Highly social pinyon jays, but not less social Clark's nutcrackers, modify their food-storing behaviour when observed by a heterospecific.

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Abstract

Behavioural flexibility can be described as the ability to use information and generalise it across contexts. Social living is thought to favour behavioural flexibility. We used a food-storing (caching) paradigm, during which individuals either ate or cached food under different conditions, to investigate whether they could flexibly adjust their caching behaviour when observed by conspecifics and heterospecifics. We examined the location and number of caches made by two corvid species differing in sociality, highly social pinyon jays (*Gymnorhinus cyanocephalus*) and less social Clark's nutcrackers (*Nucifraga columbiana*). Although pinyon jays cached a similar amount of food across conditions, they allocated more caches to areas less accessible to the observer when the observer spent more time close to the caching locations. Nutcrackers, however, reduced the number of seeds cached when observed by another nutcracker in comparison to when they cached alone, but did not significantly change their caching behaviour when observed by a pinyon jay. The differences in cache protection strategies, and the social cues (e.g., presence and behaviour of an observing bird) that elicit them, may be explained by the species' social organisation. Overall, our results provide insight into understanding how pressures associated with the social environment may influence foraging behaviours.

Keywords: caching, conspecifics, corvids, heterospecifics, nutcrackers, pinyon jays

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Behavioural flexibility, the ability of an animal to adapt its behaviour to novel circumstances, is thought to be one key component of complex cognition[1]. Flexible behaviour may have evolved in species whose environment is highly unpredictable[2]. For example, species living in groups with changing relationships (e.g., fission-fusion) may display more behavioural flexibility than less social species[2-5], as individuals in complex social groups need to rapidly adjust their behaviour to dynamic social environments. In such environments, it would be beneficial for individuals to switch among behavioural strategies that best fit the current situation, but also to apply adaptive behaviour to novel contexts.

Corvids are a taxonomic family of birds that are reported to possess many sophisticated cognitive abilities, some of which rival those of primates[6-8] such as tool use[9], future planning[10], and mirror self-recognition[11-12]. Corvid species differ in their social organisations along a spectrum, which makes them ideal candidates for investigating the relationship between sociality and behavioural flexibility. For example, pinyon jays (*Gymnorhinus cyanocephalus*) live in flocks of hundreds of individuals with high fission-fusion dynamics[13-14], whereas Clark's nutcrackers (*Nucifraga columbiana*) are less social, with a social group consisting of the mating pair and offspring of the year[13,15]. Hence, if the demands of a complex social life co-evolve with behavioural and social flexibility, then pinyon jays might be expected to show a more flexible behavioural repertoire than Clark's nutcrackers.

The socio-cognitive abilities of corvids are often assessed by their food-caching behaviours. Caching refers to the behaviour of storing food to survive when resources in the environment are scarce[16]. To protect their food caches from theft, corvids engage in a suite of *cache protection strategies*, during which individuals flexibly change their foraging behaviour depending on whether they are being observed. A well-studied example is the California scrub jay (*Aphelocoma californica*), which supresses caching in the presence of conspecifics[17], caches in locations that are less visible to the observer[17], and selectively re-caches food items in new locations after the observing bird has left[6].

To date, most studies examining cache protection strategies by corvids have focused on moderately social species (e.g., scrub jays[6,17]) and less-social species (e.g., nutcrackers[18]; adult ravens[13]; Eurasian jays[19]). In contrast, few studies have addressed the challenges encountered by highly social species (but see[20-21]), and no studies have directly compared the caching behaviour of highly social and less-social species using the same paradigm. Hence, we examined the caching behaviour of highly social pinyon jays and of less-social Clark's nutcrackers when in the presence of a conspecific observer, as well as when in the presence of a heterospecific observer. Displaying cache protection strategies when observed by a heterospecific may require even greater cognitive and behavioural flexibility, as the cacher must generalise the threat of losing their caches to a different species[22] and appropriately modify its caching behaviour. We also examined whether cachers changed their foraging behaviour based on social cues provided by the observing bird during caching and pilfering. If living in complex social structures influences behavioural flexibility, then highly social pinyon jays should be more likely to generalise their cache protection strategies when faced with novel heterospecific observers than less-social Clark's nutcrackers, but also that pinyon jays would adjust their foraging behaviour based on more subtle social cues than Clark's nutcrackers.

Methods

Subjects

Pinyon jays and Clark's nutcrackers served as caching birds (herein referred as "cachers"; *n* = 10 for each species, five female jays and six female nutcrackers) or as observing birds (herein referred as "observers"; two females for each species). All individuals were captured as adults from populations around Flagstaff (Arizona, USA) and were in captivity for approximately seven to ten years prior to this study. Five of the nutcracker cachers had previous experience with caching paradigms[11,18,23]; the five other nutcracker cachers, and all ten pinyon jay cachers had previous unrelated experimental experience (e.g., concept learning[24-25]; exploratory behaviour[26]).

All birds were housed in individual cages (pinyon jays: 51 x 51 x 72 cm, nutcrackers: 82 x 54 x 76 cm, width x depth x height, respectively), with multiple wood perches, at the University of Manitoba, Canada. Pinyon jays were housed in a colony room alongside California scrub jays, whereas nutcrackers were kept in a species-specific colony room. All colony rooms were maintained at 22°C with a 12:12 day-night cycle, with light onset at 0700 (Central Daylight time). These temperature and lighting conditions correspond to the average temperature and photoperiod during September in Flagstaff (USA), the peak caching season for pinyon jays and Clark's nutcrackers. Birds were given *ad libitum* water and grit. When not experiencing the food restriction procedure (see General procedures below), birds were fed a regular diet consisting of a mixture of parrot pellets, turkey starter, sunflower seeds, mealworms, peanuts, powder of oyster shells, and the vitamin powder supplement Prime®. Birds were monitored and weighed daily to ensure a healthy weight during the experiment.

All applicable international, national, and institutional guidelines for the care and use of animals were followed. Our research protocol was approved by University of Manitoba's Animal Care Committee (#F2014-037) and complied with the guidelines set by the Canadian Council on Animal Care.

Caching Apparatus

The caching apparatus was the same as used in Vernouillet et al.[21]. The experiment was conducted in an experimental room, separated from the colony room. Individual birds were tested in a cage (123.5 x 63.5 x 74.5 cm, width x depth x height), divided into two equally-sized compartments. The entire cage was surrounded by white curtains (Figure S1; also Figure 1 from Vernouillet et al. [21]). A transparent acrylic divider separated the two compartments, each of which contained a perch. One compartment served as the "caching compartment", whereas the other served as the "observing compartment".

Within the caching compartment, cachers were given two plastic ice cube trays (49.5 x 11 cm, length x width) each with 2 rows of 13 wells filled with sand. Trays were made visually distinctive by affixing coloured plastic MegaBlocks™ at the base of each tray. Each cacher received the same pair of distinct trays throughout the study, but the arrangement of colored blocks differed across subjects. One tray (hereafter referred to as the "pilfered tray") was positioned parallel and flush against the acrylic cage divider, whereas the other tray (hereafter referred to as the "safe tray") was positioned on the opposite wall of the caching compartment (i.e., parallel to the first tray). A food dish was placed in the caching compartment beside the cage door, between the two trays

(Figure S1). All trials were recorded using an EverFocus® 1/3″ color digital camera positioned either beside or above the experimental cage and using the motion tracking program, BiObserve® through Windows XP.

General Procedures

The experimental procedures were the same as Vernouillet et al.[21]. Briefly, each bird was given a weekly experimental session. Cachers were food deprived for 24h before the start of the *Caching phase*, by removing all the food from their home cage. This procedure created food uncertainty and motivated individuals to cache[18,21,27]. The session started with a 45-min *Caching phase*, during which the cacher was provided with a dish of 50 pine nuts to cache or consume. The observing compartment was arranged as per the condition to be completed that session (see Conditions below). This phase was immediately followed by a 3-min *Pilfering phase*, during which the pilfered tray was placed in the observing compartment, alongside the divider and in the same orientation as during the *Caching phase*. The safe tray was placed on a stool outside of both compartments (remaining visible, but inaccessible to both birds). Upon the completion of the *Pilfering phase*, all birds were returned to the colony room. After a one-hour delay, the cacher was given a 5-min *Re-caching phase*, during which both trays were returned to the cacher, such that they could eat or re-cache (i.e., move a pine seed to a different location from where it was previously cached) some of the seeds while alone. A re-cache was thus recorded when a pine seed was found in a different well of either the same tray or the opposite tray, compared to where it was originally placed. Upon completion of the *Re-caching phase*, the cacher was returned to the colony room and provided with a small amount of food to ensure a healthy bodyweight was maintained, while ensuring the bird would remain motivated to retrieve its caches the following day. During the *Retrieving phase*, which occurred 24 hours after the completion of the *Caching phase*, the cacher was placed in the caching compartment with the safe and pilfered trays, unaltered from the previous *Re-caching phase*. The cacher was permitted 45 minutes to consume or re-cache the previously cached pine seeds, during which the observing compartment of the caching cage was empty (i.e., retrieval was always conducted while alone). Additional *Retrieving phases* were administered, on the following day, every three hours if necessary, until the cacher recovered the entirety of its caches. After each phase, the researcher recorded the number and location of each pine seed (for more details, see Supplementary Material, or Vernouillet et al. [21]).

Conditions. After three weeks of baseline trials during which individuals experienced the exact same procedure as during the experiment in private (similar to the *Alone* condition), each cacher experienced three blocks of four conditions (*Alone*, *Conspecific, Heterospecific* and *Object*), with each condition randomly selected and not repeated within the same block. Each condition refers to what (if anything) was present in the observing compartment during the *Caching* and *Pilfering phases*. Observers did not participate as cachers to exclude potential effects of pilfering experience on their caching behaviour[28]. The pairing of observers to cacher remained consistent throughout the experiment (each observer watched five cachers of each species).

Alone. During the *Caching phase*, the observing compartment remained empty (Figure 1a). During the *Pilfering phase*, the pilfered tray was placed in the empty observing compartment for three minutes, and the pine seeds cached in that tray remained undisturbed. This condition was conducted to assess the baseline caching behaviour of cachers and was used to assess whether exposure to the experimental conditions changed the caching behaviour of individuals.

Object. During the *Caching phase*, an inanimate object (a black water bottle, 27.5 x 7.0 cm, height x diameter) was affixed to the perch in the observing compartment (Figure 1b). During the *Pilfering phase*, the pilfered tray was placed in the observing compartment with the object for three minutes, whereas the safe tray was placed on a stool outside of the cage, remaining visible to the cacher. The experimenter removed pine seeds from the pilfered tray after the *Pilfering phase* (but before the *Re-caching phase*). Pilfering rate was kept consistent across individuals by removing 33% of pine seeds cached during the first and second blocks, and 50% of pine seeds cached during the third block, to resemble natural variation of the pilfering rate in the wild[29]. Both trays were given back to the cacher during the *Re-caching phase*. This condition served as a control to determine whether the cacher modified its caching behaviour in response to cache loss, and when compared with the *Conspecific* and *Heterospecific* conditions, assessed the importance of social and motion cues in the display of cache protection strategies.

Conspecific. During the *Caching phase*, a bird of the same species as the cacher occupied the observing compartment (Figure 1c). During the *Pilfering phase*, the pilfered tray was placed in the observing compartment with the observer, who was given three minutes to access the tray in view of the cacher. The safe tray was placed on an inaccessible stool outside of the cage, but visible to both birds. If the observer did not pilfer enough seeds according to the pilfering rate described for the Object condition, additional pine seeds were removed by the experimenter after the *Pilfering phase* (but before the *Re-caching phase*). Similarly, if the observer pilfered more seeds than the standardized threshold, the experimenter added caches back in the tray after the *Pilfering phase* (but before the *Re-caching phase*). In both cases, the experimenter adjusted the seed number such that all areas of the tray were pilfered equally. This condition was conducted to assess whether the presence and behaviour of a conspecific observer influenced the cacher's behaviour.

Heterospecific. This condition was conducted as during the *Conspecific* condition, with the exception that the bird in the observing compartment was of a different species than the cacher (Figure 1d). This condition was conducted to assess whether the presence and the behaviour of a heterospecific observer influenced the cacher's behaviour.

Behavioural Measures

Dependent variables. During the *Caching phase*, we examined the number of pine seeds cached (in the trays and externally) and eaten. During the *Re-caching phase*, we examined the proportion of re-cached seeds. This proportion was calculated by dividing the number of caches found in new locations (compared to the location of caches documented at the end of the *Caching phase*) by the total number of pine seeds remaining after the *Re-caching phase*. All measures were evaluated at a global-level (i.e., with respect to the total number of pine seeds cached) and at a tray-level, to determine whether cachers associated the pilfering risk with the pilfered tray, but not the safe tray. At the tray level, the proportion of re-cached pine seeds corresponds to the proportion of pine seeds present in the tray at the end of the *Re-caching phase* that were found in new locations in comparison to the locations documented at the end of the *Caching phase*.

Behaviour of the observer. From the recorded sessions of the *Conspecific* and *Heterospecific* conditions, we measured the duration (in seconds) the observer spent interacting with the cacher during the *Caching phase* and with the pilfered tray during the *Pilfering phase*. During the *Caching phase*, the observer was defined as interacting with the cacher when the observer was standing within the third section of the observing compartment closest to the divider separating the two compartments. During the *Pilfering phase*, the observer was defined as interacting with the pilfered tray when searching in the tray, retrieving pine seeds, or standing on the tray.

Statistical Analyses

We performed analyses separately for each species. We used a generalized linear mixed model (GLMM) approach for our analyses, with the number of seeds cached and eaten during the *Caching phase* and the proportion of seeds re-cached during the *Pilfering phase* as dependent variables. Condition, duration of time the observer spent interacting with the cacher during the *Caching phase,* and duration of time the observer spent interacting with the pilfered tray during the *Pilfering phase* were included as fixed factors in our models to assess whether the cacher responded to the observer's behaviour during the *Caching* and *Re-caching phases*. Other fixed factors included in the models were experimental block and the cacher's sex. We performed separate analyses on the number of seeds cached in each tray and the proportion of seeds re-cached in each tray to determine whether the cachers treated the two trays differently. For these analyses, we included tray identity (pilfered vs. safe) as an additional fixed factor. Identity of the cacher was included in all models as a random factor to account for repeated measures taken on each cacher. Residual plots indicated assumptions of normality were met for the number of caches made during the *Caching phase*. We used the logarithmic number of pine seeds eaten during the *Caching phase* and the square root of the proportion of pine seeds that were re-cached during the *Re-caching phase* to meet the assumptions of normality. Analyses were conducted using R version 3.3.2[30] with the *lme4*[31], *lsmeans*[32], *psych* [33], and *qpcR*[34] packages.

To assess the fit of each model, we used Akaike's Information Criterion (*AIC*). Models were considered equivalent when $\Delta AIC < 2.0$. We obtained *p*-values for each fixed factor (i.e. tray, condition, block, sex, amount of time the observer interacted with the cacher during the *Caching phase*, amount of time the observer interacted with the pilfered tray during the *Pilfered phase*, block x condition, condition x tray, condition x block x tray, condition x amount of time the observer interacted with the cacher during the *Caching phase*, condition x amount of time the observer interacted with the pilfered tray during the *Pilfered phase*, tray x amount of time the observer interacted with the cacher during the *Caching phase*, tray x amount of time the observer interacted with the pilfered tray during the *Pilfered phase*) using likelihood ratio tests of the model with the fixed factor in question against the model without the fixed factor in question. Parameter estimation was achieved using residual maximum likelihood. Post-hoc analyses were conducted using pairwise comparisons. *P*-values of post-hoc analyses were adjusted using the Tukey method to consider multiple comparisons[32]. Alpha was set at 0.05 for all statistical analyses.

Results

Pinyon Jays

Number of pine seeds cached and eaten during the Caching phase. There were no statistical differences in the overall number of pine seeds cached by pinyon jays between conditions (*M* ± *SE*: *Alone*: 14.6 ± 2.4, *Object*: 15.0 ± 2.1, *Conspecific*: 15.6 ± 2.2, *Heterospecific*: 16.2 ± 2.2; $\chi^2_{(3)} = 0.579$, $p = 0.901$, $\Delta AIC = 6.7$; Figure 2; Table S1). No other fixed factors examined in our analyses explained the total number of seeds cached during the *Caching phase* by the pinyon jays.

Instead, we found that pinyon jays preferentially allocated their caches in the safe tray when observed. The number of pine seeds cached in each tray was best explained by the duration of time the observer spent interacting with the cacher during the *Caching phase*, regardless of the species of the observer ($\chi^2_{(2)} = 28.978$, $p < 0.001$; Table S1). As the observer spent more time interacting with the cacher, the cacher decreased the number of pine seeds cached in the pilfered tray and increased the number of pine seeds cached in the safe tray (Intercept: 7.50 ± 1.41 pine seeds; Pilfered tray estimate: -0.18 ± 0.06 pine seeds/min; Safe tray estimate: +0.24 ± 0.06 pine seeds/min; Figure 3).

There were no statistical differences in the number of pine seeds eaten by pinyon jays between conditions (see Supplementary Material, Table S2).

Proportion of re-cached pine seeds during the Re-caching phase. There were no statistical differences in the proportion of re-cached pine seeds across conditions by pinyon jays (*M* ± *SE*: *Alone*: 0.24 ± 0.05, *Object*: 0.20 ± 0.04, *Conspecific*: 0.28 ± 0.06, *Heterospecific*: 0.29 ± 0.07; $\chi^2_{(3)} = 2.573$, $p = 0.462$, $\Delta AIC = 3.4$; Table S3). No other fixed factors considered in our models explained the overall proportion of re-cached pine seeds during the *Re-caching phase* by pinyon jays (*M* ± *SE*: 0.25 ± 0.03; Table S3).

The proportion of re-cached pine seeds in each tray was best explained by the amount of time the observer spent interacting with the cacher during the *Caching phase* ($\chi^2_{(2)} = 24.315$, $p < 0.001$; Table S3). After the observer spent more time interacting with the cacher during the *Caching phase*, there was an increase in the proportion of pine seeds present in the Pilfered tray that were re-cached (i.e., found in new locations within the Pilfered tray), but not in the Safe tray, during the *Re-caching phase*

(Intercept: 0.378 ± 0.067, Pilfered tray estimate: 0.018 ± 0.006 proportion/min; Safe tray estimate: -0.000 ± 0.006 proportion/min).

Clark's Nutcrackers

Number of pine seeds cached and eaten during the Caching phase. The overall number of pine seeds cached by nutcrackers was best explained by conditions ($\chi^2_{(3)} = 11.953$, $p = 0.008$; Table S4; Figure 2). Nutcrackers cached significantly fewer pine seeds when observed by a conspecific compared to when caching alone ($M \pm SE$: *Alone*: 22.0 ± 1.6; *Conspecific*: 16.2 ± 1.8; $t = 3.39$, $p = 0.005$), and tended to cache fewer pine seeds when observed by a conspecific than when observed by a heterospecific (i.e., pinyon jay), though this difference was not significant ($M \pm SE$: *Heterospecific*: 20.3 ± 1.8; $t = -2.37$, $p = 0.089$). There was no difference in the number of pine seeds cached when caching alone and when observed by a heterospecific ($t = 1.02$, $p = 0.741$).

The number of pine seeds cached in each tray by the nutcrackers was also best explained by condition ($\chi^2_{(7)} = 33.847$, $p < 0.001$; Figure 4, Table S4). Nutcrackers cached more pine seeds in the pilfered tray than in the safe tray during the *Alone* ($M \pm SE$: Pilfered tray: 13.6 ± 1.6, Safe tray: 8.5 ± 1.1; $t = 3.152$, $p = 0.002$; Figure 4) and *Object* conditions ($M \pm SE$: Pilfered tray: 12.4 ± 1.5, Safe tray: 6.1 ± 1.1; $t = 3.867$, $p = 0.001$; Figure 4). During the *Conspecific* condition, nutcrackers showed an opposite tendency to cache more pine seeds in the safe tray than in the pilfered tray, but this difference did not reach statistical significance ($M \pm SE$: Pilfered tray: 6.6 ± 1.1, Safe tray: 9.6 ± 1.3; $t = -3.050$, $p = 0.061$; Figure 4). There were no differences in the number of pine seeds cached between trays during the *Heterospecific* condition ($M \pm SE$: Pilfered tray: 10.9 ± 1.4, Safe tray: 9.4 ± 1.3; $t = 0.977$, $p = 0.330$; Figure 4).

There were no statistical differences in the number of pine seeds eaten by Clark's nutcrackers between conditions (see Supplementary Material; Table S5).

Proportion of pine seeds re-cached during the Re-caching phase. There were no statistical differences in the proportion of pine seeds re-cached across conditions by nutcrackers ($M \pm SE$: *Alone*: 0.24 ± 0.05, *Object*: 0.24 ± 0.05, *Conspecific*: 0.23 ± 0.06, *Heterospecific*: 0.32 ± 0.11; $\chi^2_{(3)} = 1.337$, $p = 0.721$, $\Delta AIC = 4.9$; Table S4). None of the factors we considered in our models explained the overall proportion of re-cached pine seeds by nutcrackers during the *Re-caching phase* ($M \pm SE$: 0.26 ± 0.03; Table S6).

The best-ranked model explaining the proportion of pine seeds re-cached in each tray during the *Re-caching phase* included only tray identity ($\chi^2_{(1)} = 27.017$, $p < 0.001$; Table S6). Across all conditions, the proportion of pine seeds present in the Pilfered tray that were re-cached (i.e., found in new locations within the Pilfered tray) was greater than the proportion of pine seeds present in the Safe tray that were re-cached ($M \pm SE$: Pilfered tray: 0.43 ± 0.04, Safe tray: 0.19 ± 0.03).

Discussion

In the presence of a pilfering conspecific, pinyon jays preferentially allocated their caches in safer locations (see also[21]), whereas Clark's nutcrackers reduced the number of caches made overall (see also[11,18,23]). The social cues triggering the display of cache protection strategies differed between species. Pinyon jays' caching behaviour was influenced by the amount of time an observer spent interacting near the caching tray, whereas nutcrackers' caching behaviour was influenced by the mere presence or absence of a conspecific.

In the presence of a pilfering heterospecific, pinyon jays allocated their caches in safer locations in comparison to when they were caching alone, as they did when observed by a conspecific. Also, of the caches remaining after the *Re-caching phase*, a greater proportion of these caches were re-caches (i.e., found in new locations from what the observer would have witnessed) in the pilfered tray compared to the safe tray. Both the allocation of caches and the increase in re-caching depended on the duration of time the observing bird interacted close to the cacher and the caching locations during the caching session.

We found less evidence that Clark's nutcrackers modified their caching behaviour when observed by a pinyon jay compared to when they cached alone. Nutcrackers allocated their caches preferentially in the pilfered tray when they were caching alone and in the presence of an object, but not when they were caching in presence of an observing conspecific or heterospecific. This result may indicate that nutcrackers generally associated the pilfered tray with a higher risk of losing their caches when observed by another individual. This was also supported by the greater proportion of the seeds present in the pilfered tray that were moved to a new location by caching nutcrackers at the end of the re-caching phase than for the safe tray. However, despite experiencing repeated cache loss to pinyon jay observers to the same degree as with nutcracker observers, they did not reduce the amount of caches made, nor did they preferentially allocate their caches in safe locations when caching. This result may indicate that, unlike pinyon jay cachers, nutcrackers did not view the pinyon jays as a pilfering threat.

An explanation for the species differences in caching behaviour may be that observing pinyon jays spent less time interacting with cachers during the *Caching phase* compared to observing nutcrackers (Table S7). Thus, nutcrackers may have viewed pinyon jay observers as less threatening than conspecifics based on their behaviour, despite similar rates of cache loss. Pinyon jays, however, viewed both conspecifics and heterospecifics as threatening. More studies are required to determine which cues nutcrackers use to assess the pilfering risk associated to the observer.

The social cues that elicit the display of cache protection behaviours in pinyon jays and nutcrackers may also align with the demands of social living. Pinyon jays' caching and re-caching behaviours were influenced by the amount of time an observer spent interacting near the caching tray, whereas nutcrackers' caching behaviour was influenced by the mere presence or absence of a conspecific. As highly social pinyon jays rarely cache in private[14], it may be more advantageous for an individual to adjust its behaviour only when warranted by the behaviour of the observer, and not simply in the presence of an observer. On the contrary, less social species such as Clark's nutcrackers and Eurasian jays (*Garrulus glandarius*) can reduce their caching rate in the presence of another bird[18,19], since they have more opportunities to cache in private. Therefore, pinyon jays may use more nuanced social information during caching to adjust their behaviour than nutcrackers, due to the more restrictive conditions in which they cache, regardless of whether the observer pilfers the caches afterwards[21]. The difference in use of social cues may be evidence that pinyon jays have evolved greater behavioural flexibility compared to nutcrackers.

Social information can be exchanged between conspecifics and heterospecifics when multiple species share the same territory or resources. For example, some species are influenced by heterospecifics when responding to alarm calls[36,37], when choosing a breeding site[38,39], or even when foraging[40]. In the case of our study species, individual Clark's nutcrackers briefly join flocks of pinyon jays for protection during late summer and early fall, when both species collect pine seeds to cache for the winter[42]. Both species' caches are susceptible to pilfering by one another, but also by Steller's jays (*Cyanocitta stelleri*), another social jay species[43]. Here, we provide experimental evidence that one corvid species, the pinyon jay, can flexibly use the social information provided by an observer, regardless of the species, and adjust their caching behaviour accordingly. To date, only one other study evaluated whether a caching species, the mountain chickadee (*Poecile gambeli*), can adjust its caching behaviour in the presence of a pilfering heterospecific, the red-breasted nuthatch (*Sitta canadensis*;[22]). Mountain chickadees cached preferentially in hidden sites in presence of observing nuthatches but used both hidden and visible sites when they were alone, suggesting chickadees could view nuthatches as a threat for their caches. Both pinyon jays and mountain chickadees have complex social behaviour[44,45], supporting the social living hypotheses that suggest social living might promote more flexible behaviours, especially in a social context[2,5].

Our results provide equivocal evidence that social living could promote cognitive flexibility, at least in corvids[2]. Up until now, most socio-cognitive abilities thought to be present in corvids have been found in both social and non-social corvid species. For instance, both social magpies and less-social nutcrackers show evidence of mirror self-recognition[11,12]. Even in a social context, nutcrackers and more social corvids such as pinyon jays and azure-winged magpies can both perform complex social interactions with conspecifics, like cooperatively sharing food[23,46,47]. Based on our findings, one possibility is that the ability to view a conspecific as a threat might be common to all corvids, but that only highly social species adjust their caching behaviour to the social context due to the selection pressures associated with social living[2,5].

Alternatively, the species difference in caching behaviour could also be ontogenetic, as pinyon jays will likely witness a greater number of caching and pilfering events between members of their social group, and in more varied social contexts than nutcrackers. These additional learning opportunities may facilitate greater generalisation of the cognitive abilities underlying cache protection behaviours. In both cases, social living could explain the differences in behavioural flexibility between the two caching species.

In summary, the current study investigated, for the first time, whether corvids display cache protection strategies in the presence of a heterospecific in a controlled setting. We found that highly social pinyon jays and less social Clark's nutcrackers displayed different caching behaviours when observed. Pinyon jays preferentially allocate cached food in areas less accessible to a conspecific or heterospecific observer, but primarily when the observer spent more time near a caching tray. Contrarily, nutcrackers reduced the number of caches they made, but only when observed by another nutcracker. Overall, these findings suggest that corvids may differ in their use of social information and in the extent to which they interpret heterospecifics as a threat. These findings may indicate that the ability to view a conspecific as a threat is shared among corvids regardless of social organisation. However, highly social species may display more behavioural flexibility by generalising the use of cache protection strategies against heterospecifics to a greater extent and by adjusting their caching behaviour to the social context. Our results provide insight into understanding how pressures associated with the social environment may influence the caching behaviour of corvids and support the idea of more social species adjusting their behaviour more flexibly than less social species. Our findings provide a step further into understanding how complex cognition has evolved.

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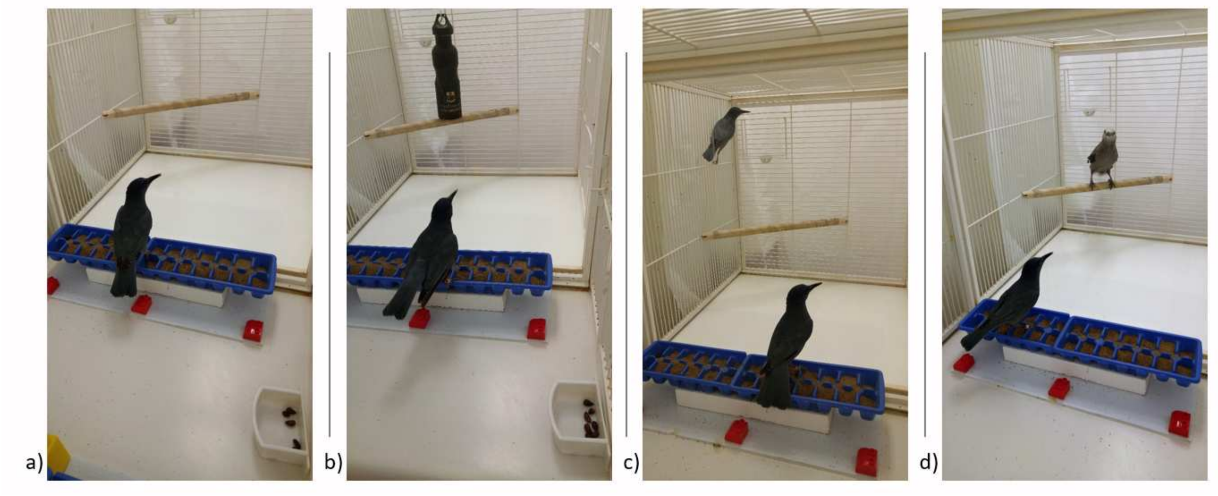

Figure 1. Pictorial representation of the experimental conditions during the *Caching phase*. The caching compartment contained the cacher (nearest bird, here a pinyon jay), and the observing compartment **a)** remained empty, contained **b)** an object, **c)** a conspecific (here, another pinyon jay), or **d)** a heterospecific (here, a Clark's nutcracker).

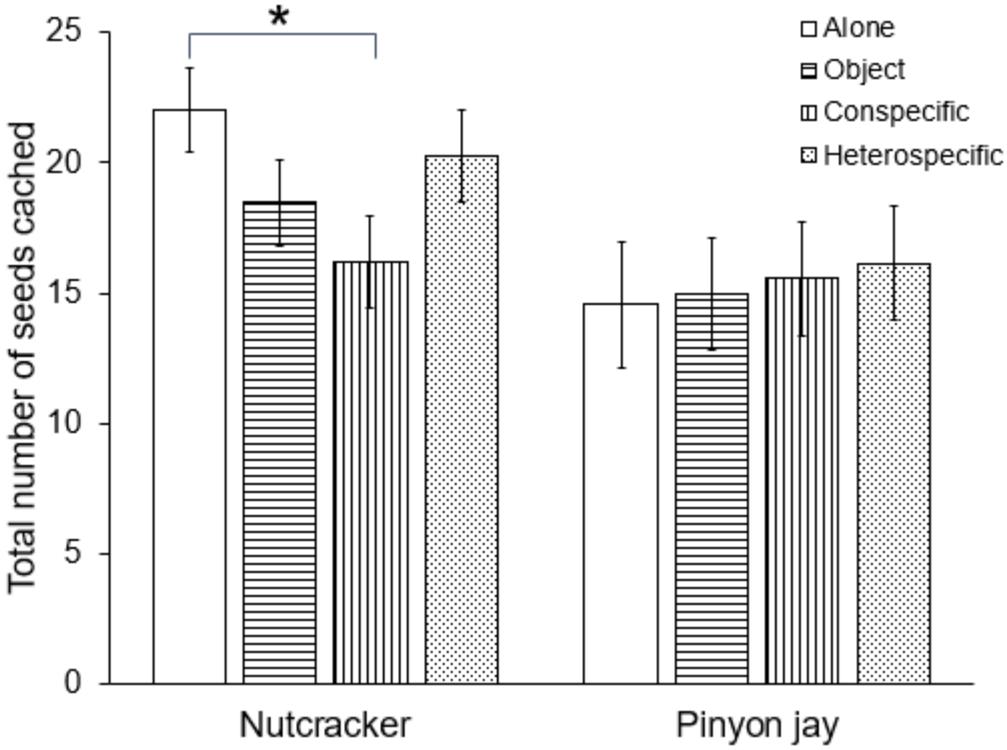

Figure 2. Total number of pine seeds cached (± *SE*) by Clark's nutcrackers and pinyon jays during the *Caching phase* during the Alone, Object, Conspecific, and Heterospecific conditions. Nutcrackers cached less when in the presence of another nutcracker (*Conspecific* condition) in comparison to when they were caching alone ($p = 0.008$). There was no difference in the number of seeds cached by pinyon jays across conditions ($p = 0.901$).

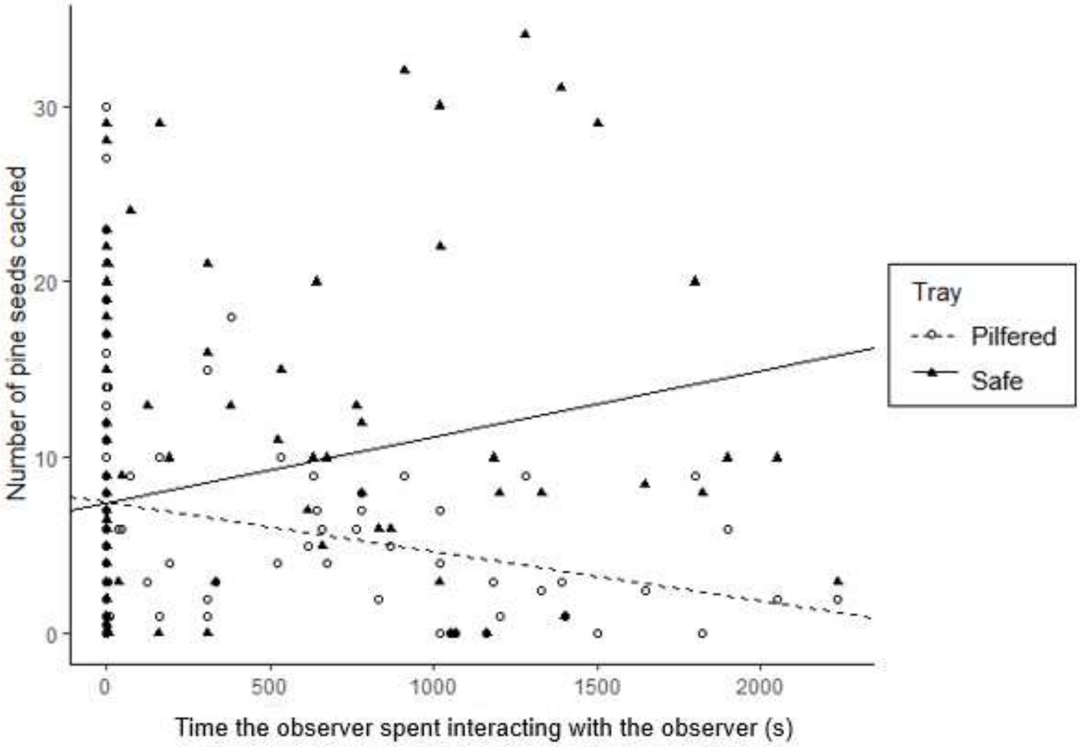

Figure 3. Number of pine seeds cached by pinyon jays in the pilfered tray and in the safe tray during the *Caching phase* depended on the amount of time the observing bird interacted with the caching bird ($p < 0.001$).

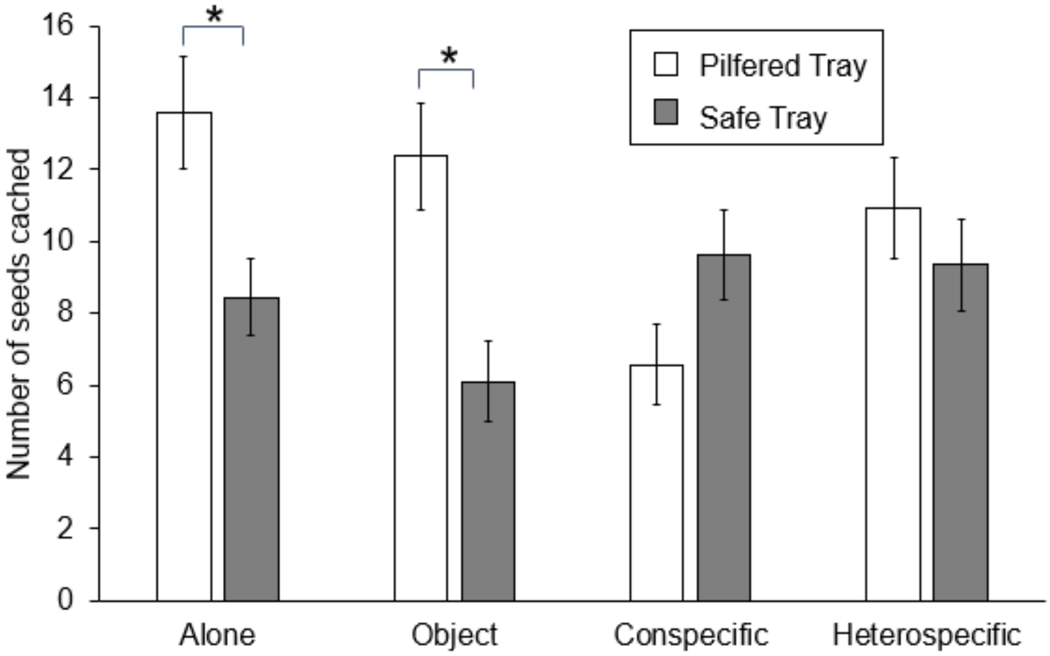

Figure 4. Number of pine seeds cached in the safe and in the pilfered trays by caching nutcrackers in each experimental condition during the *Caching phase* ($p < 0.001$).