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***What-Where-When memory in magpies (*Pica pica*).***

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1 **Abstract**

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

17

18 **Keywords:**

19 Episodic-like memory, food-hoarding birds, Corvidae

20

## 21 **Introduction**

22           The question of whether animals have a form of episodic memory has been of  
23 much interest in the literature over the last 10 years. Many authors have tried to  
24 define what episodic memory would look like in animals, if it did exist, and different  
25 criteria have been put forward (Clayton and Dickinson 1998, Clayton et al. 2003a,  
26 Dere et al. 2006, Eacott et al. 2005, Griffiths et al. 1999, Morris 2001, Schwartz et al.  
27 2005, Shettleworth 2001, Suddendorf and Busby 2003). One of the necessary, but not  
28 sufficient, criteria for having episodic memory is that the individual can remember  
29 information about a unique event they experienced in a given spatial location and at a  
30 particular time in the past, also referred to as *what-where-when* memory (Clayton and  
31 Dickinson 1998, Suddendorf and Busby 2003). Using a food-hoarding and retrieval  
32 task, Clayton and Dickinson (1998) showed that western scrub-jays (*Aphelocoma*  
33 *californica*) can recall the type of food they hoarded, where they did this, and how  
34 long ago it happened, using intervals of 4 to 124 hours. This finding was later  
35 replicated with laboratory rats (*Rattus norvegicus*), using a foraging task in the radial  
36 arm maze that was based on the food-hoarding task (Babb and Crystal 2005, 2006a, b,  
37 Naqshbandi et al. 2007).

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

46 (Correia et al. 2007, reviewed by Feenders and Smulders 2008). Because of these  
47 complications and the baggage that comes with the term episodic memory, we will  
48 only discuss the *what-where-when* aspect in the present study.

49         Because animals do not have language, to ask them whether they remember  
50 *what* they did *where* and *when*, they need to be trained with a set of behavioural rules.  
51 In the original food-hoarding task, the rule the scrub-jays had to learn is that a given  
52 food type becomes inedible after a given amount of time (Clayton and Dickinson  
53 1998). In the foraging task, the rats had to learn that a particular type of food will be  
54 replenished after a long, but not a short interval (Babb and Crystal 2005). In later  
55 experiments, both species have been trained on the obverse rule as well: scrub-jays  
56 have been tested with food that is bad after a short interval, but good after a long  
57 interval (de Kort et al. 2005), and rats have been tested with replenishment at short,  
58 but not long intervals (Naqshbandi et al. 2007). In both cases, this did not pose any  
59 significant problems for the animals.

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

71 Another aspect of the original studies by Clayton and Dickinson (1998) and  
72 Babb and Crystal (2005) is that the number of possible locations in which the animals  
73 could search for the food upon return was very limited. The scrub-jays had the choice  
74 of 16 locations across two halves of an ice-cube tray (the analysis was performed on  
75 which half the birds searched), while the rats had a choice of 8 locations. In nature,  
76 the spatial dimension of the *what-where-when* triad is likely to be continuous and  
77 large. They would also have to remember more than one item or location at a time.  
78 We therefore designed an experiment in which food-hoarding birds could hoard as  
79 many food items as they wanted anywhere in a large open tray, increasing the spatial  
80 load on their memory. We used magpies (*Pica pica*), because, like scrub-jays, they  
81 are a short-term hoarding corvid which opportunistically hoards many food types,  
82 including many that decay (Birkhead 1991). They are distantly related to scrub-jays,  
83 and therefore represent a different clade of corvids (de Kort and Clayton 2006). Both  
84 species have a similar-sized hippocampus relative to brain and body size (Pravosudov  
85 and de Kort 2005). These details suggest that magpies, like scrub-jays, should be able  
86 to remember *what* they hoarded, *where*, and *when*.

87

88

89 **Methods**

90 *Subjects*

91 4 adult (2 male and 2 female) and 2 juvenile female magpies were used.  
92 Adults were more than 3 years old and had been captured in Northumberland in June  
93 2003 under English Nature Licence number 20021809. The juveniles were less than 1  
94 year old and had been captured in Northumberland in June 2005 under English Nature  
95 Licence 20042342. The birds were housed in pairs in pens of 1.56 m (d) x 1.90 m (w)  
96 x 2.68 m (h) (two pens with an adult male and female each and one pen with the two  
97 juvenile females). The animals had access to food and water *ad libitum*. They were  
98 fed Pedigree dog food, which supplied the necessary amount of calories in the daily  
99 diet of the birds. This diet was judged to be the least preferred variety of food from  
100 the birds' point of view, providing motivation to hoard and retrieve more preferred  
101 foods during the trials. The experiments were run from January to April 2006 and the  
102 photoperiod was set at 9L:15D (coming on at 9:30 am, and turning off at 5:30 pm).  
103 Birds' body masses stayed stable throughout the study.

104

105 *Testing arena and initial training*

106 The enclosure used was three metres in diameter with 2.21 metre high walls,  
107 made from white, heavy duty curtain, and a wooden floor. An overlap in the curtain  
108 allowed access to the arena. One metre from the access, there was a one-way  
109 observation mirror. The arena contained four metal trays (75 cm (l) x 65 cm (w) x 4  
110 cm (h)), placed alongside one another to cover 150 cm x 130 cm area of the floor in  
111 the test room. Every tray was further subdivided into 16 compartments (18.5 cm x  
112 16.0 cm). Heavy small industrial wood-shavings were used to fill up the trays, which  
113 created a hoarding area for the magpies. The test trays were fitted with a number of

114 pencils decorated with beads to provide spatial landmarks within the trays (Fig. 1).  
115 The make-up of the landmarks and their locations were changed at every trial to  
116 prevent memory interference between trials.

117 The magpies were transported from the home pens to the experimental arena  
118 by turning out the lights in the home pens and shining a flash-light onto the open  
119 transport cages. The birds were trained to jump into the cage without a need for being  
120 chased. They were then carried to the experimental arena using the basket and  
121 released. The birds were allowed to hoard food in or retrieve food from the wood-  
122 shaving filled trays. This food consisted of pellets of scrambled egg (approximately  
123  $0.25 \text{ cm}^3$ , weighing 0.6-1 grams), dyed either bright red or blue, using SuperCook™  
124 food colouring. During all trials, the location, content and time of every cache created,  
125 as well as every search sweep (removal of the substrate by the magpie beak made in  
126 search of hidden food) was recorded.

127

## 128 *Experimental design and manipulations*

### 129 (i) What-where-when memory training

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

139           The cache retrieval phase occurred either in the afternoon of the same day (10  
140 trials), or the next day (10 trials; Table 1). These two types of trials were presented to  
141 the birds in a pseudo-random order (never more than 2 trials with the same retention  
142 interval in a row). Prior to retrieval, all the birds' items were replaced in the locations  
143 where they had been hoarded in the first phase of the trial. Depending on the  
144 retention interval, one type of food (red or blue pellets) was replaced with the same  
145 quantity of (inedible) wooden beads of the same size and colour. For example, if  
146 retrieval happened on the same day, then blue egg pellets would be replaced with blue  
147 beads, while if retrieval happened the next day, the red egg pellets would be replaced  
148 with red beads. The other items remained edible egg pellets of the correct colour in  
149 both cases. Which retention interval corresponded to which colour becoming inedible  
150 was counterbalanced across birds. Magpies were allowed 30 minutes to retrieve as  
151 many caches as they could find. If all the edible caches were discovered before the 30  
152 minutes had elapsed, the session was ended. After completing the retrieval session  
153 magpies were returned to their home pens.

154

155 (ii) What-where-when memory probe trial

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

163



164 (iii) Foraging Experiment

165           This experiment was conducted to doubly assure that the birds could not detect  
166 the location and/or content of a cache site using direct cues from the hidden objects.  
167 We ran 16 foraging trials with each bird. Prior to testing the birds were food deprived  
168 for 2 hours. Two birds (from the same pen) were tested per day, completing 4 trials  
169 each. In each of the four trials, a different combination of items was hidden by the  
170 experimenter: either all beads (2 caches of 3 red beads & 2 of 3 blue beads), all egg  
171 pellets (2 of 3 red pellets & 2 of blue), 2 of red egg pellets & 2 of blue beads, or 2 of  
172 blue egg pellets & 2 of red beads. The different trial types were presented in random  
173 order to every bird and the two birds tested on a given day were alternated in the  
174 arena. While one bird was in the arena, the other bird was held in the transport cage  
175 in the dark to reduce stress. The same enclosure, trays and beads were used as before,  
176 but without the trial-unique landmarks. Items were hidden 1 inch below the surface of  
177 wood shavings in the trays. They were distributed in different ways on the different  
178 trials. To determine where to hide the items, we used the following rules. Firstly,  
179 each bird's preferred cache locations were determined based on the 20 trials of the  
180 first experiment. Using the existing caching tray (Fig. 1) one hundred random sites  
181 were then generated in a computer spreadsheet. From these 100 random locations, we  
182 randomly picked two from within the bird's preferred area, and two from outside it.  
183 Distributions were therefore personalized to each individual bird. A bird was allowed  
184 to investigate the test room for 30 minutes, and location and time of all search sweeps  
185 were again recorded. Throughout testing the birds were given *ad libitum* water and  
186 any food they could find in the test arena.

187

188

189 *Data analysis*

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

197

198

199 **Results**

200

201 *What-where-when memory training trials*

202         The birds hoarded an average of 11.12 pellets (range: 3.5 to 19.2 pellets), in  
203 3.28 caches (range: 1.4 to 5.3 caches). All the pellets in a cache were usually carried  
204 together from one food bowl and deposited together. The birds never mixed the two  
205 colours in the same cache. Not all birds hoarded both colours of pellets on all trials.  
206 Trials on which the birds hoarded nothing at all were ignored in the analysis. Trials  
207 on which the birds hoarded only pellets of one colour were deemed informative to the  
208 bird (because the items of that colour would either be palatable or unpalatable on  
209 retrieval), but were treated as missing data in the analysis. On average, birds hoarded  
210 at least one colour (i.e. informative trials from the birds' point of view) on 7.17 -  
211 (range: 5-10) of the 10 long-retention trials and on 7.67 (range: 3-10) of the 10 short-  
212 retention trials. They hoarded both colours (i.e. informative trials from a data analysis  
213 point of view) on average on 6.67 (range: 3-10) long-retention trials and on 7.33  
214 (range 1-10) short-retention trials. We analyzed the results for the first 5 trials that  
215 were informative to the bird, treating those trials on which the birds only hoarded one  
216 colour as missing data in the analysis.

217         A linear mixed model with bird as a random factor and type of food item  
218 (palatable or unpalatable), trial (1-5) and retention interval (short or long) as fixed  
219 factors resulted in the following findings. By the time they had retrieved all palatable  
220 items or 30 mins had elapsed (whichever was sooner), birds had retrieved a  
221 significantly higher proportion of palatable than unpalatable items ( $F_{1,5}=128.9$ ,  
222  $p<0.0005$ ). Birds retrieved a smaller proportion of items in later trials than in earlier  
223 trials ( $F_{4,19}=4.46$ ,  $p=0.011$ ). The drop in proportion of items retrieved over trials was

224 very steep for unpalatable items, while palatable items were retrieved at similar rates  
225 throughout all trials (palatability x trial interaction:  $F_{4,19}=3.85$ ,  $p=0.019$ ; Fig. 2).  
226 There were no differences between trials with the two different retention intervals, nor  
227 were there any interactions between retention interval and trial, palatability or both  
228 (all p-values  $>0.18$ ).

229 Another measure we used was whether the first cache retrieved was a  
230 palatable or non-palatable item. If the birds know and remember which items will be  
231 palatable on a given trial, we expected that they would retrieve palatable caches first.  
232 We therefore calculated on which proportion of its trials any given bird retrieved a  
233 palatable cache first. We then calculated the probability of this proportion based on  
234 the exact probabilities of retrieving a palatable cache first by pure chance on every  
235 trial. This probability is different from trial to trial based on the ratio of red to blue  
236 caches made by the bird on those trials. We did not count the first trial for each  
237 retention interval, because this was the birds' first exposure to the rules of the  
238 experiment. Birds retrieved the palatable item first on average on 95.5% of the trials  
239 (range across birds: 78.6% to 100%). Probabilities of this happening by chance were  
240 below the 5% cut-off for each individual bird's performance (range:  $p=0.046$  to  
241  $p=3.1 \times 10^{-6}$ ).

242

#### 243 *Effects of time of day*

244 For short-retention-interval trials, the birds performed the retrieval in the  
245 afternoon of the same day, so there was only time to test 3 birds on any given day.  
246 For long-retention-interval trials, the retrieval happened the next day, so to save time,  
247 all birds were tested on the same day. This means that for two birds (H1 and H2; an  
248 adult pair from the same pen), the time of day at which hoarding took place was much

249 later on long-retention-interval trials than on short-retention-interval trials ( $t_{18}>7.2$ ,  
250  $p<0.0005$  for each bird), without any overlap after the first trial (Table 1). The times  
251 of the retrieval trials did overlap substantially, although they were still statistically  
252 later for long-retention-interval trials than for short-retention-interval trials ( $t_{18}=2.53$ ,  
253  $p=0.02$  and  $t_{18}=2.38$ ,  $p=0.03$ ; Table 1). For the other four birds (R1-R4), there was a  
254 large overlap in the hoarding times between the two trial types (all  $t_{18}<1.8$ ,  $p$ -values  $\geq$   
255 0.1; Table 1), but the retrieval times were consistently later on short-retention-interval  
256 trials than on long-retention-interval trials (all  $t_{18}>6.2$ ,  $p<0.0005$ ; Table 1). This  
257 means that in theory, the birds could tell which trial type they were in, based on either  
258 the time of day during which they hoarded (H1-H2) or the time of day during which  
259 they were allowed to retrieve (R1-R4).

260         If H1 and H2 could predict the trial type during the hoarding phase, they might  
261 have adopted a hoarding strategy based on which food would be palatable still at  
262 retrieval. We therefore analyzed whether they were more likely than R1-R4 to hoard  
263 the colour that would be palatable on retrieval than the other colour. We counted the  
264 total number of pellets hoarded of each colour on each trial, and then subtracted the  
265 number of pellets of the “unpalatable” colour from the number of the “palatable”  
266 colour (combining trials from both retention intervals). Therefore negative numbers  
267 indicate that more pellets of the “unpalatable” colour are hoarded, while positive  
268 numbers mean that the birds favoured “palatable” pellets. We excluded the first trial  
269 of each type, as the birds could not yet have obtained the information about the  
270 different trial types at that point in time. A linear mixed model with bird as the  
271 random factor indicates that this index of preference is not significantly different for  
272 the two groups of birds ( $F_{1,57}=2.099$ ,  $p=0.153$ ; H1-H2:  $-0.885 \pm 0.115$ ; R1-R4:  $-0.057$

273  $\pm 0.628$ ), that there is no change over trials in general ( $F_{1,88}=1.982$ ,  $p=0.163$ ), nor for  
274 only H1 and H2 (Interaction:  $F_{1,88}=2.371$ ,  $p=0.127$ ).

275

276 *Probe trial*

277         On the probe trial, all birds hid both colours of egg pellets. One bird hid all  
278 the unpalatable pellets in the same compartments as palatable pellets. Because we  
279 could not analyze the data to a spatial resolution more precise than the level of one  
280 compartment, it was impossible to say which pellets the bird was searching for and  
281 this bird's data were not used in the subsequent analysis. The other five birds all  
282 searched first in the location of a palatable item ( $p=0.048$ ). They continued searching  
283 in "palatable" locations before searching in the locations of the unpalatable items. By  
284 the time they had searched in all the locations where palatable items should have  
285 been, or 30 minutes had elapsed, birds had searched in on average 90% of the  
286 palatable locations, but none of the unpalatable locations ( $t_4=9.0$ ,  $p=0.0008$ ). In the  
287 half hour of searching, they also made a much higher effort searching in "palatable"  
288 locations ( $55 \pm 16$  search sweeps per bird per location) than in "unpalatable" locations  
289 ( $2 \pm 0.9$  search sweeps per bird per location) (paired t-test:  $t_4=3.4$ ,  $p=0.03$ ; Fig. 3).

290

291 *Cache detection using direct cues from the food*

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

294

295

296

297

298 **Discussion**

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

304           Whereas it is clear that magpies can show *what-where-when* memory for  
305 caches, it is unclear what exactly the nature is of the *when* component in this  
306 study. Two of the birds (H1 and H2) were in a position to potentially predict the  
307 retention interval to which they would be subjected on that particular trial, and  
308 the other four birds (R1-R4) could potentially use the time of day at retrieval to  
309 know which item colour would be edible. Encoding which items should be  
310 remembered and selectively forgetting the other type based on what time of day  
311 the hoarding takes place is theoretically possible, but at least one recent study has  
312 shown that rats cannot solve an analogous task based on this information  
313 (Roberts et al. 2008). Our post-hoc analysis also suggests that these birds did not  
314 increase how many “future palatable” pellets they hoard through the trials,  
315 although with only 2 birds in this group, the power of this analysis is very low.  
316 It therefore remains unclear whether H1 and H2 could indeed predict the trial  
317 type at hoarding.

318           All six birds solved the task above chance level. It is theoretically  
319 possible that different birds solved the task in different ways. However, the most  
320 parsimonious explanation is that the birds all used the retention interval as their  
321 main cue as to which food type they should search for. This is also consistent

322 with the existing literature on the topic (Babb and Crystal 2005, 2006a, b,  
323 Clayton and Dickinson 1998, Roberts et al. 2008).

324           Regardless of how the birds worked out which trial type they were in on  
325 any given day, they clearly were able to associate the trial type with the colour of  
326 food that was edible on that trial type, and stopped searching for the colour that  
327 would have been replaced with wooden beads. Unlike in previous experiments  
328 (Babb and Crystal 2005, 2006a, b, Clayton and Dickinson 1998, 1999, Clayton et  
329 al. 2001, 2003b, de Kort et al. 2005, Roberts et al. 2008), none of the trials relied  
330 on one food type being preferred over another one. The two food types were  
331 identical in every respect except for their colour and the meaning of the two  
332 colours was counterbalanced across birds. The birds learned which colour to  
333 retrieve in which trial type within a couple of trials.

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



347           Studies with food-hoarding birds in the past have shown many times over  
348 that they can remember several different cache locations in a single trial, out of  
349 many possible cache locations (e.g. Balda and Kamil 1989, Jacobs and Liman  
350 1991, Shettleworth and Krebs 1982). Studies of episodic-like *what-where-when*  
351 memory, however, had so far only used 2 to 8 possible alternatives to remember  
352 (Babb and Crystal 2005, 2006a, b, Clayton and Dickinson 1998, 1999, Clayton et  
353 al. 2001, 2003b, de Kort et al. 2005, Naqshbandi et al. 2007, Roberts et al. 2008).  
354 In our study, we combined the *what-where-when* feature with a continuous  
355 spatial environment in which items could be found. It is clear that the birds  
356 easily remembered where in the tray food had been hidden, and combined this  
357 with the knowledge of which type of food was in which location. This situation  
358 is closer to a real-life situation in which animals might have to combine  
359 information about *what*, *when* and *where*, and it shows that they have no problem  
360 doing this.

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

370

371

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377

378 **References**

379 Babb, S J, Crystal, J D (2005) Discrimination of what, when, and where:  
380 Implications for episodic-like memory in rats. *Learn Motiv* 36: 177-189.

381 Babb, S J, Crystal, J D (2006a) Discrimination of what, when, and where is not  
382 based on time of day. *Learning & Behavior* 34: 124-130.

383 Babb, S J, Crystal, J D (2006b) Episodic-like memory in the rat. *Curr Biol* 16:  
384 1317-1321.

385 Balda, R P, Kamil, A C (1989) A comparative study of cache recovery by three  
386 corvid species. *AnimBehav* 38: 486-495.

387 Birkhead, T R (1991) *The magpies: The ecology and behaviour of black-billed  
388 and yellow-billed magpies*. T. & A. D. Poyser Ltd

389 Clayton, N S, Dickinson, A (1998) Episodic-like memory during cache recovery  
390 by scrub-jays. *Nature* 395: 272-274.

391 Clayton, N S, Dickinson, A (1999) Scrub-jays (*Aphelocoma coerulescens*)  
392 remember the relative time of caching as well as the location and content of  
393 their caches. *J Comp Psychol* 113: 403-416.

394 Clayton, N S, Yu, K S, Dickinson, A (2001) Scrub-jays (*Aphelocoma  
395 coerulescens*) form integrated memories of the multiple features of caching  
396 episodes. *J Exp Psychol-Anim Behav Process* 27: 17-29.

397 Clayton, N S, Bussey, T J, Dickinson, A (2003a) Can animals recall the past and  
398 plan for the future? *Nat Rev Neurosci* 4: 685-691.

399 Clayton, N S, Yu, K S, Dickinson, A (2003b) Interacting cache memories:  
400 Evidence for flexible memory use by western scrub-jays (*Aphelocoma*  
401 *californica*). *J Exp Psychol-Anim Behav Process* 29: 14-22.

402 Correia, S P C, Dickinson, A, Clayton, N S (2007) Western scrub-jays anticipate  
403 future needs independently of their current motivational state. *Curr Biol* 17:  
404 856-861.

405 de Kort, S R, Clayton, N S (2006) An evolutionary perspective on caching by  
406 corvids. *Proceedings of the Royal Society B-Biological Sciences* 273: 417-  
407 423.

408 de Kort, S R, Dickinson, A, Clayton, N S (2005) Retrospective cognition by  
409 food-caching western scrub-jays. *Learn Motiv* 36: 159-176.

410 Dere, E, Kart-Teke, E, Huston, J P, De Souza Silva, M A (2006) The case for  
411 episodic memory in animals. *Neuroscience & Biobehavioral Reviews* 30:  
412 1206-1224.

413 Eacott, M J, Easton, A, Zinkivskay, A (2005) Recollection in an episodic-like  
414 memory task in the rat. *Learn Mem* 12: 221-223.

415 Feenders, G, Smulders, T V (2008) Episodic-like memory in food-hoarding  
416 birds. In: Dere, E, Easton, A (Ed.) *Handbook of episodic memory*. in press.

417 Griffiths, D, Dickinson, A, Clayton, N (1999) Episodic memory: What can  
418 animals remember about their past? *Trends in Cognitive Sciences* 3: 74-80.

419 Jacobs, L F, Liman, E R (1991) Grey squirrels remember the location of buried  
420 nuts. *Anim Behav* 41: 103-110.

421 Morris, R G M (2001) Episodic-like memory in animals: Psychological criteria,  
422 neural mechanisms and the value of episodic-like tasks to investigate  
423 animal models of neurodegenerative disease. *Philosophical Transactions of*  
424 *the Royal Society of London - Series B: Biological Sciences* 356: 1453-  
425 1465.

426 Naqshbandi, M, Feeney, M C, McKenzie, T L B, Roberts, W A (2007) Testing  
427 for episodic-like memory in rats in the absence of time of day cues:  
428 Replication of babb and crystal. *Behav Process* 74: 217-225.

429 Pravosudov, V V, de Kort, S R (2005) Is the western scrub-jay (*aphelocoma*  
430 *californica*) really an underdog among food-caching corvids when it comes  
431 to hippocampal volume and food caching propensity? *Brain Behav Evol*  
432 67: 1-9.

433 Roberts, W A, Feeney, M C, MacPherson, K, Petter, M, McMillan, N, Musolino,  
434 E (2008) Episodic-like memory in rats: Is it based on when or how long  
435 ago? *Science* 320: 113-115.

436 Schwartz, B L, Hoffman, M L, Evans, S (2005) Episodic-like memory in a  
437 gorilla: A review and new findings. *Learn Motiv* 36: 226-244.

438 Shettleworth, S J (2001) Animal cognition and animal behaviour. *Anim Behav*  
439 61: 277-286.

440 Shettleworth, S J, Krebs, J R (1982) How marsh tits find their hoards : The roles  
441 of site preference and spatial memory. *JExpPsych:AnimBehProc* 8: 354-  
442 375.

443 Suddendorf, T, Busby, J (2003) Mental time travel in animals? *Trends in*  
444 *Cognitive Sciences* 7: 391-396.

445 Tulving, E (2001) Episodic memory and common sense: How far apart?  
446 Philosophical Transactions of the Royal Society of London - Series B:  
447 Biological Sciences 356: 1505-1515.  
448 Zentall, T R, Clement, T S, Bhatt, R S, Allen, J (2001) Episodic-like memory in  
449 pigeons. Psychon Bull Rev 8: 685-690.  
450

451 **Table Caption**

452 Table 1: The ranges of starting times for the hoarding (max 1 hour) and retrieval

453 (max 30 min) sessions for all birds, under both experimental conditions.

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458 **Figure captions**

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

460

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

467

468 Fig. 3 Mean number of search sweeps per bird within 1 tray radius of palatable and  
469 unpalatable cache sites during the probe trial. Different symbols represent different  
470 birds.

471

472

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

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480 Table 1

481



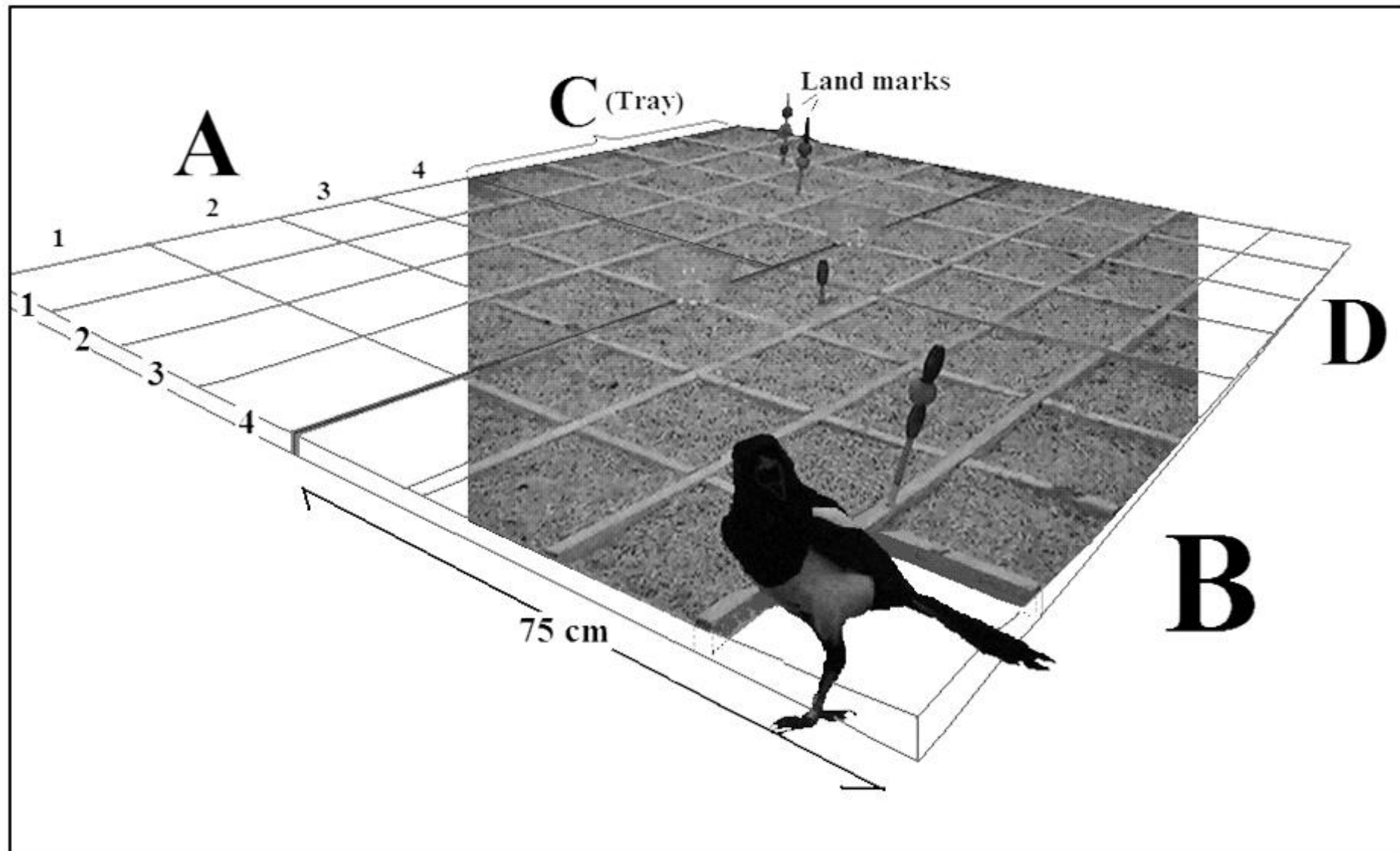


Figure 1

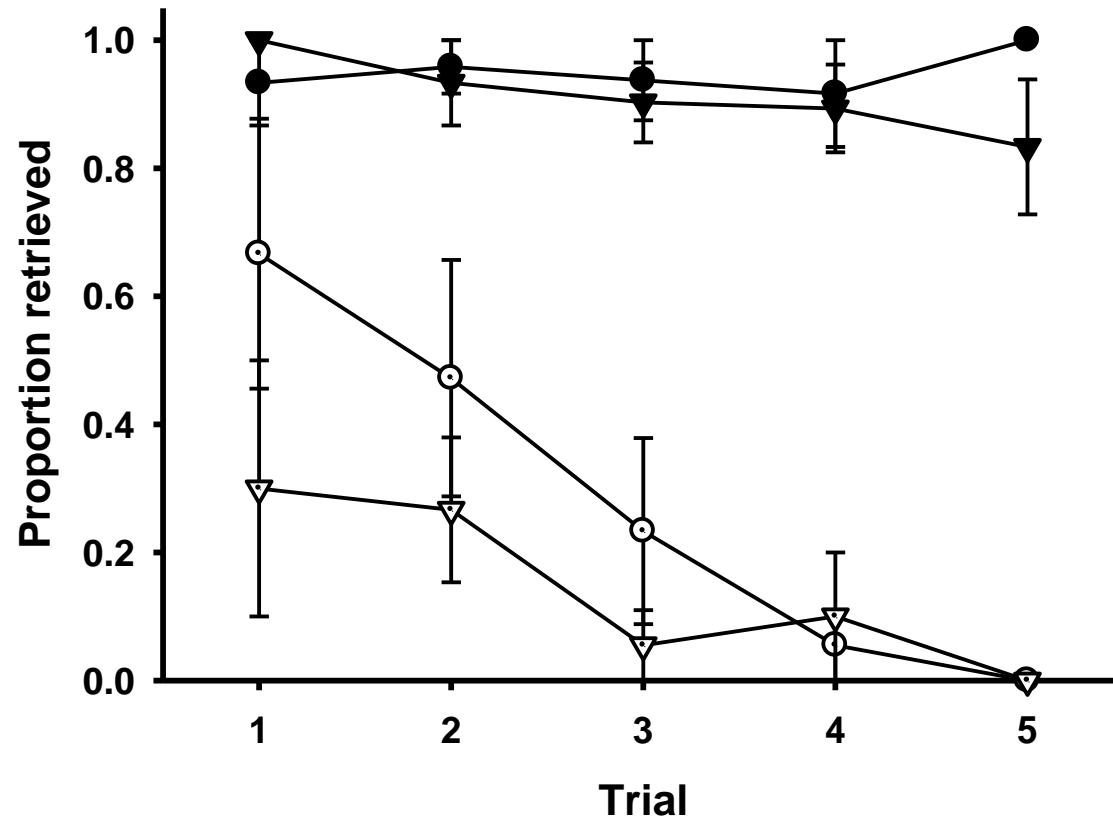


Figure 2

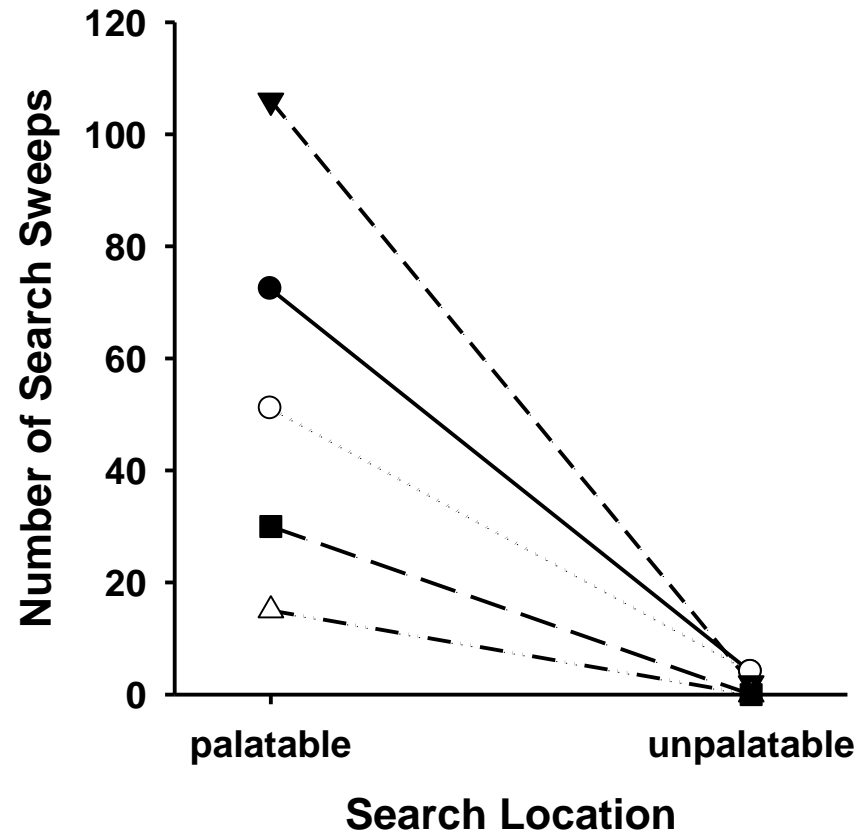


Figure 3