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# Pilfering Eurasian jays use visual and acoustic information to locate caches

**Rachael C. Shaw · Nicola S. Clayton**

**Abstract** Pilfering corvids use observational spatial memory to accurately locate caches that they have seen another individual make. Accordingly, many corvid cache-protection strategies limit the transfer of visual information to potential thieves. Eurasian jays (*Garrulus glandarius*) employ strategies that reduce the amount of visual and auditory information that is available to competitors. Here, we test whether or not the jays recall and use both visual and auditory information when pilfering other birds' caches. When jays had no visual or acoustic information about cache locations, the proportion of available caches that they found did not differ from the proportion expected if jays were searching at random. By contrast, after observing and listening to a conspecific caching in gravel or sand, jays located a greater proportion of caches, searched more frequently in the correct substrate type and searched in fewer empty locations to find the first cache than expected. After only listening to caching in gravel and sand, jays also found a larger proportion of caches and searched in the substrate type where they had heard caching take place more frequently than expected. These experiments demonstrate that Eurasian jays possess observational spatial memory and indicate that pilfering jays may gain information about cache location merely by listening to caching. This is the first evidence that a corvid may use recalled acoustic information to locate and pilfer caches.

**Keywords** Corvid · *Garrulus glandarius* · Observational spatial memory · Auditory information · Pilfering

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## Introduction

Observational spatial memory enables individuals to remember the locations of caches that they have seen others make (Bugnyar and Kotrschal 2002) and increases their search accuracy when locating caches to pilfer (Dally et al. 2006). Faced with pilferers that can accurately locate caches using observational spatial memory, caching individuals utilise cache-protection tactics which limit the transfer of visual information about cache location to potential pilferers (Bugnyar and Kotrschal 2002; Dally et al. 2006). Although observational spatial memory has been demonstrated for all other corvid species that have been tested to date (summarised in Shaw and Clayton 2012), it has yet to be tested in Eurasian jays.

When caching, Eurasian jays utilise tactics which may limit opportunities for conspecifics to observe them, such as caching at a distance from competitors (Shaw and Clayton 2012). In addition to visual cache-protection tactics, Eurasian jays, like Western scrub jays (*Aphelocoma californica*, Stulp et al. 2009), also employ cache-protection tactics in the auditory domain. Compared to when alone, jays reduce the proportion of caches made in a noisy gravel substrate when a competitor can hear but cannot see them (Shaw and Clayton 2013). Suppressing acoustic information when caching may avoid drawing the attention of nearby, out-of-view competitors that could subsequently

attempt to view caching (Dally et al. 2006). The jay's auditory cache-protection tactics may also mitigate the risks posed by out-of-view conspecifics that can use auditory information to locate caches that they have heard another individual make. Potentially, pilfering jays may gain spatial information about cache location by listening to caching and recall and use this to guide their search for caches to pilfer. However, it has yet to be experimentally evaluated whether any food-caching species is capable of using auditory cues in this manner.

The purpose of this study was therefore twofold: firstly, to establish whether, like other corvids, Eurasian jays use observational spatial memory when pilfering a conspecific's caches and secondly, to test whether jays can use auditory information gained by listening to caching to improve their pilfering performance. An individual jay's pilfering performance was assessed in three conditions: a baseline when jays had no information about cache locations (no information condition), after jays had observed and heard caching (seen and heard condition) and after jays had heard but had not observed caching (heard only condition). To create caching locations that were both visually and acoustically distinct, caching took place in two substrates that differed in their visual and acoustic properties. Each condition had two trials: one in which caches were placed in a noisy gravel substrate (the noisy trial) and the other in which caches were placed in the quiet sand substrate (the quiet trial).

In the baseline 'no information' condition, we predicted that Eurasian jays, like other corvids (e.g. Western scrub jays: Watanabe and Clayton 2007), would not use olfactory cues to locate hidden food (Hitchcock and Sherry 1990) and so would be no more accurate when pilfering than if they were searching for caches randomly. In contrast, we predicted that the jays would be able to recall visual information about cache location and so their pilfering performance would be better than a random search strategy in the 'seen and heard' condition. Finally, in the 'heard only' condition, we predicted that, given the jays' sensitivity to the acoustic properties of sand and gravel when caching (Shaw and Clayton 2013), jays may be able to use the noise associated with caching in gravel and the relative absence of noise associated with caching sand to guide their search behaviour to the correct substrates and increase their success above a random search strategy when locating caches to pilfer.

## Methods

Nine adult jays (aged 4 years in 2011; four females, five males) were tested outside of the breeding season between 26 October 2011 and 17 February 2012 and 29 August

2012 and 4 September 2012. Jays were housed in an outdoor aviary complex throughout the experiment (H × W × L: 3 × 10 × 28 m). General housing and husbandry are described in detail elsewhere (Shaw and Clayton 2012, 2013).

### Apparatus

Testing took place in two adjacent indoor compartments (H × W × L: 3 × 1 × 1 m) accessible from the aviary via opaque trap doors (hereafter the 'caching/pilfering' and the 'observing' compartments; Fig. 1). Compartment interiors were not visible from the aviary when the trap doors were closed. In the 'caching/pilfering' compartment (Fig. 1a), two caching trays were placed on a wooden platform that was positioned 1 m above (and preventing access to) the floor. Trays were 5 × 25 × 25 cm seedling trays each containing 16 pots (5 cm diameter). Each tray had a 7-cm-wide cloth strip running down the centre, separating the pots into two groups of eight, each arranged in a 2 × 4 array (Fig. 1b). One array in each tray was filled with white sand (the 'quiet' substrate) and the other with brown gravel (the 'noisy' substrate). All subjects had prior experience caching in similar substrates and caching trays (see Shaw and Clayton 2013 for details). The 'observing' compartment contained one central perch positioned next to a window (20 × 30 cm) cut into the opaque white sheet which covered the wire mesh separating the 'caching/pilfering' and 'observing' compartments. The window was situated in the centre of the wall and 1 m above the platform in the 'caching/pilfering' compartment (Fig. 1a).

### Procedures

Testing took place between 1,000 and 1,300, and subjects received no more than one trial per day. To ensure that subjects were mildly hungry, all food was removed from the aviary at least an hour before testing. A within-subject, repeated-measures design was used, and all subjects were tested individually in three conditions ('no information', 'seen and heard' and 'heard only'), with two trials in each condition (a 'noisy' and a 'quiet' trial). Subjects initially had two baseline trials (one 'noisy' and one 'quiet' trial) in the 'no information' condition in which they searched for 15 min for caches that they had neither seen nor heard being made. Before the trial began, the experimenter (R.C.S.) hid five nuts in five separate pots in one array: in the 'quiet' trial, all caches were in the sand array of one tray, while in the 'noisy' trial, all caches were in the gravel array of the other tray. The caches were placed in the trays before the trays were carried from the video observation hut to the aviary, ensuring that no subjects could hear caching take place in the 'no information' condition. The

**(a)** Caching phase    **(b)** Pilfering phase
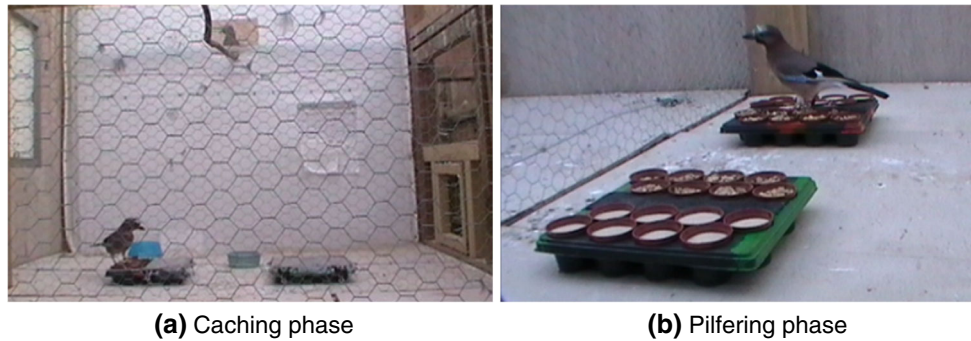
**Fig. 1 a** During the caching phase in a 'seen and heard' trial, the subject (visible in 'observing compartment' through the small window in *top centre* of image) observes a cacher in the 'caching/pilfering' compartment. Plastic covers on the trays allow the cacher access to half of one tray only. **b** During the pilfering phase, both trays are uncovered and placed in the exact same position as during the caching phase. The tray in the foreground illustrates how each tray contains eight sand pots (*near*) and eight gravel pots (*far*)

order of the 'noisy' and 'quiet' trials was counterbalanced between individuals. Three subjects (Ayton, Adlington and Purchas) did not approach either tray in their initial baseline trials; thus, they had two additional 'no information' trials after being tested in the remaining two conditions. These three subjects had also observed a conspecific caching in both substrates in a previous experiment (see Shaw and Clayton 2013). However, this previous experiment took place in different compartments and the jays did not have the opportunity to pilfer any caches.

The 'seen and heard' and 'heard only' conditions began with a caching phase in which the subject was in the 'observing' compartment for 15 min, while a conspecific (the 'cacher') was given a bowl containing 20 peanuts and two caching trays in the 'caching/pilfering' compartment (Fig. 1a). In the 'seen and heard' condition, transparent Perspex covered the window between compartments, allowing the subject to view the cacher (Fig. 1a). In the 'heard only' condition, the Perspex was covered with opaque card, preventing visual access to the cacher. The order of the two conditions was counterbalanced between individuals. Within each condition, there was a 'noisy' and a 'quiet' trial: the cacher had access to the sand array of one tray in the 'quiet' trial and the gravel array of the other tray in the 'noisy' trial (the video in the supplementary materials exemplifies how caching looked and sounded in the two substrates). To control the tray locations that a cacher could access, both arrays of one tray were entirely covered with transparent plastic and the other tray was half-covered to leave only one array available for caching in. Within each condition, the order of the 'noisy' and 'quiet' trials and the array that was first available for the cacher was counterbalanced between individuals.

After caching, the subject and cacher were both released and excluded from the compartments. The locations of caches in the trays and in out-of-tray locations in the 'caching/pilfering' compartment were recorded. All caches made in the trays were removed and rehidden in the same

locations by the experimenter, with the substrate smoothed over to remove any visual cues. Initially, out-of-tray caches (which typically consisted of peanuts wedged into crevices but remaining partially visible) were left intact. However, only one subject (Romero) consistently searched in the trays when out-of-tray caches remained. Therefore, four subjects (Adlington, Ayton, Ohuruogu and Purchas) had all trials repeated with out-of-tray caches removed (only data from the repeated trials were analysed) and three subjects (Hoy, Pendleton and Wilson) were only tested with out-of-tray caches removed. After 15 min, the trays were returned to their original positions with the plastic covers removed, the food bowl was removed, and the subject was enclosed in the 'caching/pilfering' compartment for the 15-min pilfering phase. At the end of the pilfering phase, the subject was released, the locations of caches remaining in the trays were recorded, and any items that had been pilfered from the trays and recached in out-of-tray locations were also recorded. All trials were recorded using Panasonic SDR-S70 cameras.

To encourage the cacher to cache in trays throughout the experiment, cachers were allowed to recover any tray caches that they had made in the previous trial (with any pilfered caches replaced) the subsequent morning after 1-h deprivation and before testing took place that day. Additionally, the particular trays and their precise location remained constant throughout the 'seen and heard' and 'heard only' trials to minimise disruption to caching behaviour. To minimise caching behaviour variation between conditions, a subject had the same cacher for all trials. In total four jays acted as cachers, three of these (Pendleton, Ayton and Wilson) did so prior to being tested as subjects and one (Ohuruogu) did so after being tested as a subject.

Analysis

Three of the nine jays tested were not included in the analysis: one (Wiggins) did not search for caches in any of

the experimental conditions, one (Hoy) could not be used as an observer because none of the cachers would reliably cache when in his presence, and one (Pendleton) stopped searching in the trays over the course of his trials. The Observer XT (Noldus) was used to analyse the videos of the pilfering phase for the remaining six (three males, three females) subjects. Frame-by-frame analysis (30 frames $s^{-1}$) was used to count the number of times that a subject dug and the precise location in which digging occurred, as well as pilfering. Occasionally, subjects recached peanuts that they had found: any digs made in a location containing a cache made by the subject, or in a location that the subject had cached in during the immediately preceding trial, were not included in the analysis, as it was unlikely that the subject was searching for a cache to pilfer in these circumstances. To assess the reliability of video coding, an independent observer (P. Marques) who was completely unfamiliar with the birds and with the experimental aims and conditions scored the precise location of every dig that occurred during a trial (pot, substrate and tray) in 14 % of the videos (five different trials from five different subjects). The observer and experimenter had a high level of agreement (Cohen's $k = 0.86$).

The following measures of pilfering performance were analysed: the proportion of caches found out of the total number of caches available (hereafter *search success*), the number of unique empty pots searched in until the first cache was found (hereafter *search efficiency*) and the proportion of these searched empty pots that contained the correct substrate or were in the correct tray. *Search efficiency* was measured only until the first cache was found, as locating an item may affect subsequent search behaviour (Hitchcock and Sherry 1990); for example, finding a cache may have caused jays to direct their subsequent search in adjacent locations, or begin searching for a location in which to recache the item. Occasionally, a bird encountered a correct location, but delayed pilfering until later in the trial, or did not pilfer at all. However, this behaviour can still be considered as a correct decision relative to the cues that the bird may have used to guide search behaviour (Feenders and Smulders 2011). Therefore, *search success* included caches that were found but not retrieved and *search efficiency* was measured as the number of unique incorrect locations searched until the first correct location was encountered. In some trials, the subject never encountered or pilfered a correct location; therefore, for the analysis of *search efficiency*, the data for these trials consisted of all unique locations searched throughout the entire trial.

For both *search success* and *search efficiency*, in each condition, the birds' performance was compared to the random search behaviour expectation. This was calculated following the methods of Watanabe and Clayton (2007).

For *search success*, the proportion of caches that a subject was expected to locate by random search was calculated as the number of locations containing caches divided by the total number of locations available (e.g. in a trial with caches in five locations, the random expectation = 5/32). For the random search expectation for *search efficiency*, the expected number of unique sites searched before encountering a location containing a cache was calculated using the hypergeometric distribution. This was an exact probability calculated as $q/p$, where $p$ is the number of sites containing a cache divided by the total number of available cache sites ($p = n_{\text{cache locations}}/32$) and $q = 1 - p$. Finally, the proportion of empty locations searched that contained the correct substrate and the proportion that were in the correct tray were compared to the expectation if birds were searching randomly (i.e. 50 % of locations in the correct substrate and 50 % of locations in the correct tray).

The observed and expected values for each measure did not fulfil the assumption of normally distributed data required for parametric tests, and the sample size was too small for generalised linear mixed model approaches (Bolker et al. 2009). When pilfering, subjects slightly preferred searching in sand, which was reflected in the trend (non-significant at $\alpha = 0.05$) for more search errors to be made in sand than gravel across all conditions [median errors in sand = 5, median gravel = 1; Wilcoxon signed-rank test: $T = 2$, $N = 6$ (ties = 0), $0.10 > P_{\text{two-tailed}} > 0.05$]. An individual's pilfering performance was biased by their preference for a particular substrate type. Accordingly, five birds preferentially searched in sand during both baseline trials. Subsequently, in the 'seen and heard' and 'heard only' conditions, four of these five birds made a greater proportion of their searches in the correct substrate in their 'quiet' trials on average than in their 'noisy' trials on average (the fifth showed no difference between the two trial types), while the individual with a preference for gravel in the baseline showed the reverse pattern. Using the mean of the 'noisy' and 'quiet' trials within each condition allowed us to investigate the effect of condition on the subjects' pilfering performance without undue influence from these substrate preferences. There was no difference in the number of caches available to pilfer in the 'noisy' and 'quiet' trials within the 'seen and heard' and within the 'heard only' conditions ['seen and heard': 'noisy' median = 2.5 caches, 'quiet' median = 2 caches, $T = 6$, $N = 6$ (ties = 1), $P_{\text{two-tailed}} > 0.1$; 'heard only': 'noisy' median = 2.5 caches, 'quiet' median = 2.5 caches, $T = 8.5$, $N = 6$ (ties = 0), $P_{\text{two-tailed}} > 0.1$]. We could therefore calculate the mean of the 'noisy' and 'quiet' trials within each condition for all measures and carry out non-parametric analyses on these means.

Within each condition, Wilcoxon signed-rank tests were used to compare the random search expectations to the

observed measures of *search success*, *search efficiency*, the proportion of empty locations searched that contained the correct substrate and the proportion of empty locations that were in the correct tray. As we were testing the specific predictions outlined in the introduction, all comparisons of these measures with the random search expectation were one tailed. All tests were exact (Mundry and Fischer 1998), and $\alpha$ was 0.05.

## Results

### No information condition

When subjects had no visual or acoustic information about caching, their pilfering performance was poor; in the 'no information' condition, subjects did not differ from the random search expectation in terms of their *search success* [$T = 6$, $N = 6$ (*ties* = 0), $P > 0.1$; Fig. 2a]. Moreover, *search efficiency* was poor and subjects searched more empty locations than expected [$T = 1$, $N = 6$ (*ties* = 0), $P < 0.05$; Fig. 2b]. Subjects also searched in the wrong substrate more frequently than expected by chance before finding their first cache [$T = 0$, $N = 6$ (*ties* = 1), $P < 0.05$; Fig. 3a]. By contrast, there was no evidence that subjects were biased towards a particular tray, as they did not deviate from the chance expectation in the proportion of searches that were made in the correct tray [$T = 7$, $N = 6$ (*ties* = 1), $p > 0.1$; Fig. 3b].

### Seen and heard condition

All subjects observed part of at least one caching event in both trials of the 'seen and heard' condition (with the exception of Romero, who did not observe any caching events in the 'quiet' trial of the 'seen and heard' condition). Observing a conspecific caching resulted in pilfering performance that was better than the random search expectation. Subjects had greater *search success* [$T = 0$, $N = 6$ (*ties* = 0), $P < 0.025$; Fig. 2a] and *search efficiency* [$T = 0$, $N = 6$ (*ties* = 0), $P < 0.025$; Fig. 2b] than expected by chance. Additionally, subjects searched in the correct substrate more frequently than predicted by chance [$T = 0$, $N = 6$ (*ties* = 1), $P < 0.05$; Fig. 3a]. However, too many individuals showed no deviation from the random search expectation in the proportion of searches made in the correct tray to permit a Wilcoxon test (Fig. 3b).

### Heard only condition

Listening to caching improved the jays' pilfering performance, as subjects had greater *search success* than expected had they been searching randomly [$T = 1$, $N = 6$



**(a)** *Search success*

**(b)** *Search efficiency*
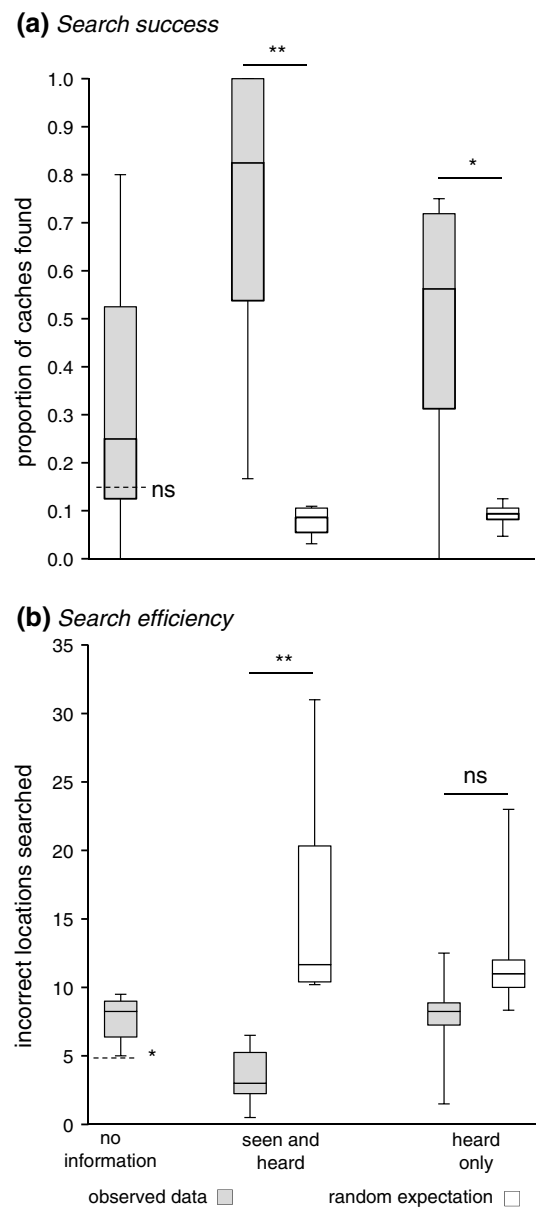
**Fig. 2** Averages of the 'noisy' and 'quiet' trials within each of the three conditions (*grey boxes*) for **a** *search success* (the proportion of cache locations found) and **b** *search efficiency* (the number of empty locations visited until the first location was found). The random search expectations are shown as a *dashed line* in the 'no information' condition and *white boxes* in the 'seen and heard' and 'heard only' conditions. The random search expectations for *search success* and *search efficiency* were calculated following the methods described in the analysis section (ns: $p > 0.05$; *$p < 0.05$; **$p < 0.025$; *whiskers* range, *boxes* upper quartile, median and lower quartile)

(*ties* = 0), $P < 0.05$; Fig. 2a]. However, their *search efficiency* did not differ from the random expectation [$T = 3$, $N = 6$ (*ties* = 0), $P > 0.05$; Fig. 2b]. Nonetheless, when acoustic information about caching was available, the jays directed their search to the correct substrate more frequently than expected if their search behaviour had been
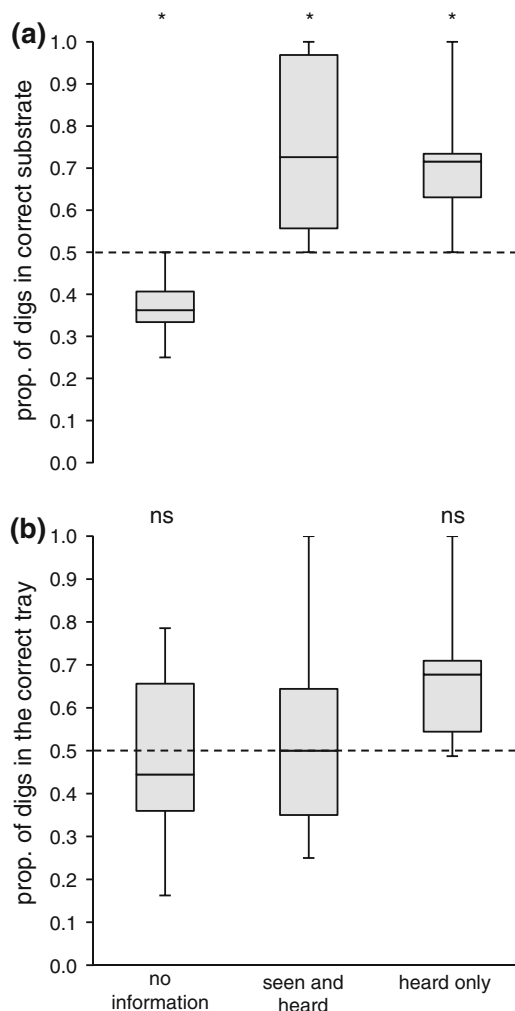
**Fig. 3** The proportion of empty locations searched that were **a** in the correct substrate and **b** in the correct tray within each condition. The *dashed lined* represents the expectation if birds were searching randomly (ns: $p > 0.05$; *$p < 0.05$; *whiskers* range, *boxes* upper quartile, median and lower quartile). The results of the 'seen and heard' condition for (**b**) could not be statistically analysed

random [$T = 0$, $N = 6$ (ties $= 1$), $P < 0.05$; Fig. 3a]. While there was evidence that jays directed their search effort towards the *substrate* that caching took place in, there was no evidence that search effort was also directed towards the *tray* in which jays had heard caching take place more frequently than expected [$T = 1$, $N = 6$ (ties $= 1$), $P > 0.05$; Fig. 3b].

**Discussion**

Observing caching events improved the pilfering performance of Eurasian jays as predicted. In the 'seen and heard' condition, subjects had greater *search success* (i.e. found a greater proportion of caches) as well as greater

*search efficiency* (i.e. searched in fewer empty locations to find the first cache) than expected had they been searching randomly. By contrast, in the baseline 'no information' condition, subjects did not differ from the random search expectation in terms of their *search success*. Moreover, search errors were more frequently made in the incorrect substrate and their *search efficiency* was worse than expected. Although the birds' poor performance in these latter two measures may have been merely due to chance, an alternative possibility is that the jays' search patterns were not truly random when they had no information about cache location and were instead biased by their previous pilfering experience. For example, carry-over effects between trials may have caused the jays to search initially in or near to cache sites that they had pilfered in the preceding trial, before switching to a random search strategy when they found the initial search strategy to be unsuccessful. It is therefore very unlikely that the jays relied on the presence of visual or olfactory cues in the substrate to locate caches. Instead, pilfering Eurasian jays learn about cache location through observing caching conspecifics. Jays remember this information and use it to direct their search behaviour when they have the opportunity to pilfer.

In the absence of visual information, listening to caching improved the jay's pilfering performance. Accordingly, in the 'heard only' condition, the subjects' *search success* was greater than expected had they been searching randomly. Subjects also searched locations that contained the correct substrate more frequently than expected. Thus, after listening to caching, subjects may have used recalled acoustic cues to focus their search effort in the appropriate substrates. By contrast, when subjects had no visual or acoustic information during caching, they searched in the incorrect substrate. Therefore, listening to caching may have helped pilfering jays to identify the substrate in which caches were made, even if it did not allow them to pinpoint the general spatial location of caches, as reflected in the fact that their *search efficiency* was no better than the random search expectation and they did not direct their search to the correct tray. Potentially, the jays did not perceive or could not recall the specific direction that the sound of caching was coming from (e.g. on the left or right of the 'caching/pilfering' compartment). Additionally, there may have been insufficient spatial separation between the trays to enable birds to determine a specific direction from which sound was being produced while they were listening to caching.

Using acoustic cues requires that a pilferer ignores acoustic signals that are uninformative (e.g. other naturally occurring noises such as the non-caching movements of the cacher) and pays attention only to relevant sound cues that indicate caching behaviour. The ability to distinguish between these informative and uninformative acoustic cues

may be acquired with experience. In the current experiment, jays were required to associate any noises made by particular substrates (e.g. gravel) with caches having been made in that particular location (e.g. the gravel-filled pots as opposed to sand-filled pots). As all subjects had prior experience caching in both substrates (Shaw and Clayton 2013), they may have previously learnt the sounds associated with caching in these substrates. Subjects may have also needed to infer that a lack of noise associated with caching in a particular substrate meant that no caching had taken place there. The cognitive demands of using recalled acoustic cues may therefore exceed the demands of similar visual tasks and could explain why the jay's pilfering performance in the 'heard only' condition was not as strong as their performance in the 'seen and heard' condition.

In our experiments, there was a general tendency for subjects to make more search errors in sand than in gravel. One possible explanation for this finding is that the jays were biased towards the less salient stimulus when recalling cache locations. For example, pigeons trained to choose between two stimuli, one that is rewarded after being signalled for a short duration and one that is rewarded after being signalled for a long duration, will make more errors by choosing the short-duration stimulus when there is a long retention interval between when the stimulus is presented and when the choice is made (Spetch 1987). As caching in gravel produces much more noise than caching in sand (see video in supplementary materials), it is likely to be more salient, both when a bird observes caching and when it merely listens to it. As the subject's memory trace for caching events fades during the 15-min time delay between the caching and the pilfering phases of the experiment, birds may have systematically favoured the less salient event when choosing where to pilfer. This may explain the subjects' bias towards searching in sand when pilfering. However, an alternative explanation is that the birds simply prefer sand over gravel. Indeed, it should be noted that our previous research has shown that the jays also prefer caching in sand rather than gravel (Shaw and Clayton 2013). As all of the subjects in the current study had participated in this previous experiment, their preference as pilferers for searching in sand could be due to either a preference for sand per se, or a pre-existing association that they had formed as cachers between sand and the presence of caches.

In the jay's preferred forest habitat (Andrén 1990), there are frequent barriers to visual information, making it likely that visual signals attenuate more rapidly than acoustic signals. If increasing pilfering performance above a random search strategy is sufficiently beneficial to individuals and acoustic cues are frequently the only information available when a conspecific is caching, then together these factors may have selected for the ability to recall and use

acoustic information gained by eavesdropping on caching episodes to locate caches. The use of such 'acoustic spatial memory' by pilferers is complemented by the finding that jays suppress vocalisations in the presence of a cacher (Shaw and Clayton 2013), as vocalising would both disclose a pilferer's presence to the cacher and potentially interfere with their ability to eavesdrop.

In common with many other corvid species (see Shaw and Clayton 2012 for a summary), our results demonstrate that Eurasian jays use observational spatial memory to improve their pilfering success rate. Our findings also raise the additional, intriguing possibility that when searching for caches to pilfer, jays can recall and use information gained merely by eavesdropping on caching, potentially differentiating between different sounds associated with caching to know where to direct their search. Further study of the use of 'acoustic spatial memory' in corvid species that differ in their ecology from the secretive and forest-dwelling Eurasian jay presents an exciting avenue for future research.

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