referred to as the “mirrored tray”) was positioned parallel to the caching tray in the adjacent cage compartment (i.e., on the opposite side of the acrylic barrier), to which the bird did not have access. The mirrored tray was identical to the caching tray with the exception that the positions of the coloured blocks were “reflected.” The adjacent cage compartment also contained an identical dish with pine nuts, positioned such that the adjacent cage, and all of its contents, appeared as a reflected version of the focal bird's compartment.

During the *Retrieving Phase*, in addition to the caching and mirrored trays present during the *Caching Phase*, the birds were also provided with a “re-caching tray,” identifiable with a different combination of coloured blocks. The re-caching tray was placed along the far wall opposite to the acrylic barrier and parallel to the caching tray (Figure 1). As the re-caching tray was not present during the *Caching Phase*, it provided the birds with potential cache sites that were not associated with the observer and therefore the risk of cache loss. The birds were given 15 min to recover any pine nuts that had been cached during the *Caching Phase*, either by eating the pine nuts or re-caching them in the caching or re-caching tray. Additional *Retrieving Phases* were conducted as necessary until all caches made during the *Caching Phase* were consumed. The number and location of pine nuts cached were recorded after both the *Caching* and *Retrieving Phases* by physically searching the wells of the caching and re-caching trays.

2.2.3 | Familiarization

All birds initially participated in Familiarization trials prior to the experimental conditions to acclimate them to the testing environment, including the acrylic barrier and all trays (i.e., caching, re-caching and mirrored trays). These trials followed the procedures outlined above, except during early Familiarization trials, pine nuts were scattered about the cage to encourage the birds to interact with the caching tray. Familiarization trials were conducted until the birds were reduced to their target weight and had made at least one cache in 2/3 consecutive trials (range: 10–22 trials for individual birds).

2.2.4 | Baseline

Following Familiarization, the birds completed six Baseline trials. During Baseline, a bird experienced both the *Caching Phase* and the *Retrieving Phase* alone. The adjacent cage compartment contained

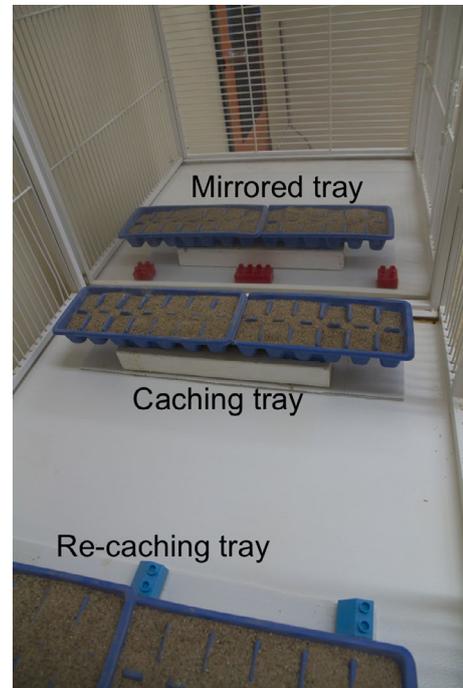


FIGURE 1 Photograph showing the two-compartment testing environment from the perspective of the focal bird's compartment. The caching and mirrored trays were present during both the *Caching* and *Retrieving Phases*, whereas the re-caching tray was only present during the *Retrieving Phase*. A clear acrylic barrier separated the caching and mirrored trays during all phases

only the mirrored tray. A clear acrylic barrier separated the two cage compartments. Baseline trials established a bird's normal caching and recovery tendencies prior to introducing an observer (see below). This Baseline was key to establish, as the presence of an observer may result in the testing environment itself becoming associated with the risk of cache theft, potentially influencing caching even in conditions during which the observer was absent.

Upon completing Baseline, each bird participated in six trials of each experimental condition: Alone, Blurry Alone, Mirror, Blurry Mirror, Observed and Blurry Observed. Corvids learn quickly to adapt their caching behaviours to the social context during this paradigm (e.g., Clary & Kelly, 2011; Emery et al., 2004), often within three trials. Therefore, although we did not expose the birds to mirrors prior to the experimental conditions, conducting six trials allowed us to assess how extended experience with the mirrors affected caching behaviours over time. Experimental trials were conducted in randomized order within each of six blocks of trials, such that each block contained one trial of each condition (i.e., trials of each condition were selected without replacement in each block).

2.2.5 | Alone/Blurry Alone

Similar to the Baseline condition, each bird cached while alone in both conditions, as the adjacent cage compartment remained empty except for the mirrored tray. During the Alone condition, a clear acrylic barrier separated the two cage compartments. The Alone

condition allowed us to assess caching behaviours without the presence of a conspecific, and determine whether the environment itself became associated with a risk of being observed. During the Blurry Alone condition, a film of faux window frosting (Artscape Inc. Texture Twelve) was applied to a second acrylic barrier, which was placed behind the clear barrier. The Blurry Alone condition allowed us to assess whether the mere presence of the faux window frosting caused birds to engage in more cache protection behaviours (i.e., changes in the number of pine nuts cached, eaten or re-cached), either because they found the blurry barrier to be inherently threatening or because of the added uncertainty as to whether they were being observed.

2.2.6 | Mirror/Blurry Mirror

For the Mirror and Blurry Mirror conditions, respectively, either a regular mirror or a blurry mirror was inserted behind the clear acrylic barrier during the *Caching Phase*. The same faux window frosting used in the Blurry Alone condition was applied to create the blurry mirror. During the *Retrieving Phase*, only the clear acrylic barrier separated the two compartments. The Mirror condition was designed to assess whether the birds interpreted the mirror image as another bird or as a reflection of themselves. If the mirror image was interpreted as a conspecific, the birds were expected to engage in more cache protection behaviours compared to the Alone conditions. If the mirror image was interpreted as their own reflection, we predicted no difference in cache protection behaviours when compared to the Alone conditions. The Blurry Mirror condition removed the clear identity information (see Figure S1a) provided by a regular mirror, leaving only contingent motion. Thus, if limiting the information provided by the mirror to contingent motion facilitated mirror self-recognition (as suggested by Clary & Kelly, 2016b), then we predicted birds would engage in less cache protection behaviours compared to the Mirror condition.

2.2.7 | Observed/Blurry Observed

During the Observed and Blurry Observed conditions, a conspecific bird was placed in the adjacent cage compartment. The presence of the conspecific required the focal bird to make their caches while being observed. The Blurry Observed condition was conducted by placing the blurry acrylic barrier (as used during the Blurry Alone condition) behind the clear acrylic barrier (Figure S1b). The conspecific observer had access to the mirrored tray and a dish of pine nuts during both the Observed and Blurry Observed conditions. As such, the focal bird was exposed to similar eating and caching behaviours from the observer as they would have seen from their self-generated behaviours during the Mirror and Blurry Mirror conditions. During the *Retrieving Phase*, the clear acrylic barrier separated the two compartments. The Observed and Blurry Observed conditions assessed whether the birds engaged in cache protection behaviours after being observed by a conspecific, as shown in previous research (e.g., Emery & Clayton,

2001), and in the case of the Blurry Observed condition, whether uncertainty about the observer's identity influenced cache protection behaviours.

2.3 | Mark test

2.3.1 | Apparatus

The mark test was conducted in the same two-compartment experimental cage used during the preceding caching task, using the same recording equipment. Depending on the trial type, the two cage compartments were separated by either a regular mirror, a blurry mirror or a non-reflective white plastic barrier. The scrub jays were marked on the throat region with small adhesive stickers (diameter = 6 mm). We used a red test mark ($M \pm SD = 6,260 \pm 593 \mu\text{g}$) and a plumage-matched control mark ($M \pm SD = 4,109 \pm 437 \mu\text{g}$). As scrub jays' throat feathers are mottled with blue, grey and white feathers, the control mark was made by photographing the throat feathers, white balancing the image and printing the pattern onto sticker sheets. Sheets were then hole-punched to obtain the final circular mark. The visual system of California scrub jays has not been studied, although corvids of the genus *Corvus* have some ultraviolet (UV) sensitivity (Håstad, Victorsson, & Ödeen, 2005; Ödeen & Håstad, 2003), so the mark may have differed in UV reflectance from the plumage of the scrub jays, but was otherwise well camouflaged to human vision (for photographs see Figure S2).

2.3.2 | Procedures

After completion of the caching task, but prior to the mark test, all birds were given additional opportunities to learn the properties of mirrors. Each bird experienced ten 20-min trials, once per day, during which they were placed in the experimental cage with a vertically positioned half-mirror separating the two compartments. The half-mirror allowed the birds to experience the disappearance of their image at the mirror's edge, and the ability to move into the adjacent compartment to explore behind the mirror. This procedure provided the scrub jays with similar experiences as those of the nutcrackers examined by Clary and Kelly (2016b), which had extended mirror exposure prior to the mark test.

Procedures for the mark test closely replicated those used by Clary and Kelly (2016b). The birds experienced each of three mark conditions (Red Mark, Control Mark and No Mark) during three viewing conditions (Opaque Barrier, Mirror and Blurry Mirror). Each day, the scrub jays completed two 20-min trials, separated by approximately two and a half hours. To prepare a bird for a trial during the Red and Control Mark conditions, one experimenter covered the bird's head with the sleeve of their laboratory coat, while a second experimenter placed the mark at a location on the bird's throat region not normally viewable to the bird. While placing the mark, the other experimenter pressed down on various other body parts so the tactile sensation of being marked was not exclusively to the throat region. The Red Mark condition provided both tactile and

visual information, whereas the Control Mark condition provided only tactile cues (see Figure S2 for pictures of mark placement and Figure S3 for the Red Mark visibility during the Blurry Mirror condition). For the No Mark condition, a sticker was placed on the bird's throat, as described above, but then immediately removed before pressing other body parts as described above. The No Mark condition measured a bird's baseline propensity to make actions directed to the throat region.

The birds completed two trials of each combination of mark and viewing condition (18 total trials). The order of trials was pseudo-randomized such that each bird experienced each mark/viewing combination before the same combination was repeated. If scrub jays are capable of mirror self-recognition with either the regular or blurry mirror, the birds were predicted to make more self-directed actions to the throat region during mirror conditions with the Red Mark, compared to conditions with the Control Mark and with No Mark. If the blurry mirror facilitated mirror self-recognition by only providing contingent motion, as opposed to the regular mirror which provided both identity and contingent motion information, then the birds were predicted to show more self-directed actions to the Red Mark during the Blurry Mirror condition compared to the Mirror condition.

2.4 | Statistical analysis

For the caching task, the absolute number of pine nuts cached and eaten was measured during the *Caching Phase*, and the absolute number of pine nuts re-cached, eaten and recovered (defined as pine nuts re-cached + eaten; see Clary & Kelly, 2011; Emery et al., 2004) during the first *Retrieving Phase*. The proportion of pine nuts re-cached and recovered (from the total pine nuts available per trial) during the first *Retrieving Phase* was also examined.

For the mark test, the video recordings were scored to obtain the number of self-directed behaviours made with the beak or foot to the mark (i.e., throat area) and non-mark regions of the body, the frequency of feather ruffling, and the number of social behaviours. Observed social behaviours included aggressive displays (defined as a bird standing upright while flaring the tail feathers) and attempts to attack the other bird or reflection (defined as a bird flying at the barrier in an attempt to grapple with its talons). Two experimenters scored the videos, with one individual being naïve to the experimental question. To determine inter-rater reliability, 20/126 of the videos were scored by both individuals. The scoring of these behaviours was highly correlated between the two individuals ($r = .98$).

To analyse the data, we used linear mixed-effects models with Condition, Trial and their interaction inputted as fixed effects for the caching task. Condition, Mark Type and their interaction were inputted as fixed effects for the mark test. For both the caching task and the mark test, Subject was inputted as a random effect to account for the repeated measurements of each bird. When dealing with missing values, as in the case of the proportional analyses (i.e., a proportion could not be calculated for trials during which a bird did not cache), degrees of freedom were estimated by Satterthwaite's

approximation. Residual plots indicated the models were both linear and homoscedastic.

For the caching task, we evaluated the main effect of condition by including Baseline trials, but removed Baseline trials when evaluating the main effect of trial and the interaction of condition and trial. This procedure was adopted because the Baseline trials gave no information as to whether the birds' changed their behaviour due to their experiences during the experimental conditions. Alpha was set at 0.05 for all analyses and Tukey adjustments, which control the family-wise error rate, were used for post hoc comparisons for the caching task. All analyses were conducted in R version 3.5.3 (R Core Team, 2019) using the packages *lme4* (Bates, Maechler, Bolker, & Walker, 2015), *lmerTest*, (Kuznetsova, Brockhoff, & Christensen, 2017) and *multcomp* (Hothorn, Bretz, & Westfall, 2008).

3 | RESULTS

3.1 | Caching task

During the *Caching Phase*, there was a main effect of Condition for the number of pine nuts cached ($F_{(6, 240)} = 3.101, p = .006$; Figure 2). The birds cached the most pine nuts during the Observed condition ($M \pm SEM = 12.69 \pm 0.061$), statistically more than during the Mirror ($M \pm SEM = 9.67 \pm 0.60, z = 3.760, p = .003$) and Blurry Alone conditions ($M \pm SEM = 10.14 \pm 0.55, z = -3.174, p = .025$), but not statistically different than during the Baseline condition ($M \pm SEM = 10.83 \pm 0.70, z = 2.311, p = .238$). No other conditions were statistically different from one another. When Baseline trials were removed, there was no main effect of Trial ($F_{(5, 175)} = 1.879, p = .100$), nor a Condition by Trial interaction ($F_{(25, 175)} = 0.550, p = .960$).

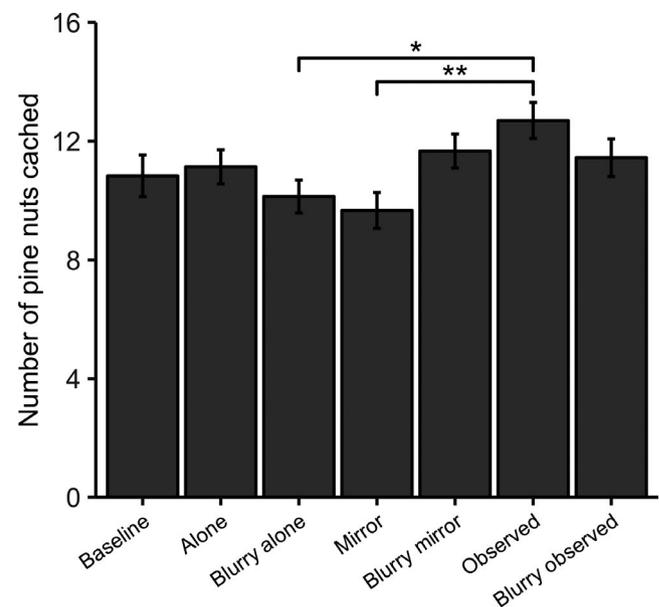


FIGURE 2 Mean number of pine nuts cached during the *Caching Phase* of each condition of the caching task. Error bars represent standard error of the mean. * indicates $p < .05$, ** indicates $p < .01$

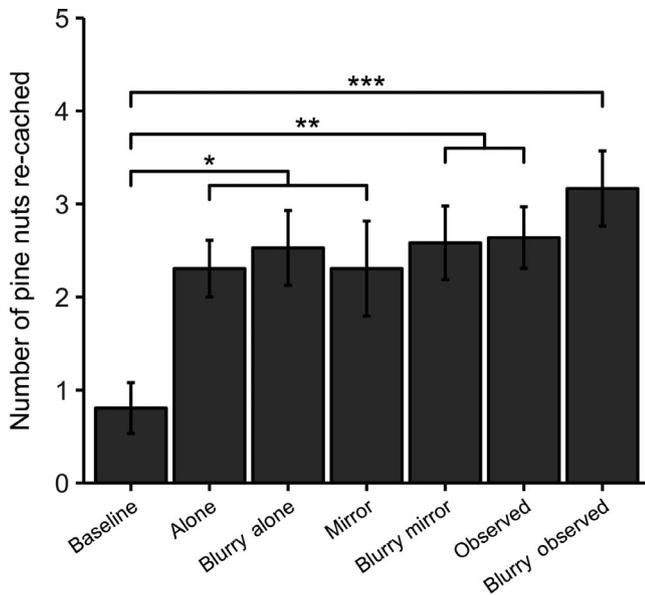


FIGURE 3 Mean number of pine nuts re-cached during the *Retrieving Phase* of each condition of the caching task. Error bars represent standard error of the mean. * indicates $p < .05$, ** indicates $p < .01$, *** indicates $p < .001$

For the number of pine nuts eaten during *Caching Phase*, there was no main effect of Condition ($F_{(6, 240)} = 1.470, p = .189$). With the Baseline condition removed from the analysis, there was a main effect of Trial ($F_{(5, 175)} = 7.200, p < .001$), as there was a reduction in the number of pine nuts eaten from trial two ($M \pm SEM = 12.06 \pm 0.33$) compared to trials four ($M \pm SEM = 10.58 \pm 0.29, z = 3.293, p = .013$), five ($M \pm SEM = 10.11 \pm 0.40, z = 4.349, p < .001$) and six ($M \pm SEM = 10.11 \pm 0.28, z = 4.349, p < .001$). There was no interaction between Condition and Trial ($F_{(25, 175)} = 0.429, p = .993$).

During the *Retrieving Phase*, there was a main effect of Condition when analysing the number of pine nuts re-cached ($F_{(6, 240)} = 4.219,$

$p < .001$; Figure 3), with the number of pine nuts re-cached lower during the Baseline condition ($M \pm SEM = 0.81 \pm 0.27$) compared to all other conditions (Alone: $M \pm SEM = 2.31 \pm 0.30, z = 2.972, p = .047$; Blurry Alone: $M \pm SEM = 2.53 \pm 0.40, z = 3.413, p = .012$; Observed: $M \pm SEM = 2.64 \pm 0.33, z = 3.633, p = .005$; Blurry Observed: $M \pm SEM = 3.17 \pm 0.40, z = 4.679, p < .001$; Mirror: $M \pm SEM = 2.31 \pm 0.51, z = 2.972, p = .047$; and Blurry Mirror: $M \pm SEM = 2.58 \pm 0.40, z = 3.523, p = .008$). No other conditions statistically differed from one another. With the Baseline condition removed, there was a main effect of Trial ($F_{(5, 175)} = 6.790, p < .001$; Figure 4), as the birds showed an increase in the number of pine nuts re-cached comparing trial one ($M \pm SEM = 1.31 \pm 0.27$) to trials four ($M \pm SEM = 2.79 \pm 0.44, z = 3.575, p = .004$), five ($M \pm SEM = 3.21 \pm 0.37, z = 4.426, p < .001$) and six ($M \pm SEM = 3.00 \pm 0.35, z = 4.426, p < .001$). There was no interaction between Condition and Trial ($F_{(25, 175)} = 0.889, p = .620$).

The same pattern of results was found when analysing re-caches as a proportion of the pine nuts available. There was a main effect of Condition ($F_{(6, 233)} = 4.052, p < .001$), as the birds re-cached a greater proportion of pine nuts in all conditions (Alone: $M \pm SEM = 0.21 \pm 0.04, z = 3.484, p = .009$; Blurry Alone: $M \pm SEM = 0.22 \pm 0.03, z = 3.740, p = .004$; Mirror: $M \pm SEM = 0.21 \pm 0.04, z = 3.599, p = .006$; Blurry Mirror: $M \pm SEM = 0.20 \pm 0.03, z = 3.310, p = .016$; Observed: $M \pm SEM = 0.19 \pm 0.02, z = 3.210, p = .023$; and Blurry Observed: $M \pm SEM = 0.25 \pm 0.03, z = 4.395, p < .001$) compared to the Baseline condition ($M \pm SEM = 0.06 \pm 0.02$). With Baseline trials removed, there was a main effect of Trial ($F_{(5, 169)} = 6.942, p < .001$) as the birds increased the proportion of pine nuts re-cached from trial one ($M \pm SEM = 0.10 \pm 0.02$) compared to trials four ($M \pm SEM = 0.21 \pm 0.03, z = 3.354, p = .010$), five ($M \pm SEM = 0.26 \pm 0.03, z = 4.547, p < .001$) and six ($M \pm SEM = 0.25 \pm 0.03, z = 4.723, p < .001$). There was no interaction between Condition and Trial ($F_{(25, 169)} = 0.868, p = .649$).

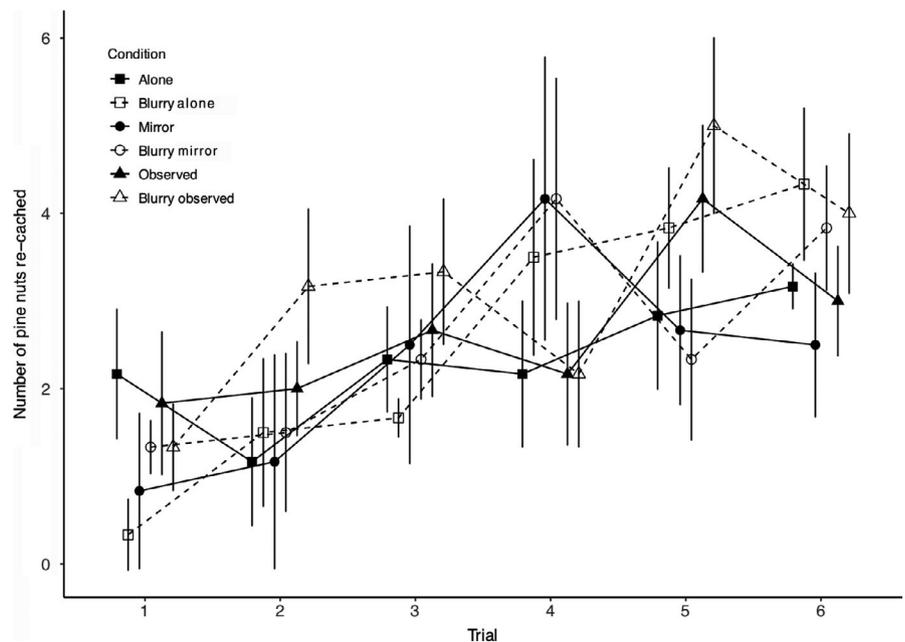


FIGURE 4 Mean number of pine nuts re-cached during the *Retrieving Phase* of each trial for each condition of the caching task. Error bars represent standard error of the mean

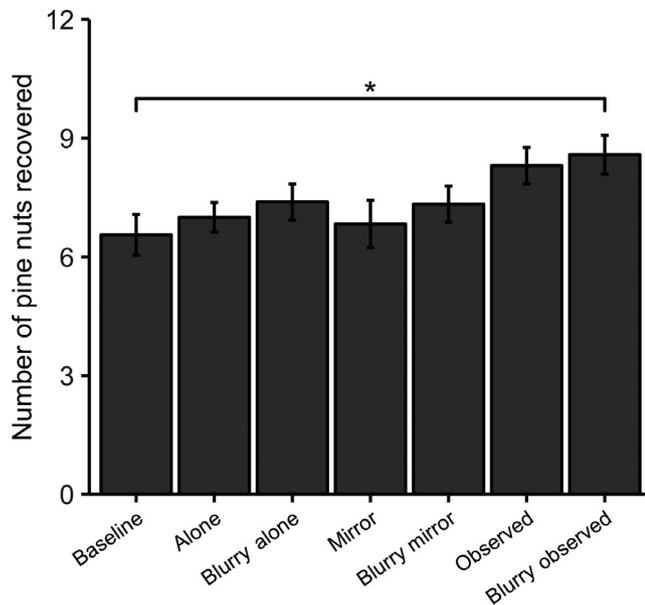


FIGURE 5 Mean number of pine nuts recovered during the *Retrieving Phase* of each condition of the caching task. Error bars represent standard error of the mean. * indicates $p < .05$

When analysing the number of pine nuts recovered during the *Retrieving Phase*, there was a main effect of Condition ($F_{(6, 240)} = 2.777, p = .013$; Figure 5), in which the scrub jays recovered more cached pine nuts during the Blurry Observed condition ($M \pm SEM = 8.58 \pm 0.49$) than during the Baseline condition ($M \pm SEM = 6.56 \pm 0.52, z = 3.168, p = .026$). No other conditions statistically differed from one another. With Baseline trials removed, there was no main effect of Trial ($F_{(5, 175)} = 0.775, p = .569$), nor a Condition by Trial interaction ($F_{(25, 175)} = 0.848, p = .676$).

When using a proportional analysis of the pine nuts recovered during the *Retrieving Phase*, there were some differences from the analysis described above. Although there was still a main effect of Condition ($F_{(6, 233)} = 2.939, p = .009$; Figure 6), there were no statistical differences between conditions after the Tukey adjustment. The proportion of pine nuts recovered during the Mirror ($M \pm SEM = 0.75 \pm 0.03, z = 2.836, p = .069$) and Blurry Observed ($M \pm SEM = 0.74 \pm 0.03, z = 2.609, p = .12$) conditions were the closest to approach a statistical difference with the proportion of pine nuts recovered during the Baseline condition ($M \pm SEM = 0.62 \pm 0.03$). With Baseline trials removed, there was no main effect of Trial ($F_{(5, 169)} = 0.795, p = .555$), nor a Condition by Trial interaction ($F_{(25, 169)} = 0.627, p = .915$).

The caching and eating behaviour of the observer was similar to the behaviour of the focal birds during the Mirror conditions. The number of pine nuts the observer cached ($M \pm SEM = 9.29 \pm 0.91$) across all Observed and Blurry Observed trials was not statistically different from the number of pine nuts the focal birds cached ($M \pm SEM = 10.67 \pm 0.75$) across all Mirror and Blurry Mirror trials ($F_{(1, 44)} = 0.050, p = .833$). The number of pine nuts the observer ate ($M \pm SEM = 10.25 \pm 0.78$) across all Observed and Blurry Observed trials was not statistically different from the number of pine nuts

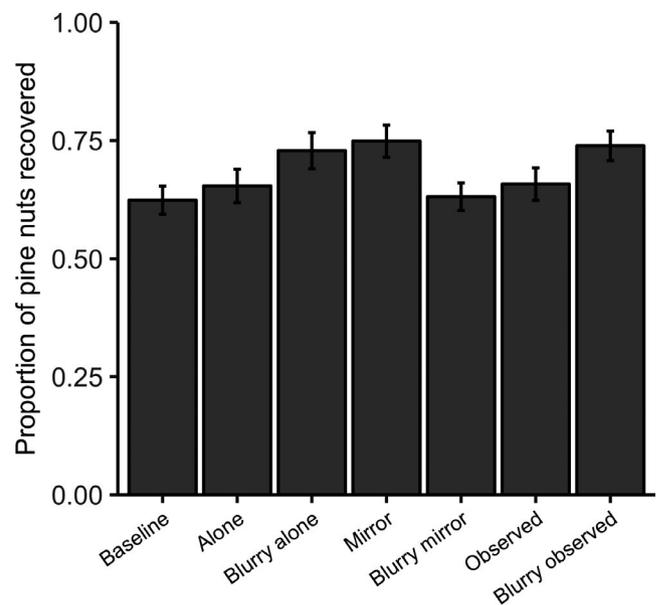


FIGURE 6 Mean proportion of pine nuts recovered during the *Retrieving Phase* of each condition of the caching task. Error bars represent standard error of the mean. After the Tukey adjustment, none of the conditions differed statistically

eaten by the focal birds ($M \pm SEM = 10.67 \pm 0.36$) across all Mirror and Blurry Mirror trials ($F_{(1, 3.1)} = 0.035, p = .863$).

3.2 | Mark test

For the number of actions directed to the mark region, there was no main effect of Condition ($F_{(2, 111)} = 1.808, p = .169$), Mark Type ($F_{(2, 111)} = 2.296, p = .106$), nor an interaction between Condition and Mark Type ($F_{(4, 111)} = 2.0345, p = .094$; Figure 7). However, our planned comparisons revealed that the birds tended to make more actions directed to the Red Mark during the Opaque Barrier condition ($M \pm SEM = 7.86 \pm 5.16$), than during either the Mirror ($M \pm SEM = 1.00 \pm 0.52, z = 2.824, p = .031$) or Blurry mirror conditions ($M \pm SEM = 0.36 \pm 0.37, z = 3.088, p = .014$). The higher number of mark region actions during the Opaque Barrier condition with the Red Mark was largely driven by two trials, during which the birds clearly noticed the mark and perseverated in their attempts to remove it (Table 1).

For non-mark region actions, there was no main effect of Condition ($F_{(2, 111)} = 1.688, p = .190$), Mark Type ($F_{(2, 111)} = 0.507, p = .604$), nor a Condition by Mark Type interaction ($F_{(4, 111)} = 0.291, p = .883$). For feather ruffles, there was no main effect of Condition ($F_{(2, 111)} = 2.552, p = .082$), Mark Type ($F_{(2, 111)} = 1.105, p = .335$) nor any interaction between Condition and Mark Type ($F_{(4, 111)} = 1.408, p = .236$). Social behaviours were limited to two individuals during the Mirror condition: Nero showed aggressive bouts in all Mirror condition trials (Mirror/No Mark: $M = 16.5$; Mirror/Control mark: $M = 9.5$; Mirror/Red Mark: $M = 5.5$), and Phineas, the observer from the caching task who had less mirror experience prior to the mark test, showed aggressive behaviours during only the first Mirror/No Mark trial (5 aggressive bouts).

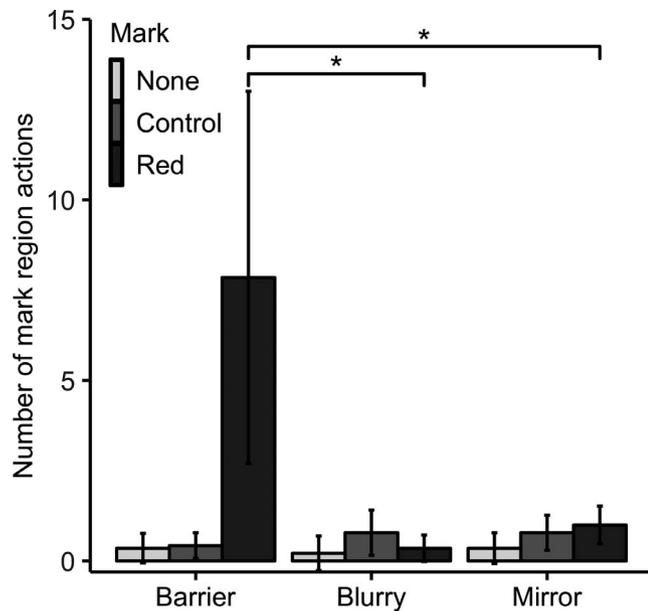


FIGURE 7 Mean number of actions towards the mark region (i.e., throat area) during the mark test. Error bars represent standard error of the mean. * indicates $p < .05$

4 | DISCUSSION

The current study investigated the mirror self-recognition abilities of California scrub jays across two experiments: a caching task and the mark test. Overall, our results show limited evidence of mirror self-recognition in scrub jays. We found some evidence of mirror self-recognition during the caching task, as scrub jays increased cache protection behaviours from Baseline when observed by another individual but not when they were in the presence of a mirror. During the mark test, however, we did not find any evidence of mirror self-recognition, as birds did not use either the regular or blurry mirror to direct attempts to remove the red mark.

Results from the caching task replicated a previous finding that scrub jays tend to increase caching when in the presence of an observer (Emery et al., 2004), yet a similar increase was not shown when caching with either a regular or blurry mirror. In fact, the most apparent statistical difference in caching behaviour in our study was found for the number of caches made between the Observed

and Mirror conditions, suggesting the mirrored reflection might not have been interpreted as a conspecific. Alternatively, it is also plausible the birds interpreted the reflection as an “odd” conspecific (de Waal, Dindo, Freeman, & Hall, 2005), which caused them to produce caching behaviour atypical for when in the presence of another individual.

Furthermore, the scrub jays did not show an increase in the number of pine nuts re-cached nor recovered during the Mirror/Blurry Mirror conditions compared to the Alone/Blurry Alone conditions, as would be expected if the reflection was interpreted as a potential thief. Instead, the birds statistically increased both re-caching and recovery rates from the Baseline condition only when the birds were being observed by a conspecific (see also Dally et al., 2010) behind a blurry barrier. There was not a similar increase in both re-caching and recovery during the Blurry Mirror condition suggesting that uncertainty regarding a conspecific's identity, but not a reflection's identity, resulted in increased cache protection behaviours. This increase in cache protection during the Blurry Observed condition was not just a response to some inherent quality of the blurry acrylic barrier, as neither the Blurry Alone nor Blurry Mirror conditions were statistically different from Baseline for the number of pine nuts recovered. This finding helps clarify an outstanding issue from Clary and Kelly (2016b): whether the birds could visually resolve the blurred image enough to understand it as another individual. Here, despite the degraded view through the barrier, the birds' behaviour supported that they were not only aware of the presence of an observer, but perceived the greatest risk to their caches during the Blurry Observed condition.

Interestingly, we did not find a difference in the number of pine nuts re-cached between the Alone condition and the Observed condition as has been found in other studies (Dally, Emery, & Clayton, 2004, 2005; Dally et al., 2006; Emery & Clayton, 2001; Emery et al., 2004). Rather, we found the birds increased re-caching behaviour more generally after the Baseline trials, likely as the birds came to associate the testing environment with the risk of being observed, thereby “compromising” the Alone and Blurry Alone conditions. Thus, although some of our predictions were met to support an interpretation of mirror self-recognition (i.e., no statistical difference in re-caching or recovery behaviours during Alone and Mirror conditions), the lack of a statistical difference for cache protection

TABLE 1 Number of mark region directed actions during trial 1/trial 2 for each bird during each condition with each mark type

Subject	Barrier/No Mark	Barrier/Control	Barrier/Red	Blurry/No Mark	Blurry/Control	Blurry/Red	Mirror/No Mark	Mirror/Control	Mirror/Red
Dr. Ham	1/0	1/0	0/66	0/0	0/0	0/0	0/0	1/0	1/0
Lena	0/0	0/0	1/0	0/0	0/0	0/0	0/0	0/0	0/0
Nero	0/0	0/1	1/0	0/2	3/0	0/0	0/0	0/3	0/0
Calvin	1/0	1/2	2/35	0/0	1/0	2/2	0/3	1/1	1/6
Woody	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
NotCalvin	0/0	0/0	3/1	0/0	0/3	0/0	0/1	0/2	0/0
Phineas	2/1	0/1	0/1	0/1	0/4	0/1	0/1	2/1	4/2

behaviours between the Alone and Observed conditions (aside from the difference in pine nuts recovered between the Baseline and Blurry Observed conditions), and between the Observed and Mirror conditions, undermines the confidence we can place in this conclusion. Overall, the pattern of results may support mirror self-recognition, particularly for the number of pine nuts recovered. The scrub jays tended to recover more pine nuts during both Observed conditions compared to both Mirror conditions and both Alone conditions; however, these differences were not statistically reliable after controlling the family-wise error rate. Although we provided additional trials relative to previous caching studies (e.g., Clary & Kelly, 2011; Emery et al., 2004), it is possible the birds still did not have enough trials for mirror self-recognition to present more clearly.

There may be alternative interpretations of the results from the caching task. For example, the birds may have interpreted the mirror image as a moving object, rather than as themselves or a conspecific. This lack of understanding would also predict no change in caching behaviour between the Alone and Mirror conditions. However, this interpretation may not be likely, as one bird (Nero) showed social behaviours with the mirror, as has been shown with many other bird species studied (e.g., Derégnaucourt & Bovet, 2016), suggesting that the reflection was responded to as another bird. Alternatively, the scrub jays may have shown no difference in cache protection behaviours during the Alone and Mirror conditions because the reflection was interpreted as a non-threatening or inattentive conspecific, as it would have cached simultaneously with the focal bird. However, this may also be unlikely, as anytime the focal bird attended to the “conspecific” when caching, the mirror image would also be attending to the focal bird. Therefore, the attentiveness of the “conspecific” in the mirror would necessarily be dependent on the focal bird's behaviour.

Results from the mark test did not show convincing evidence of mirror self-recognition by the scrub jays. The birds did not attempt to remove the red mark during either the Mirror or Blurry Mirror conditions more than during the Barrier condition. In fact, the birds were most likely to attempt to remove the red mark during the Barrier condition, during which no specular information was available. Thus, on some trials, the birds may have detected the red mark in their periphery as a result of exaggerated head movements during preening or feather ruffling. The Control Mark was very rarely detected, indicating tactile cues (i.e., sensing the weight of the mark on the feathers) were not apparent enough to the birds to stimulate self-directed behaviours.

In comparison to the nutcrackers studied by Clary and Kelly (2016b), the scrub jays showed less compelling evidence of self-recognition overall and did not have an advantage for self-recognition with the blurry mirror compared to the regular mirror. One possible explanation for this difference is that the scrub jays were not nearly as occupied with preening as the nutcrackers during the mark test (as measured by the number of non-mark region actions across all conditions [scrub jays: $M \pm SEM = 2.76 \pm 0.65$; nutcrackers: $M \pm SEM = 16.82 \pm 2.18$]). Motivational differences between the species to maintain their plumage may have made it more likely

to find nutcrackers capable of mirror self-recognition under these same conditions, as the nutcrackers were more likely to engage in self-directed behaviour overall. Motivational differences have been raised as a potential problem with the mark test (Suddendorf & Butler, 2013; de Veer & van den Bos, 1999), as the test depends on the animal's motivation to scrutinize the mirror image as well as to remove the mark once it is identified. To address this, future studies might include a condition during which the birds are marked on an easily visible part of their bodies as a baseline measure for their motivation to remove a mark (see Vanhooland et al., in press).

Differences in mirror experience prior to the mark test may have also contributed to the different mirror responses of the nutcrackers and scrub jays. The scrub jays may have lacked the prior mirror experience necessary to understand how the mirror could be used to guide their self-directed behaviours. The nutcrackers received a greater number of caching trials, with longer durations, and as such had more experience with mirrors than the scrub jays prior to the mark test (scrub jays: ~ 7.3 hr; nutcrackers: ~ 23.5 hr). This additional experience during which the nutcrackers could learn the properties of the mirrors may have better prepared them for the mark test. However, this also highlights one potential advantage of using the caching task rather than the mark test to measure mirror self-recognition: its ecological relevance. During the caching task, behaviour indicative of mirror self-recognition may emerge as a by-product of the bird's natural behaviour, instead of requiring the bird to learn to use the mirror as an instrument for self-grooming, as is necessary during the mark test.

Admittedly, our mixed findings contribute to an already muddled picture of whether corvids possess the cognitive abilities necessary for mirror self-recognition. To date, only a few individuals from two corvid species have shown preliminary evidence of mirror self-recognition (Eurasian magpies: Prior et al., 2008; Clark's nutcrackers: Clary & Kelly, 2016b). However, considering the substantial evidence that corvids share many complex cognitive traits with great apes (Emery & Clayton, 2004), corvids would be predicted to also be capable of mirror self-recognition. So why has more widespread detection of this trait in corvids been so elusive? One possible explanation is corvids are not capable of mirror self-recognition, and previous cases of corvids passing tests of mirror self-recognition are false positives. Although possible, this explanation seems unlikely considering that even within the great apes, only a small proportion of individuals within each species pass the mark test (Povinelli, Rulf, Landau, & Bierschwale, 1993). Thus, the inherent nature of the mark test may render it more prone to producing false negatives than false positives. This may be especially true when using the mark test on animals for which the test was not originally intended. For example, the tetrachromatic vision of most avian species may complicate the interpretation of the mark test. Most commercially available mirrors are constructed by adhering a thin metal film (typically aluminium) onto a sheet of glass. Common forms of glass, however, absorb wavelengths in the UVA spectrum (315–400 nm; Cetinkaya Colak & Aral, 2011), and these wavelengths may

be important for avian visual signalling (Bleiweiss, 2004; Mays & Hopper, 2004; Mays et al., 2004). Therefore, the reflection seen by a bird may not be an accurate rendition of its true appearance. If this is the case, variability in the types of mirrors used, as well as variability in a species' reliance on UV reflectance on their plumage for visual recognition, may contribute to the inconsistent findings of mirror self-recognition among corvids. This may also explain why some avian species use mirrors for non-social tasks (e.g., to locate hidden objects) during which UV information may not be as important, yet do not show evidence supporting mirror self-recognition (Medina et al., 2011; Pepperberg et al., 1995). Thus, the use of "first surface" mirrors, in which the reflective surface is not placed behind a glass barrier, may facilitate future investigations of avian mirror self-recognition.

The idiosyncrasies of the mark test also highlight the need for alternative self-recognition tasks to be developed (e.g., Dale & Plotnik, 2017). The results of Clary and Kelly (2016b) suggested the caching task may be a suitable analogue for the mark test for corvids, yet with the advantage of being a more ecologically relevant approach, which may provide a more realistic estimate of the proportion of individuals within a species capable of mirror self-recognition. Furthermore, use of blurry mirrors allows for the possibility that mirror self-recognition is a graded, rather than binary ability (Clary & Kelly, 2016b; de Waal, 2019). By developing a more diverse toolkit for assessing mirror self-recognition in non-human animals, more confident conclusions may be drawn about the relationship between mirror self-recognition and complex social cognitive abilities. However, if this relationship exists, as suggested by the early comparative literature, then it would be unexpected for scrub jays to be incapable of mirror self-recognition, considering how research of scrub jay behaviour has advanced our understanding of the potential social cognitive abilities of non-human animals. As such, the apparent failure of the scrub jays to show evidence of mirror self-recognition, as measured during the mark test, may serve as a warning against relying solely on the mark test to identify mirror self-recognition. Instead, future work should shift towards developing more ecologically relevant paradigms to supplement the mark test, thereby providing converging lines of evidence capable of bolstering our understanding of which animals are capable of mirror self-recognition and how the cognition underlying this ability has evolved.

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CONFLICT OF INTEREST

All authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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