

Magpies can use local cues to retrieve their food caches

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Abstract Much importance has been placed on the use of spatial cues by food-hoarding birds in the retrieval of their caches. In this study, we investigate whether food-hoarding birds can be trained to use local cues (“beacons”) in their cache retrieval. We test magpies (*Pica pica*) in an active hoarding-retrieval paradigm, where local cues are always reliable, while spatial cues are not. Our results show that the birds use the local cues to retrieve their caches, even when occasionally contradicting spatial information is available. The design of our study does not allow us to test rigorously whether the birds prefer using local over spatial cues, nor to investigate the process through which they learn to use local cues. We furthermore provide evidence that magpies develop landmark preferences, which improve their retrieval accuracy. Our findings support the hypothesis that birds are flexible in their use of memory information, using a combination of the most reliable or salient information to retrieve their caches.

Keywords Spatial memory · Cue use · Food-hoarding birds · Corvidae · *Pica pica*

Introduction

Food-hoarding birds like corvids and parids make caches when food is abundant, in order to retrieve these supplies when food is scarce (e.g., Clayton and Dickinson 1999;

Clayton et al. 1996; MacDougall-Shackleton et al. 2003; Male and Smulders 2007; Pravosudov 1985; Pravosudov and Grubb 1997; Shettleworth et al. 1995). They are able to remember the location of their storage sites with high accuracy by specifically using spatial information (e.g., Balda 1980; Balda and Kamil 1992; Cowie et al. 1981; Herz et al. 1994; Kamil and Balda 1985; Sherry et al. 1981; Tomback 1977; Vanderwall 1982). The preference for spatial memory was shown in a number of studies where birds were either trained on one-trial associative memory tasks to relocate food in one of many feeders (e.g., Brodbeck 1994; Clayton and Krebs 1994; Sherry and Vaccarino 1989; Shiflett et al. 2003), or in an operant task of (non)matching-to-sample requiring the bird to remember a local (e.g., color) or spatial (e.g., left corner) cue of a stimulus in order to obtain a food reward (e.g., Brodbeck and Shettleworth 1995; Hampton and Shettleworth 1996; Healy 1995; Healy and Krebs 1992). The overall result of those experiments is that food-hoarding species prefer to use the spatial cues first, whereas non-hoarding species use the two cue types equally often.

Even though food-hoarding birds prefer spatial cues, they can use local cues under specific conditions. In a recent study where the local cues were made specifically salient by making the baited feeder one color and the distractors all the same different color, food-hoarding mountain chickadees (*Poecile gambeli*) used the local cues from the very beginning (LaDage et al. 2009). This clearly shows that food-hoarding birds can use local cues and that they prefer those, if they are simpler to use and more salient than the spatial cues, at least in a one-trial associative memory task. This then begs the question of whether food-hoarding birds can make use of local cues in the context of their natural hoarding behavior. So far, only two studies have tested the use of local cues in the birds’ natural

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hoarding-retrieval behavior but with only one caching location available: Brodbeck (1994) showed that black-capped chickadees (*Poecile atricapillus*) used spatial cues first and then local cues to retrieve previously cached food, whereas Watanabe (2005) showed that Western scrub jays (*Aphelocoma californica*) were able to retrieve their caches based on local (visual) cues but only if no competitive (contradictory) spatial information was available.

In our study, we trained European magpies (*Pica pica*) in a more complex setup, compared to the previous studies, where the birds freely chose the cache location but were required to use local cue information to subsequently retrieve their caches. We analyzed whether the birds were able to accurately retrieve their caches by relying on the local cues only; we also included a few trials with competitive local and spatial cues in which we could probe for the birds' preferences for local or spatial cues. We further examined whether the birds had preferences for particular local cues and whether this explained their retrieval performance.

Methods

The data presented here were derived from one step in a series of training steps in which we were trying to train the birds to locate caches purely based on local cues. In the subsequent steps, we meant to reduce the size of the caching trays. However, this proved not to be successful and the rest of the training was abandoned. Here, we present the data from the last step in the training protocol that was successful. Because the procedure was intended as a training unit, it was not fully designed as an experiment. We did not perform any probe trials without food present because we were worried it would interfere with the motivation to hoard and hence with training in the further steps. We also did not tightly control the experience each bird had with conflicts between local and spatial cues, such that some birds had more experience with this than others. Nevertheless, we consider the collected data to provide sufficiently interesting results to the scientific community.

Subjects

Six magpies (two males, four females) had been captured in Northumberland in 2003 and 2005 (English Nature licenses #20021809 and 20042342). They were housed as pairs (two male–female pairs, one female-only pair) in aviaries in one indoor room under a light–dark regime of 14.5:9.5 L:D (the birds had experienced this photoperiod for more than three months prior to testing). The birds had ad libitum access to dog food and water and were supplemented once per week with eggs and fruits.

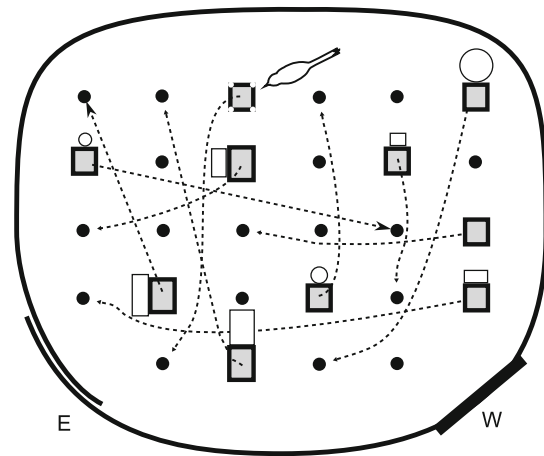


Fig. 1 Schematic view of the test arena, top view. Shown is one example arrangement of 10 cache trays (gray squares) with attached objects (open outlines) on a total of 28 possible positions (black dots) and rearranging the trays by shuffling prior to retrieval (dashed lines/arrows). Trays and the schematic magpie are drawn to scale with respect to the surrounding arena boundary (appr. 250 × 290 cm). W one-way window for observation, E entry/exit to the arena

Testing procedure

The tests took place in a room adjacent to the housing room, fitted with a near-circular test arena (diameter 2.5–2.9 m, height 2.2 m). This arena was built of a black floor and white heavy-duty curtains as walls. An overlap in the wall-curtains provided an entry/exit. A one-way window was mounted on one side for the experimenter to observe the bird without interference (Fig. 1).

The arena floor was divided into an equidistant array of 28 positions in a 5 × 6 rectangular array with two corners missing. On 10 of these 28 positions, a small wooden tray was placed (inner size varying from 10.0 × 11.5 cm to 11.5 × 15.0 cm, depth 4.2 cm), filled with fine wood chips. Objects were placed adjacent to the trays so that eight trays were marked by prominent objects (e.g., milk bottle, cardboard box, and brick), one tray had four green beads attached to its frame, and one tray had no marking at all. This gave a total of 10 visually distinct trays that were used in all trials. The birds had briefly been trained on a simpler version (3–6 trays on 6–28 locations) of the current task before they were introduced to the current design. Some of the described objects had marks of red or blue–colors that the same birds in a previous study had associated with food of different decay times (Zinkivskay et al. 2009). Thus, it is possible that those previously formed associations could lead to a bias in object preferences. However, such a bias seems unlikely in our case because the birds had not experienced any colored food for more than 3 months before the present study, and in that period, the birds had been faced with red and blue colored patches

Table 1 Overview the order of trials and what type of tray the bird was using for caching

Bird ID	Trial number															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	2n	1s+1n	4n	3n	2n	1n	–	–	2n	–	2d+1n	2n	1s+1n	2n	1n	2n
2	3n	1d+2n	1n	3n	1n	2n	2n	1n	1d	2n	1d	2n	2n	3n	1n	4n
3	3n	1s+2n	2n	6n	–	2n	3n	1d+2n	2n	2n	2n	3n	2n	5n	2n	1d+1n
4	3n	2s	2n	1n	–	2n	2n	1n	2n	1n	–	2n	–	5n	2n	1d+2n
5	–	1s	1n	–	2n	–	–	1d+2n	–	–	–	–	1n	–	–	–
6	–	1n	1n	–	2n	–	–	1d	–	–	–	–	1d	–	–	–

Listed are (for each trial where hoarding and retrieval occurred) whether the position of a cache tray was actually covered during retrieval, either by the same cache tray (*s*) or by a different tray (*d*), or not covered by any tray (*n*). Numbers indicate the number of trays of each kind which were used for hoarding

in their home cages on various objects (e.g., wooden blocks) serving as environmental enrichment.

On average, two trials were performed per week, for a total of 16 trials per bird. Both birds housed together in one aviary were caught at the same time into small transport cages, and one of the birds remained in the transport cage while the other was tested. Due to this procedure, the length of food deprivation, i.e., the time a bird spent in the small cage prior to testing, depended on the length of the previous bird's session. However, the motivation to hoard or retrieve varied from bird to bird and from day to day, even in the same bird. Thus, any pre-fixed length of food deprivation prior to testing would not have led to the same motivational effect across birds or across the trials. The between-pairs order was randomized from trial to trial, but within each pair, we used a fixed order based on the individual birds' known level of hoarding motivation.

Each of the 16 trials was divided into two sessions: one hoarding session and one retrieval session, approximately 24 h apart. For the hoarding session, a bowl with 15 mealworms was placed into the arena (in varying positions on different trials) and a bird let in. The experimenter recorded the number of worms eaten and/or the time (to the minute) of a caching event including location and number of worms stored. The session was finished as soon as all worms had been eaten and/or hoarded or 60 min elapsed, whichever occurred first. The bird was then taken back into its home cage, and the cache location(s) and number of cached worms were verified.

On the following day, the caches (using the exact same number of worms, freshly killed/decapitated to prevent movements) were placed back into the appropriate tray(s), but the trays were now shuffled around in a random pattern. The bird was let into the arena to retrieve as many caches as it wanted. The experimenter recorded at what time (to the minute) and which tray was visited. A visit was defined as the bird probing the tray by lowering at least the tip of its

beak into the wood chips, most times including almost the full length of the beak. As soon as all cache sites were emptied or 30 min had elapsed (whichever occurred first), the bird was brought back to its home cage. In case a bird did not hoard during the first day, it was placed in the arena the following day for 60 min, but with no caches and no food available.

Between hoarding and retrieval, the trays were moved around the arena, at varying distances across the 5×6 array. In 8/16 trials, completely different positions were used during retrieval. In 5/16 trials, one or two positions covered by a tray during hoarding were also covered by a tray (but a different one) during retrieval. In 3/16 trials, up to three trays were kept in the same position during both sessions and up to three positions were covered with a different tray during retrieval, resulting in a total of 5–6 positions remaining covered during both hoarding and retrieval. All birds experienced the same new tray arrangement independent of which trays they had used for hoarding. This means that even though some positions may have been covered during hoarding and retrieval (by different trays), an individual bird may not have experienced a conflict between local and spatial cues if it actually did not use that specific position for caching. Looking at it from a different angle, some birds may have been reinforced on both spatial and local cues more often than other birds; this could potentially have caused some variance in the retrieval performance. Table 1 provides an overview of the series of trials and whether the bird was caching at a position that was covered during retrieval by the same or a different tray.

Data analysis

We asked two main questions: (1) How accurate is retrieval performance based on local cues? and (2) Do birds have a consistent preference for using a specific tray? To answer

the first question, we analyzed whether each bird's retrieval performance was better than expected by chance with respect to the actual number of caches in each individual trial. To do this, we used the number of errors each individual made before successfully retrieving the first cache, with "errors" being defined as the number of different empty trays visited prior to the first visit to a correct, cache-containing tray. We focused only on the first retrieval because some birds only hid one item on some trials and because a bird's motivation to search for additional cache sites (if available) may be influenced by what the bird retrieved from the first successful retrieval. If a bird directed a search toward a correct tray (i.e., where a cache was actually placed) but did not actually retrieve the food (because it searched too superficially or in the wrong subpart of the tray), this visit was still counted as successful; this is because the bird made a correct decision relative to the local cue used to locate the tray, even though it may have needed additional spatial cues to locate the cache within the tray. We emphasize that we focused on the birds' abilities to use local cues to relocate the correct tray. Revisits to trays were not counted as additional errors. We therefore treated the behavior as sampling without replacement and compared the birds' actual number of errors to the number expected by chance (accounting for the trial-specific number of caches made), as calculated using the hypergeometric distribution.

In another approach, we examined whether the birds' first visit is more likely than chance to be directed toward a correct tray. Because birds hid different numbers of items on different trials, the probability of finding a cache on the first look differs from trial to trial. A binomial test is therefore not appropriate, as it assumes that the probability of a "success" is constant. Instead, we calculated the exact probabilities for each bird to have performed at least as well as it did, if it had searched randomly (which is equivalent to a P value in a statistical test). For this, we first calculated the probability of finding an item on the first look for each trial for a given bird and then combined these probabilities appropriately to calculate the P value. We illustrate this calculation with a simple example of a bird that hoarded in 2, 3, and 1 of 10 trays, respectively, in three consecutive trials. The probability of finding the item on the first look by chance is therefore 0.2 for trial 1, 0.3 for trial 2, and 0.1 for trial 3. Now imagine that the bird finds a cache on the first look in two of these three trials. The P value is then calculated as follows: (1) There are three different possible combinations allowing the bird to find a cache on the first look in 2 of 3 trials. The probability of doing this is therefore the sum of the probabilities of each of the three possibilities: $(0.2 \cdot 0.3 \cdot 0.9) + (0.2 \cdot 0.7 \cdot 0.1) + (0.8 \cdot 0.3 \cdot 0.1) = 0.092$. (2) The probability of doing better than that (i.e., finding a cache on the first look in all three

trials) is: $(0.2 \cdot 0.3 \cdot 0.1) = 0.006$. (3) The P value is the probability of doing as well as the bird did or better by chance and is therefore equal to the sum of the two previously calculated probabilities: $P = 0.098$.

To answer the second question (about tray preferences), we analyzed whether birds use certain trays more often than expected by chance across trials. To determine this, we used the probability calculation described above and an alpha level of 0.1. This alpha level was chosen because our sample size was low for some birds (7 trials). It is a conservative choice, because we were interested in extracting retrieval performance that is very likely not influenced by preferences. Making it easier for a tray to be designated as "preferred", therefore, makes it more likely that this tray will be excluded in our subsequent analysis.

In order to avoid pseudoreplication, and because individual birds sometimes behaved very differently, we decided to analyze individual birds' behaviors separately and then combined them using a meta-analysis technique. Therefore, the above calculations were done on a bird-by-bird basis with 'trials' as the unit of analysis. We then used the meta-analysis method of Stouffer, also called the Z transform test, to combine the data from the six birds. This analysis transforms individual P values into z -scores and then combines them to a general Z value of which the according P value can be obtained from a standard normal table (Whitlock 2005).

Result

Hoarding behavior

Each bird participated in all 16 trials. Only trials in which the birds hoarded food were analyzed. We had to exclude 2 trials (in two different birds) from the retrieval analysis (but not from the preference analysis) because of inconsistencies in the notetaking.

Across all trials in which the birds hoarded at least one item (72 trials, range 6–16 per bird), we recorded a median of 2 caches (range 1–6) made per trial per bird. The birds ate a median of 8 worms (range 2–14) and cached 6 worms (range 1–13). We recorded a total of 66 trials where retrieval occurred, with a median of 12.5 trials per bird (range 5–16) (Table 2a). A session where the bird actually hoarded lasted a median of 7 min (range 1–60) and the associated retrieval session 8 min (range 1–30).

Retrieval performance

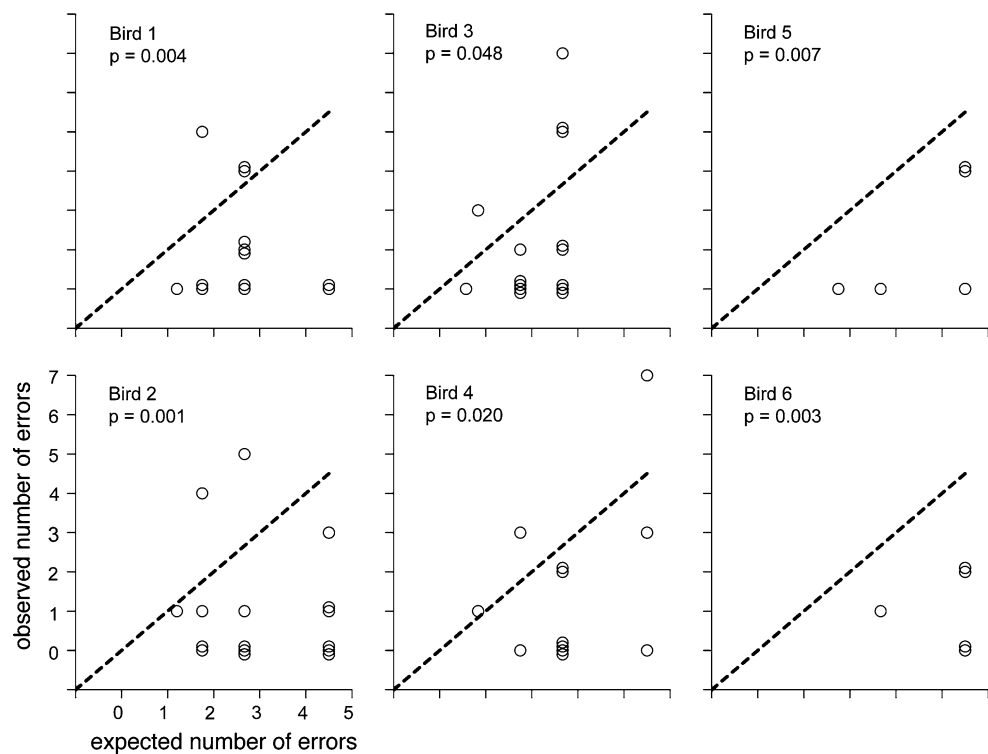
First, we analyzed the number of errors made until the first cache was discovered; this number was matched with the

Table 2 Overview of the retrieval performance of the individual birds

Bird ID	General retrieval performance						Tray preferences—retrieval performance							
	Hoarding	Retrieval	No error	Including all trials and trays		Pref trays	Excluding pref tray(s)			First hit = correct pref tray		First error = (empty) pref tray		
	(a)			(b)			(c)			(d)		(e)		
	<i>n</i>	<i>n</i>	<i>n</i>	<i>P</i> (<i>t</i> test)	<i>P</i> (prob)	#	<i>P</i> (<i>t</i> test)	<i>P</i> (prob)	<i>n</i>	<i>P</i> (prob)	<i>n</i>	<i>P</i> (prob)	<i>n</i>	
1	13	13	7	0.004	0.009	1	0.013	0.012	11	0.139	6	0.297	3	
2	16	16	8	0.001	0.005	2	0.010	0.040	11	0.160	8	0.270	7	
3	16	15	8	0.048	0.022	2	0.253	0.079	15	0.011	12	0.002	7	
4	14	12	6	0.020	0.019	2	0.140	0.186	11	0.263	9	0.031	5	
5	7	5	3	0.007	0.025	3	n/a	n/a	1	n/a		n/a		
6	6	5	2	0.003	0.097	0	0.003*	0.097*	5	n/a		n/a		
Stouffer's pooled <i>P</i>				0.001	0.001		0.001	0.001		0.007		0.002		

Shown are sample sizes (*n*) and *P* values resulting from either the *t* test, *P*(*t* test) or the trial-specific probability calculation, *P*(prob), and Stouffer's pooled *P* value of the overall group performance. (a) number of actual hoarding and retrieval trials and trials with no error occurring to retrieve first cache. (b) overall retrieval performance. (c) retrieval performance excluding preferred trays. (d) preference to first retrieve from preferred tray. (e) preference to direct first error to empty preferred tray. *P* values highlighted **bold** are significant (<0.05); pref tray = preferred tray; # = number of trays; n/a indicates cases with too few or no valid trials; the asterisk (*) marks numbers that were not recalculated with respect to tray preference because this bird did not have any preferred tray

Fig. 2 Individuals' general retrieval performance. Plotted are the observed number of errors against the number of errors as expected by random search behavior. Number of errors are defined as number of different empty trays visited prior to the first visit to a correct, cache-containing tray. The *dashed line* indicates the case where the observed data are identical with the expected data. *P* values (paired *t* test) are shown for each bird

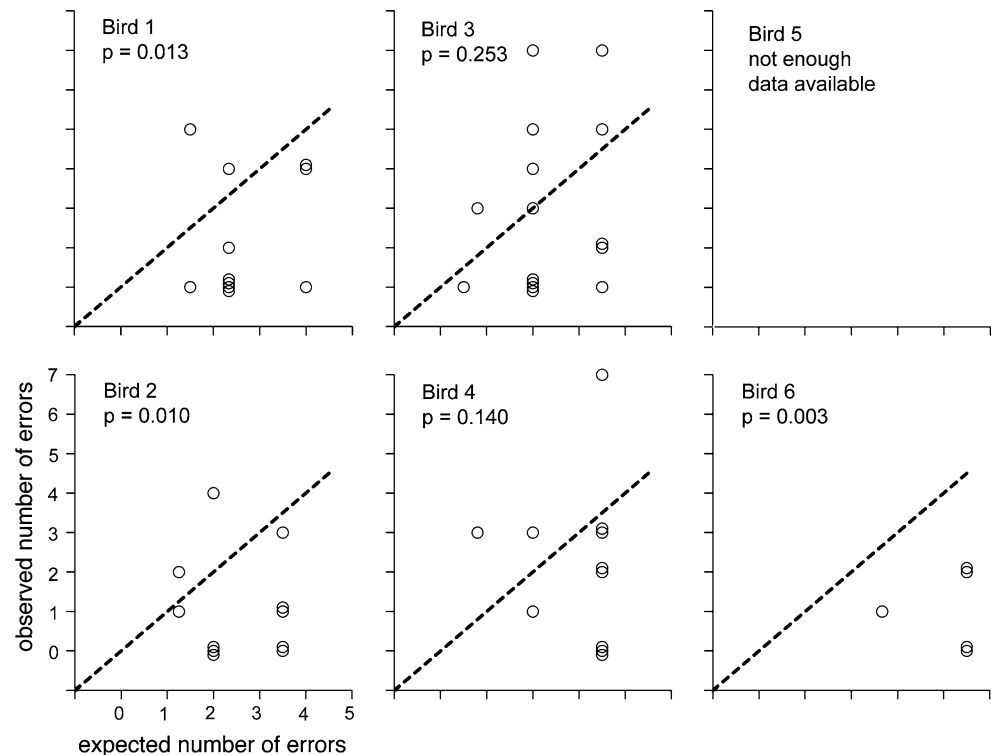


average expected number of errors a bird would make prior to retrieval if the bird were searching randomly (random sampling without replacement), given the number of caches present in each particular trial. These numbers were compared using a one-tailed paired *t* test for each individual bird leading to significant differences for all birds ($t \geq 1.785$, range $t_{14} = 1.785$ to $t_{15} = 3.738$; $P < 0.05$, range 0.001–0.048; Fig. 2; Table 2b).

We then analyzed the number of trials in which the birds looked in a correct location on the first visit, using the probability calculation explained in the methods. Five birds performed better than expected by chance (*P* values ranging from 0.005 to 0.025), and one bird did not ($P = 0.097$; Table 2b).

Both of these analyses resulted in a significant Stouffer's pooled *P* value (<0.001) for the group of birds, showing

Fig. 3 Individuals' retrieval performance excluding preferred trays from the analysis. Further details as in Fig. 1



that the birds' performance is unlikely to be due to random search behavior (Table 2b).

Tray preferences

Non-random performance can be obtained by remembering the correct trays in each trial, but also by having preferred trays and simply knowing and using these trays. We therefore asked whether the birds had a preference for hoarding in one or more specific trays. We counted the number of trials in which each tray was used for hoarding and, by calculating the trial-specific probabilities, found that five of the birds significantly preferred hoarding in 1–3 of the 10 trays ($P < 0.1$).

Subsequently, we reanalyzed the retrieval performance of those five birds by excluding the preferred tray(s) and any visits the birds made to those. Example, if a bird cached in one preferred and two non-preferred trays, we counted the number of errors the bird made prior to retrieving from one of the non-preferred trays. Accordingly, the expected retrieval performance was corrected for the number of preferred trays, i.e., (number of trays to choose from) = (total number of trays) – (number of preferred trays). One bird had 3 preferred trays; in 4 of 5 valid retrieval trials, it exclusively used the preferred trays, so we excluded this bird from further analysis. Taking preferred trays out of the picture, we analyzed the number of errors made prior to retrieval using a one-tailed paired t test. Two birds performed better than chance, making fewer errors

than expected ($t_{10} = 2.609$, $P = 0.013$ & $t_{10} = 2.758$, $P = 0.010$), whereas the other two birds were not different from chance ($t_{10} = 1.144$, $P = 0.140$ & $t_{14} = 0.681$, $P = 0.253$) (Fig. 3; Table 2c). Additionally, we also calculated the probability of finding their caches on the first look as often as they did (just like for the raw retrieval performance). The same two birds still retrieved their caches better than expected by chance ($P \leq 0.040$), whereas the other two birds were again not different from chance ($P \geq 0.079$). Both approaches resulted in significant Stouffer's pooled P value (< 0.001) for the group of birds (Table 2c).

To further characterize the extent of the birds' tray preferences, we used the above-described probability calculation to analyze whether they were more likely to visit these trays first than any other trays. To examine this, we first focused on trials in which the birds hoarded in at least one of the preferred trays as well as in at least one other, non-preferred tray (35 trials total, 6–12 per bird). We analyzed whether in the retrieval session, the birds first searched the preferred cache-containing tray when compared to any non-preferred cache-containing tray, irrespective of any errors preceding the first hit. We found one of the four birds doing so more often than expected by chance ($P = 0.012$). This bird is one of the two whose retrieval performance was no longer better than chance after preferred trays were taken out of the analysis. The performances of the other three birds were not different from chance level ($P > 0.138$, range 0.139–0.263).

However, Stouffer's analysis suggests that across all birds, they were more likely to search preferred trays before non-preferred trays (pooled $P = 0.007$; Table 2d).

We then asked whether these birds would look in preferred trays first, if they had not been used in a given trial. We analyzed those trials where at least one preferred tray had not been used for caching and where the birds made at least one error prior to the first retrieval (22 trials total, 3–7 per bird). We calculated the probability of directing an error toward this preferred empty tray before a non-preferred empty tray. The results show that in two of the four birds, the first error in a specific trial was more often than chance directed toward a preferred tray that had not been used for hoarding ($P = 0.031$ and $P = 0.002$). These were the two birds whose retrieval performance was no longer better than chance after preferred trays were taken out of the analysis. The other two birds had no significant preference for their preferred trays when making their first error ($P = 0.270$ and $P = 0.297$; Table 2e). However, again, Stouffer's test indicates that across all four birds, errors are more likely to be directed toward preferred than non-preferred trays (pooled $P = 0.002$; Table 2e).

Spatial versus local cues

In a total of 10 trials (including at least one trial from each bird), the spatial position at which a cache had been made held a different, empty tray during retrieval. For these trials, we asked whether the birds first searched at the tray covering the correct position (henceforth called 'correct position') rather than the tray with the correct local cues (henceforth called 'correct cue'), thus preferring spatial over local cues. Different birds had different numbers of trials in which correct locations were reinforced throughout the study (Table 1). Based on this variability in experience, we would only expect a very strong bias toward the use of spatial cues to result in significant preferences for correct position in those competitive trials. However, previous studies point in the direction of such a strong preference for spatial cues (Brodbeck 1994; Watanabe 2005; Hurly et al. 2010), so we considered it worth investigating.

We found that in only one case, the bird first looked at the correct position before looking at the correct cue. In 6 trials, the birds directed their first search toward a correct cue. In 3 trials, the birds made errors prior to retrieval but they looked at the correct cue before looking in the correct location. The probability that in 9 of these 10 trials (or better), a local cue is used first for retrieval by chance is 0.052. This clearly shows that the birds do not have a strong preference for using spatial cues at this point in time, and it strongly suggests that (after their experience in this study) the birds preferred using local cues.

Discussion

The birds in our study were presented with the same 10 cache trays that in most cases changed spatial locations between hoarding and retrieval, leaving local cues as the only consistently reliable information to determine the position of hoarded food. Our findings show that under these conditions, magpies develop individual preferences for hoarding near particular visual cues and were guided by those preferences when searching for food during retrieval sessions. In addition, they were able to remember the trial-specific cues near which they had hoarded food and used these to retrieve the food, even on the rare occasions that spatial and local cues were in conflict. This shows that the birds could rely on the local cues to identify the correct cache tray.

Our experimental design purposely incorporated a positive reinforcement for using local cues, although the unbalanced design did not allow for analysis of the learning itself. Nevertheless, the procedure was successful in training the birds to use local cues. This finding is also important in the context of beacon-based orientation. Previous studies on a range of species have shown a strong bias to use spatial information in order to find a feeder even if during training the stationary feeder was directly associated with a visually prominent beacon (e.g., rats: Cheng 1986; squirrels: Devenport and Devenport 1994; hummingbirds: Hurly et al. 2010), unless the geometric information is ambiguous, e.g., a circular test arena (Pecchia and Vallortigara 2010). The magpies, when trained to non-stationary food sources, however, used the tray-associated landmarks for beaconing and learned to ignore the geometric cues.

We used prominent, distinguishable objects as local cues directly attached to the trays. Some birds showed signs of distress when new objects were placed in the home cage or when used in previous trials. Thus, to keep motivational and stress levels constant in order to elicit comparable cognitive performance across trials, using the same objects throughout the experiment seemed most reasonable. This decision has a number of ramifications. Firstly, with the repeated use of one set of landmarks, we cannot exclude interference from information obtained in previous trials. From the current data set, we cannot analyze whether this is the case or not, because the behavior of the birds was too variable and complex. Nevertheless, the fact that in 34 of 66 trials (51.1%), the birds did not make a single error prior to retrieving from the first cache indicates at least some capability of the birds to separate the current trial from previous ones.

A second ramification of the repeated use of local cues is that birds can develop preferences for particular trays or landmarks, which are consequently used to form simple

rules. Five of the six birds indeed developed a preference for hoarding in at least one of the ten trays. The Stouffer test shows that the birds indeed use these hoarding preferences to guide their retrieval behavior, although there may be some individual variation in how strongly they are guided by this information. The use of individual tray preferences can be thought of as a cognitive strategy to simplify the task of retrieving the food items in the repeated and overall very similar trials. Whether this would also be an adaptive strategy in a more natural setting remains to be seen. Preferences do not explain the entire performance of these birds, however. The overall retrieval performance was still better than chance even when excluding the preferred trays. Thus, even though the birds seem to be guided by their tray preference, they also accurately retrieved from non-preferred trays.

One can argue that the birds in our study may have used olfactory cues (or other cues emanating from the mealworms) to retrieve the caches, because in our design, the caches were always filled with freshly killed mealworms during retrieval. As mentioned in the Methods, we did not use any probe trials with empty caches, because unrewarded trials led to a reduction in hoarding motivation (personal observation), and we wanted to continue the training to the next step. However, Zinkivskay et al. (2009) showed that magpies do not find scrambled egg that was randomly distributed in a large probing tray suggesting that the birds cannot locate these food items by olfaction. A recent experiment with one new magpie also suggests that they cannot detect dead mealworms buried in the same type of wood chips as in the current study (data not shown). Studies in other corvid species suggested that they do not use olfactory cues for retrieval either (Bunch and Tomback 1986; Vanderwall 1982). Buitron and Nuechterlein (1985) did show that magpies can use olfactory cues to find hidden food, but only if the cues are very strong. In our study, the trays were filled with wood chips that were not exchanged on a regular basis. This means that the wood chips in all trays had been repeatedly in contact with cached items and were likely to smell of worms. Even though we cannot exclude the role of olfactory cues because a freshly killed worm is likely to emanate stronger and different odors than contaminated wood chips, we find it very unlikely that the magpies in our study could have used olfaction to accurately retrieve the caches.

Based on the evidence presented, we argue that all six birds tested were able to retrieve their caches accurately based on local cues. Given that in our set up, the local cues were the only reliable cues to the position of the food, our data agree with LaDage et al.'s (2009) argument that use of local and/or spatial information is likely to be context dependent (using the “easiest” or most reliable cue). Our results do seem to partially contradict those of Watanabe

(2005). He tested scrub jays in an active caching task, requiring the birds to memorize local cues, which were then contrasted with spatial cues at retrieval. The birds in his study still preferred using spatial cues, and only used local cues when there was not a tray available in the correct location. In his setup, in contrast to ours, however, the birds did not have a choice during hoarding as only one cache tray was available. Thus, the spatial information may have been more salient. Watanabe could show that after the birds had received several training trials where the cache tray changed location prior to retrieval, they changed their retrieval behavior from primarily choosing the spatial location to equally choosing local and spatial cues for retrieval under competitive conditions and significantly changed to local cues under non-competitive conditions. Our findings are in line with Watanabe's results with respect to the non-competitive condition under which the birds primarily used the local cues to accurately retrieve the caches. In contrast to Watanabe's competitive condition, our competitive tests provide strong evidence that the magpies did not primarily use spatial cues but rather relied on the local cues. This discrepancy between the two studies may be due to the experimental design. Giving the birds more choices of constantly moving local cues, and extended training on those, may reinforce the usefulness of the local cues and the uselessness of the spatial cues more than Watanabe's training conditions. A more carefully designed follow-up experiment would allow us to test this hypothesis in depth.

In conclusion, we provide first evidence that magpies can use local visual cues to retrieve their caches correctly, even after 24 h. When trained that this is the only relevant cue, they do so even if there is competitive spatial information available. Our data also suggest that magpies can use cognitive strategies (such as the development of preferences which can be used at both hoarding and retrieval) to simplify the memory task. Thus, magpies make flexible use of whichever cues are relevant.

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Conflict of interest The authors declare that they have no conflict of interest.

References

- Balda RP (1980) Recovery of cached seeds by a captive *Nucifraga caryocatactes*. *Z Tierphysiol Tierernahr-J Comp Ethol* 52:331–346

- Balda RP, Kamil AC (1992) Long-term spatial memory in clark nutcracker, *Nucifraga columbiana*. *Anim Behav* 44:761–769
- Brodbeck DR (1994) Memory for spatial and local cues—a comparison of a storing and a nonstoring species. *Anim Learn Behav* 22:119–133
- Brodbeck DR, Shettleworth SJ (1995) Matching location and color of a compound stimulus—comparison of a food-storing and a nonstoring bird species. *J Exp Psychol Anim Behav Process* 21:64–77
- Buitron D, Nuechterlein GL (1985) Experiments on olfactory detection of food caches by black-billed magpies. *Condor* 87:92–95
- Bunch KG, Tomback DF (1986) Bolus recovery by gray jays—an experimental-analysis. *Anim Behav* 34:754–762
- Cheng K (1986) A purely geometric module in the rat's spatial representation. *Cognition* 23:149–178
- Clayton NS, Dickinson A (1999) Motivational control of caching behaviour in the scrub jay, *Aphelocoma coerulescens*. *Anim Behav* 57:435–444
- Clayton NS, Krebs JR (1994) Memory for spatial and object-specific cues in food-storing and nonstoring birds. *J Comp Physiol A Sens Neural Behav Physiol* 174:371–379
- Clayton NS, Mellor R, Jackson A (1996) Seasonal patterns of food storing in the jay *Garrulus glandarius*. *Ibis* 138:250–255
- Cowie RJ, Krebs JR, Sherry DF (1981) Food storing by marsh tits. *Anim Behav* 29:1252–1259
- Devenport JA, Devenport LD (1994) Spatial navigation in natural habitats by ground-dwelling sciurids. *Anim Behav* 47:727–729
- Hampton RR, Shettleworth SJ (1996) Hippocampus and memory in a food-storing and in a nonstoring bird species. *Behav Neurosci* 110:946–964
- Healy SD (1995) Memory for objects and positions—delayed non-matching-to-sample in storing and nonstoring tits. *Q J Exp Psychol B* 48:179–191
- Healy SD, Krebs JR (1992) Delayed-matching-to-sample by marsh tits and great tits. *Q J Exp Psychol B* 45B:33–47
- Herz RS, Zanette L, Sherry DF (1994) Spatial cues for cache retrieval by black-capped chickadees. *Anim Behav* 48:343–351
- Hurly TA, Franz S, Healy SD (2010) Do rufous hummingbirds (*Selasphorus rufus*) use visual beacons? *Anim Cogn* 13:377–383
- Kamil AC, Balda RP (1985) Cache recovery and spatial memory in clark nutcrackers (*Nucifraga columbiana*). *J Exp Psychol Anim Behav Process* 11:95–111
- LaDage LD, Roth TC, Fox RA, Pravosudov VV (2009) Flexible cue use in food-caching birds. *Anim Cogn* 12:419–426
- MacDougall-Shackleton SA, Sherry DF, Clark AP, Pinkus R, Hernandez AM (2003) Photoperiodic regulation of food storing and hippocampus volume in black-capped chickadees, *Poecile atricapillus*. *Anim Behav* 65:805–812
- Male LH, Smulders TV (2007) Hyperdispersed cache distributions reduce pilferage: a field study. *Anim Behav* 73:717–726
- Pecchia T, Vallortigara G (2010) Reorienting strategies in a rectangular array of landmarks by domestic chicks (*Gallus gallus*). *J Comp Psychol* 124:147–158
- Pravosudov VV (1985) Food searching and storing by *Parus cinctus lapponicus* and *Parus montanus borealis* (Paridae). *Zoologicheskij Zhurnal* 64:1036–1043
- Pravosudov VV, Grubb TC (1997) Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food supply. *Behav Ecol* 8:332–339
- Sherry DF, Vaccarino AL (1989) Hippocampus and memory for food caches in black-capped chickadees. *Behav Neurosci* 103:308–318
- Sherry DF, Krebs JR, Cowie RJ (1981) Memory for the location of stored food in marsh tits. *Anim Behav* 29:1260–1266
- Shettleworth SJ, Hampton RR, Westwood RP (1995) Effects of season and photoperiod on food storing by black-capped chickadees, *Parus atricapillus*. *Anim Behav* 49:989–998
- Shiflett MW, Smulders TV, Benedict L, DeVoogd TJ (2003) Reversible inactivation of the hippocampal formation in food-storing black-capped chickadees (*Poecile atricapillus*). *Hippocampus* 13:437–444
- Tomback DF (1977) Foraging strategies of the clark's nutcracker. *Living Bird* 17:123–161
- Vanderwall SB (1982) An experimental analysis of cache recovery in clarks nutcracker. *Anim Behav* 30:84–94
- Watanabe S (2005) Strategies of spatial learning for food storing in scrub jays. *J Ethol* 23:181–187
- Whitlock MC (2005) Combining probability from independent tests: the weighted z-method is superior to Fisher's approach. *J Evol Biol* 18:1368–1373
- Zinkivskay A, Nazir F, Smulders TV (2009) What-where-when memory in magpies (*Pica pica*). *Anim Cogn* 12:119–125