

What–Where–When memory in magpies (*Pica pica*)

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Abstract Some animals have been shown to be able to remember which type of food they hoarded or encountered in which location and how long ago (*what–where–when* memory). In this study, we test whether magpies (*Pica pica*) also show evidence of remembering these different aspects of a past episode. Magpies hid red- and blue-dyed pellets of scrambled eggs in a large tray containing wood shavings. They were allowed to make as many caches as they wanted. The birds were then returned either the same day or the next day to retrieve the pellets. If they returned the same day, one colour of pellets was replaced with wooden beads of similar size and colour, while if they returned the next day this would happen to the other colour. Over just a few trials, the birds learned to only search for the food pellets, and ignore the beads, of the appropriate colour for the given retention interval. A probe trial in which all items were removed showed that the birds persisted in searching for the pellets and not the beads. This shows that magpies can remember which food item they hoarded where, and when, even if the food items only differ from each other in their colour and are dispersed throughout a continuous caching substrate.

Keywords Episodic-like memory · Food-hoarding birds · Corvidae

Introduction

The question of whether animals have a form of episodic memory has been of much interest in the literature over the last 10 years. Many authors have tried to define what episodic memory would look like in animals, if it did exist, and different criteria have been put forward (Clayton and Dickinson 1998; Clayton et al. 2003a; Dere et al. 2006; Eacott et al. 2005; Griffiths et al. 1999; Morris 2001; Schwartz et al. 2005; Shettleworth 2001; Suddendorf and Busby 2003). One of the necessary, but not sufficient, criteria for having episodic memory is that the individual can remember information about a unique event they experienced in a given spatial location and at a particular time in the past, also referred to as *what–where–when* memory (Clayton and Dickinson 1998; Suddendorf and Busby 2003). Using a food-hoarding and retrieval task, Clayton and Dickinson (1998) showed that western scrub-jays (*Aphelocoma californica*) can recall the type of food they hoarded, where they did this, and how long ago it happened, using intervals of 4–124 h. This finding was later replicated with laboratory rats (*Rattus norvegicus*), using a foraging task in the radial arm maze that was based on the food-hoarding task (Babb and Crystal 2005, 2006a, b; Naqshbandi et al. 2007).

Another criterion for episodic memory is that information should be encoded automatically, without knowing at the time of encoding that the information will be of use later on (Zentall et al. 2001). This condition is not met by either the jay or the rat studies. In both cases, the animals “know” that the food will be present in the future and could therefore “consciously” commit the information to memory. Episodic memory in humans also typically includes an aspect of auto-noëtic consciousness or mental time travel back to the experienced episode (Tulving 2001). This is

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impossible to assess with certainty in animals, although hints do exist for scrub-jays (Correia et al. 2007, reviewed by Feenders and Smulders 2008). Because of these complications and the baggage that comes with the term episodic memory, we will only discuss the *what–where–when* aspect in the present study.

Because animals do not have language, to ask them whether they remember *what* they did *where* and *when*, they need to be trained with a set of behavioural rules. In the original food-hoarding task, the rule the scrub-jays had to learn is that a given food type becomes inedible after a given amount of time (Clayton and Dickinson 1998). In the foraging task, the rats had to learn that a particular type of food will be replenished after a long, but not a short interval (Babb and Crystal 2005). In later experiments, both species have been trained on the obverse rule as well: scrub-jays have been tested with food that is bad after a short interval, but good after a long interval (de Kort et al. 2005), and rats have been tested with replenishment at short, but not long intervals (Naqshbandi et al. 2007). In both cases, this did not pose any significant problems for the animals.

In all these experiments, however, the rule the animals learned was about the “interesting”, preferred food. The alternative food was always the same, always available, and always the least preferred option for the animals. To run these kinds of experiments with many different species of animals, it would be good to have a procedure that does not rely on identifying a preferred and a non-preferred food type for each species (or indeed each individual), but could be run with whichever food type works well to reward these animals. In the current study, we present a method to do this by manipulating just one aspect of the food (in our case: its colour). Doing this also allows us to counterbalance the experimental design, with half the animals learning one rule, and the other half the opposite rule, controlling for any unforeseen confounds of having the same rule for all animals.

Another aspect of the original studies by Clayton and Dickinson (1998) and Babb and Crystal (2005) is that the number of possible locations in which the animals could search for the food upon return was very limited. The scrub-jays had the choice of 16 locations across two halves of an ice-cube tray (the analysis was performed on which half the birds searched), while the rats had a choice of eight locations. In nature, the spatial dimension of the *what–where–when* triad is likely to be continuous and large. They would also have to remember more than one item or location at a time. We therefore designed an experiment in which food-hoarding birds could hoard as many food items as they wanted anywhere in a large open tray, increasing the spatial load on their memory. We used magpies (*Pica pica*), because, like scrub-jays, they are a short-term hoarding corvid which opportunistically hoards many food types,

including many that decay (Birkhead 1991). They are distantly related to scrub-jays, and therefore represent a different clade of corvids (de Kort and Clayton 2006). Both species have a similar-sized hippocampus relative to brain and body size (Pravosudov and de Kort 2005). These details suggest that magpies, like scrub-jays, should be able to remember *what* they hoarded, *where*, and *when*.

Methods

Subjects

Four adult (two males and two females) and two juvenile female magpies were used. Adults were more than 3 years old and had been captured in Northumberland in June 2003 under English Nature Licence number 20021809. The juveniles (<1-year-old) had been captured in Northumberland in June 2005 under English Nature Licence 20042342. The birds were housed in pairs in pens of 1.56 m (d) × 1.90 m (w) × 2.68 m (h) (two pens with an adult male and female each and one pen with the two juvenile females). The animals had access to food and water ad libitum. They were fed Pedigree dog food, which supplied the necessary amount of calories in the daily diet of the birds. This diet was judged to be the least preferred variety of food from the birds’ point of view, providing motivation to hoard and retrieve more preferred foods during the trials. The experiments were run from January to April 2006 and the photoperiod was set at 9L:15D (coming on at 9:30 a.m., and turning off at 5:30 p.m.). Birds’ body masses stayed stable throughout the study.

Testing arena and initial training

The enclosure used was 3 m in diameter with 2.21 m high walls, made from white, heavy duty curtain, and a wooden floor. An overlap in the curtain allowed access to the arena. One metre from the access, there was a one-way observation mirror. The arena contained four metal trays [75 cm (l) × 65 cm (w) × 4 cm (h)], placed alongside one another to cover 150 cm × 130 cm area of the floor in the test room. Every tray was further subdivided into 16 compartments (18.5 cm × 16.0 cm). Heavy small industrial wood-shavings were used to fill up the trays, which created a hoarding area for the magpies. The test trays were fitted with a number of pencils decorated with beads to provide spatial landmarks within the trays (Fig. 1). The make-up of the landmarks and their locations were changed at every trial to prevent memory interference between trials.

The magpies were transported from the home pens to the experimental arena by turning out the lights in the home pens and shining a flash-light onto the open transport cages.

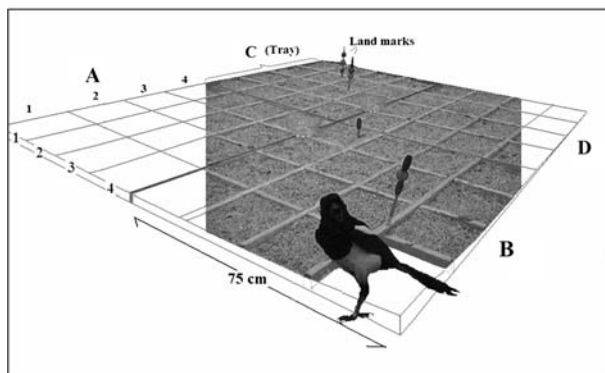


Fig. 1 Diagram of the hoarding trays, with landmarks and a magpie to scale

The birds were trained to jump into the cage without a need for being chased. They were then carried to the experimental arena using the basket and released. The birds were allowed to hoard food in or retrieve food from the wood-shaving filled trays. This food consisted of pellets of scrambled egg (approximately 0.25 cm^3 , weighing $0.6\text{--}1 \text{ g}$), dyed either bright red or blue, using SuperCookTM food colouring. During all trials, the location, content and time of every cache created, as well as every search sweep (removal of the substrate by the magpie beak made in search of hidden food) was recorded.

Experimental design and manipulations

What–where–when memory training

This study followed a repeated measures design, in which every bird partook in 20 experimental trials. In every trial, the birds were introduced to the testing arena where they were presented with two food bowls, placed on either side of the arena centre. Each bowl contained 15 egg pellets, red in one bowl, blue in the other. The position of red and blue food was counterbalanced across trials. Birds were allowed to explore, eat and hoard the food pellets. The session was ended after all food pellets had been eaten and/or hoarded, or after 1 h elapsed, whichever came first. All items were removed by the experimenter to prepare the arena for the next bird and the bird was returned to its home pen.

The cache retrieval phase occurred either in the afternoon of the same day (ten trials), or the next day (ten trials; Table 1). These two types of trials were presented to the birds in a pseudo-random order (never more than two trials with the same retention interval in a row). Prior to retrieval, all the birds' items were replaced in the locations where they had been hoarded in the first phase of the trial. Depending on the retention interval, one type of food (red or blue pellets) was replaced with the same quantity of (inedible) wooden beads of the same size and colour. For

Table 1 The ranges of starting times for the hoarding (max 1 h) and retrieval (max 30 min) sessions for all birds, under both experimental conditions

Bird ID	Short retention interval		Long retention interval	
	Hoarding	Retrieval	Hoarding	Retrieval
H1	10:00–12:10	14:00–16:05	12:15–15:50	13:00–15:30
H2	10:30–14:00	13:30–17:00	13:40–17:00	13:15–16:10
R1	10:00–12:00	14:00–16:00	09:30–14:10	10:30–12:45
R2	11:00–12:58	14:30–16:35	09:30–12:15	11:00–13:00
R3	10:30–12:35	14:00–16:00	11:05–13:25	11:00–14:00
R4	11:30–13:30	14:30–16:30	11:30–13:55	11:30–14:30

example, if retrieval happened on the same day, then blue egg pellets would be replaced with blue beads, while if retrieval happened the next day, the red egg pellets would be replaced with red beads. The other items remained edible egg pellets of the correct colour in both cases. Which retention interval corresponded to which colour becoming inedible was counterbalanced across birds. Magpies were allowed 30 min to retrieve as many caches as they could find. If all the edible caches were discovered before the 30 min had elapsed, the session was ended. After completing the retrieval session magpies were returned to their home pens.

What–where–when memory probe trial

This trial was designed to test whether the birds were using memory or if they used direct cues from the egg and/or beads during the cache retrieval phase of the trial. The procedure of the probe trial was identical to that of the one-day retention interval trial, except that none of the caches were returned to the arena for the retrieval phase. As before, the magpies were allowed to search the substrate for 30 min. Time and location (i.e. which compartment) of all search sweeps were recorded and after completing this session magpies were returned to their home pens.

Foraging experiment

This experiment was conducted to doubly assure that the birds could not detect the location and/or content of a cache site using direct cues from the hidden objects. We ran 16 foraging trials with each bird. Prior to testing the birds were food deprived for 2 h. Two birds (from the same pen) were tested per day, completing four trials each. In each of the four trials, a different combination of items was hidden by the experimenter: either all beads (two caches of three red beads and two of three blue beads), all egg pellets (two of

three red pellets and two of blue), two of red egg pellets and two of blue beads, or two of blue egg pellets and two of red beads. The different trial types were presented in random order to every bird and the two birds tested on a given day were alternated in the arena. While one bird was in the arena, the other bird was held in the transport cage in the dark to reduce stress. The same enclosure, trays and beads were used as before, but without the trial-unique landmarks. Items were hidden 1 in. below the surface of wood shavings in the trays. They were distributed in different ways on the different trials. To determine where to hide the items, we used the following rules. First, each bird's preferred cache locations were determined based on the 20 trials of the first experiment. Using the existing caching tray (Fig. 1) 100 random sites were then generated in a computer spreadsheet. From these 100 random locations, we randomly picked two from within the bird's preferred area, and two from outside it. Distributions were therefore personalized to each individual bird. A bird was allowed to investigate the test room for 30 min, and location and time of all search sweeps were again recorded. Throughout testing the birds were given ad libitum water and any food they could find in the test arena.

Data analysis

As retrieval was ended after the birds had retrieved all their egg pellet caches or 30 min had elapsed, we calculated the proportion of the bead-containing caches that were retrieved during that same period. We also calculated the proportion of egg-pellet-containing caches retrieved if the birds did not retrieve all of them. These proportions were arcsine square-root transformed for statistical analysis. Most statistical analyses were conducted using SPSS 15.0. Results are considered significant if $P \leq 0.05$ and all descriptive statistics are expressed as mean \pm SEM.

Results

What–where–when memory training trials

The birds hoarded an average of 11.12 pellets (range 3.5–19.2 pellets), in 3.28 caches (range 1.4–5.3 caches). All the pellets in a cache were usually carried together from one food bowl and deposited together. The birds never mixed the two colours in the same cache. Not all birds hoarded both colours of pellets on all trials. Trials on which the birds hoarded nothing at all were ignored in the analysis. Trials on which the birds hoarded only pellets of one colour were deemed informative to the bird (because the items of that colour would either be palatable or unpalatable on retrieval), but were treated as missing data in the analysis.

On average, birds hoarded at least one colour (i.e. informative trials from the birds' point of view) on 7.17 (range 5–10) of the ten long-retention trials and on 7.67 (range 3–10) of the ten short-retention trials. They hoarded both colours (i.e. informative trials from a data analysis point of view) on average on 6.67 (range 3–10) long-retention trials and on 7.33 (range 1–10) short-retention trials. We analyzed the results for the first five trials that were informative to the bird, treating those trials on which the birds only hoarded one colour as missing data in the analysis.

A linear mixed model with bird as a random factor and type of food item (palatable or unpalatable), trial (1–5) and retention interval (short or long) as fixed factors resulted in the following findings. By the time they had retrieved all palatable items or 30 min had elapsed (whichever was sooner), birds had retrieved a significantly higher proportion of palatable than unpalatable items ($F_{1,5} = 128.9$, $P < 0.0005$). Birds retrieved a smaller proportion of items in later trials than in earlier trials ($F_{4,19} = 4.46$, $P = 0.011$). The drop in proportion of items retrieved over trials was very steep for unpalatable items, while palatable items were retrieved at similar rates throughout all trials (palatability \times trial interaction: $F_{4,19} = 3.85$, $P = 0.019$; Fig. 2). There were no differences between trials with the two different retention intervals, nor were there any interactions between retention interval and trial, palatability or both (all P values > 0.18).

Another measure we used was whether the first cache retrieved was a palatable or non-palatable item. If the birds know and remember which items will be palatable on a given trial, we expected that they would retrieve palatable caches first. We therefore calculated on which proportion of

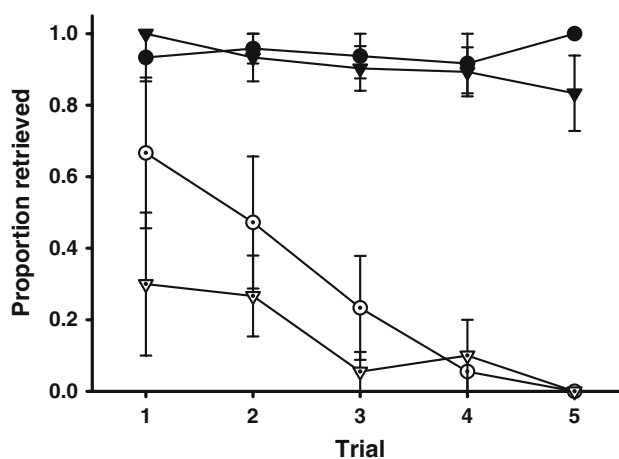


Fig. 2 Proportion of palatable and unpalatable caches retrieved by the time all palatable caches had been retrieved or 30 min had elapsed. Averages from the first five informative trials (i.e. trials in which birds cached at least one colour) are plotted. *Circles* represent long retention interval trials, while *triangles* represent short retention intervals. *Closed symbols* represent palatable items, while *open symbols* represent unpalatable items. Error bars represent standard errors of the mean

its trials any given bird retrieved a palatable cache first. We then calculated the probability of this proportion based on the exact probabilities of retrieving a palatable cache first by pure chance on every trial. This probability is different from trial to trial based on the ratio of red to blue caches made by the bird on those trials. We did not count the first trial for each retention interval, because this was the birds' first exposure to the rules of the experiment. Birds retrieved the palatable item first on average on 95.5% of the trials (range across birds 78.6–100%). Probabilities of this happening by chance were below the 5% cut-off for each individual bird's performance (range $P = 0.046$ to $P = 3.1 \times 10^{-6}$).

Effects of time of day

For short-retention-interval trials, the birds performed the retrieval in the afternoon of the same day, so there was only time to test three birds on any given day. For long-retention-interval trials, the retrieval happened the next day, so to save time, all birds were tested on the same day. This means that for two birds (H1 and H2; an adult pair from the same pen), the time of day at which hoarding took place was much later on long-retention-interval trials than on short-retention-interval trials ($t_{18} > 7.2$, $P < 0.0005$ for each bird), without any overlap after the first trial (Table 1). The times of the retrieval trials did overlap substantially, although they were still statistically later for long-retention-interval trials than for short-retention-interval trials ($t_{18} = 2.53$, $P = 0.02$ and $t_{18} = 2.38$, $P = 0.03$; Table 1). For the other four birds (R1–R4), there was a large overlap in the hoarding times between the two trial types (all $t_{18} < 1.8$, P values ≥ 0.1 ; Table 1), but the retrieval times were consistently later on short-retention-interval trials than on long-retention-interval trials (all $t_{18} > 6.2$, $P < 0.0005$; Table 1). This means that in theory, the birds could tell which trial type they were in, based on either the time of day during which they hoarded (H1–H2) or the time of day during which they were allowed to retrieve (R1–R4).

If H1 and H2 could predict the trial type during the hoarding phase, they might have adopted a hoarding strategy based on which food would be palatable at retrieval. We therefore analyzed whether they were more likely than R1–R4 to hoard the colour that would be palatable on retrieval than the other colour. We counted the total number of pellets hoarded of each colour on each trial, and then subtracted the number of pellets of the “unpalatable” colour from the number of the “palatable” colour (combining trials from both retention intervals). Therefore negative numbers indicate that more pellets of the “unpalatable” colour are hoarded, while positive numbers mean that the birds favoured “palatable” pellets. We excluded the first trial of each type, as the birds could not yet have obtained the

information about the different trial types at that point in time. A linear mixed model with bird as the random factor indicates that this index of preference is not significantly different for the two groups of birds ($F_{1,57} = 2.099$, $P = 0.153$; H1–H2: -0.885 ± 0.115 ; R1–R4: -0.057 ± 0.628), that there is no change over trials in general ($F_{1,88} = 1.982$, $P = 0.163$), nor for only H1 and H2 (Interaction: $F_{1,88} = 2.371$, $P = 0.127$).

Probe trial

On the probe trial, all birds hid both colours of egg pellets. One bird hid all the unpalatable pellets in the same compartments as palatable pellets. Because we could not analyze the data to a spatial resolution more precise than the level of one compartment, it was impossible to say which pellets the bird was searching for and this bird's data were not used in the subsequent analysis. The other five birds all searched first in the location of a palatable item ($P = 0.048$). They continued searching in “palatable” locations before searching in the locations of the unpalatable items. By the time they had searched in all the locations where palatable items should have been, or 30 min had elapsed, birds had searched in on average 90% of the palatable locations, but none of the unpalatable locations ($t_4 = 9.0$, $P = 0.0008$). In the half hour of searching, they also made a much higher effort searching in “palatable” locations (55 ± 16 search sweeps per bird per location) than in “unpalatable” locations (2 ± 0.9 search sweeps per bird per location) (paired t test: $t_4 = 3.4$, $P = 0.03$; Fig. 3).

Cache detection using direct cues from the food

Over the 16 test trials each bird received, five magpies were unable to find any of the hidden items, and one magpie found one bead on the last trial day.

Discussion

In this study, we have shown that magpies, like western scrub-jays, can remember the type of food they hoarded, in which location this was, and when this hoarding took place. All birds knew which items to search for to obtain food reward and which items to ignore (because they had been replaced with inedible wooden beads).

Whereas it is clear that magpies can show *what–where–when* memory for caches, it is unclear what exactly the nature is of the *when* component in this study. Two of the birds (H1 and H2) were in a position to potentially predict the retention interval to which they would be subjected on that particular trial, and the other four birds (R1–R4) could potentially use the time of day at retrieval to know which

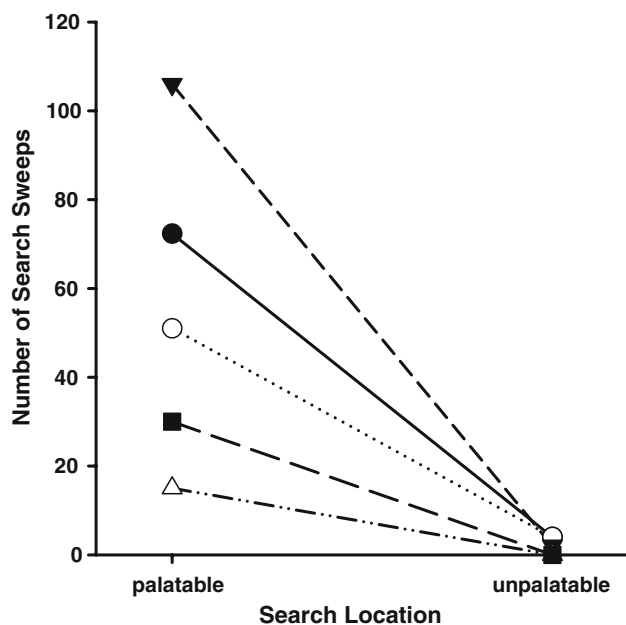


Fig. 3 Mean number of search sweeps per bird within one tray radius of palatable and unpalatable cache sites during the probe trial. *Different symbols represent different birds*

item colour would be edible. Encoding which items should be remembered and selectively forgetting the other type based on what time of day the hoarding takes place is theoretically possible, but at least one recent study has shown that rats cannot solve an analogous task based on this information (Roberts et al. 2008). Our post hoc analysis also suggests that these birds did not increase how many “future palatable” pellets they hoard through the trials, although with only two birds in this group, the power of this analysis is very low. It therefore remains unclear whether H1 and H2 could indeed predict the trial type at hoarding.

All six birds solved the task above chance level. It is theoretically possible that different birds solved the task in different ways. However, the most parsimonious explanation is that the birds all used the retention interval as their main cue as to which food type they should search for. This is also consistent with the existing literature on the topic (Babb and Crystal 2005, 2006a, b; Clayton and Dickinson 1998; Roberts et al. 2008).

Regardless of how the birds worked out which trial type they were in on any given day, they clearly were able to associate the trial type with the colour of food that was edible on that trial type, and stopped searching for the colour that would have been replaced with wooden beads. Unlike in previous experiments (Babb and Crystal 2005, 2006a, b; Clayton and Dickinson 1998, 1999; Clayton et al. 2001, 2003b; de Kort et al. 2005; Roberts et al. 2008), none of the trials relied on one food type being preferred over another one. The two food types were identical in every respect

except for their colour and the meaning of the two colours was counterbalanced across birds. The birds learned which colour to retrieve in which trial type within a couple of trials.

Some have argued that the reason scrub-jays can learn that insects go bad, while peanuts do not, is that animal food is more likely to decay than seeds, and that instead of learning this rule, birds could have an evolved “knowledge” that animal food goes bad. However, our results suggest that animals can learn and apply a completely arbitrary rule as quickly as a rule that is consistent with natural patterns. It is of course possible that the ability to learn and apply such rules is itself an adaptation to the food-hoarding lifestyle. Western scrub-jays have also been shown to be flexible about the types of rules they can learn, learning that wax worms can “ripen” (de Kort et al. 2005). However, the fact that rats can solve an analogous task using chocolate and berry flavoured pellets (Babb and Crystal 2005, 2006a, b; Roberts et al. 2008), suggests the cognitive ability is more widespread and food hoarding just provides a convenient behavioural system in which to study this type of memory.

Studies with food-hoarding birds in the past have shown many times over that they can remember several different cache locations in a single trial, out of many possible cache locations (e.g. Balda and Kamil 1989; Jacobs and Liman 1991; Shettleworth and Krebs 1982). Studies of episodic-like *what–where–when* memory, however, had so far only used two to eight possible alternatives to remember (Babb and Crystal 2005, 2006a, b; Clayton and Dickinson 1998, 1999; Clayton et al. 2001, 2003b, de Kort et al. 2005; Naqshbandi et al. 2007; Roberts et al. 2008). In our study, we combined the *what–where–when* feature with a continuous spatial environment in which items could be found. It is clear that the birds easily remembered where in the tray food had been hidden, and combined this with the knowledge of which type of food was in which location. This situation is closer to a real-life situation in which animals might have to combine information about *what*, *when* and *where*, and it shows that they have no problem doing this.

In conclusion, we show that magpies can remember *what* type of food they hid *where*, and *when*, and they can do this using a completely arbitrary rule about the colour of the food. This arbitrary rule allowed us to counterbalance the experimental design, with different birds searching for different food types at different retention intervals. We believe that this procedure is an improvement on previous procedures, which have made assumptions about food types and have relied on existing food preferences. We hope that it will make it easier in the future to test *what–where–when* memory in other food-hoarding species, to provide a better overview of how this trait is distributed across different clades.

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