

Spatial memory of Paridae: comparison of a storing and a non-storing species, the coal tit, *Parus ater*, and the great tit, *P. major*

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Abstract. The performances of the coal tit (a food storer) and the great tit (a non-storer) were compared in two experiments in which the bird was rewarded in phase 2 of a trial for returning to sites where it had seen food in phase 1 ('window-shopping'). In both experiments the differences in performance between the species were small. In the first experiment the storing species was better than the non-storer at returning to the site where it had seen a seed, and in the second experiment the storing species was better at discriminating in phase 2 between sites visited in phase 1 that contained a seed and sites visited in phase 1 that were empty. A third experiment demonstrated that the motivational variables of reward size and deprivation were unlikely to account for the difference between the species. The results might indicate that there are differences in the spatial memory of the storing and non-storing species, but a difference in perceptual discrimination cannot be excluded.

Two approaches to comparing learning and memory of different species can be distinguished. In the traditional approach (Thorndike 1911; Bitterman 1975) the performances of very different species such as goldfish, *Carassius auratus*, and pigeons, *Columba livia*, are compared in arbitrary laboratory tasks like discrimination reversal and probability learning. Macphail (1982) claimed that this approach has so far provided no conclusive evidence for qualitative or quantitative differences between species once 'contextual' variables like sensory, motor and motivation differences are taken into account. Recently some authors (e.g. Domjan & Galef 1983; Kamil 1987; Rozin & Schull 1988) have advocated what Kamil (1987) termed the synthetic approach, combining the method and the theory of psychology with the insights of ethologists and behavioural ecologists into how animals use learning and memory in nature. According to this view, closely related species should be compared with regard to abilities that they naturally need to use to different degrees. Proponents of the synthetic approach predict that quantitative or qualitative specializations of learning and memory will be found that correspond to differences in ecology (Domjan & Galef 1983; Sherry & Schacter 1987). However, little systematic research using this approach has been done.

Food-storing birds provide an excellent opportunity to test the notion that memory differs between species in an adaptive way. Some parids (titmice) and corvids (crows) store food in the wild and rely

on memory to find it again. They may store items in hundreds of different places for periods of hours or days (reviews in Shettleworth 1985; Balda et al. 1987; Sherry 1987). Other species, living in similar areas and with similar feeding habits, store very little or not at all. The importance of good spatial memory to a food-storing way of life suggests that food-storing species may have evolved a particularly large-capacity, long-lasting and accurate spatial memory, which might be qualitatively or quantitatively different from the spatial memory used in normal foraging. This speculation is encouraged by recent neuroanatomical studies showing that the hippocampus in food-storing birds is significantly larger relative to brain and body size than in non-storing birds (Krebs et al. 1989; Sherry et al. 1989). The hippocampus is the area of the brain implicated in some aspects of spatial and other memory in mammals (Rawlins 1985) and birds (Bingman et al. 1984; Sherry & Vaccarino 1989). Moreover, hippocampal damage reduces performance in recovery of stored food in black-capped chickadees, *Parus atricapillus* (Sherry & Vaccarino 1989). Regarding behavioural evidence for specialized memory, Balda & Kamil (1989) have described differences in cache recovery among three corvid species that could reflect differences in memory.

In the experiments reported here we compare the performance of a storing and a non-storing species of *Parus* using a test of memory called 'window-shopping' (Shettleworth & Krebs 1986). This test

was designed to capture the essential features of food-storing memory without requiring the birds to store food, thereby allowing the performance of storing and non-storing species to be compared. The initial hypothesis is that the performance of a storing species on this task should be superior to that of a non-storer and that the difference should reflect differences in memory. A window-shopping trial consists of two phases: the first phase corresponds to storing food except that instead of putting food into each site itself, the bird sees food behind a small window while foraging. The windows are covered by small cloth flaps which the birds are trained to lift to inspect the contents of the hole behind the window. Thus, as in storing food, the bird visits a number of places and learns that food is in some of them. In the second phase of each trial, after a retention interval, the bird is allowed to return and eat the food it saw behind the window in the earlier phase. The food is still hidden behind cloth flaps in the sites where it was seen in phase 1, but now the windows are open so that when the flap is lifted the food can be taken out of the hole and eaten.

Food-storing black-capped chickadees can perform the window-shopping task at above chance level when the interval between the two phases is about 2 h (Shettleworth & Krebs 1986). In the present study we compared the performance of coal tits with that of the non-storing great tit. We first compared the species in a simple version of the task in which a single seed was hidden on each trial in one of seven sites; the retention interval was 30 min. In the second experiment we compared performance in a more complicated version of the task in which seeds were seen in seven out of 60 sites in phase 1 and the retention interval was 120 min. The reason for using a simple version of the task in the first experiment was that we wanted to start from a situation in which we expected both species to perform well and then increase the difficulty of the task to see if a species difference might emerge. In the final experiment we tested whether or not two motivational variables, reward size and deprivation level, influence performance in the complex window-shopping task.

EXPERIMENT 1

Our aim in this experiment was to compare the performances of coal tits and great tits in a simple

version of the window-shopping task referred to above, with one out of seven sites rewarded and a retention interval of 30 min.

Methods

Subjects

The subjects were four great tits and four coal tits caught in deciduous woodland near Stanton St John, Oxfordshire. Both species were fed a mixture of dried insects, grated apple and carrot, and hard-boiled egg together with peanuts, sunflower seeds and mealworms. The birds were kept indoors in standard holding cages measuring 0.44 m wide \times 0.77 m long \times 0.44 m high each connected by a trapdoor to the experimental room. Both the living and experimental rooms were maintained on a 10:14 h light:dark cycle.

Experimental environment

The birds were tested in a room, 3.75 \times 3.9 \times 2.4 m high; along the 3.9-m wall were eight trapdoors connecting the birds' living cages with the room and the 3.75-m wall had a door with a smoked one-way Plexiglas window through which the experimenter could view the birds.

In the experimental room were seven wooden blocks (9.0 cm wide \times 15.0 cm high \times 4.0 cm thick; see Shettleworth & Krebs 1986). Each had a small hole (0.5 cm diameter) in its front face covered by a piece of transparent plastic measuring 2.5 \times 1.3 \times 0.1 cm. Through this piece of plastic, or 'window', the contents of the hole were visible but not accessible and the window could be moved so that in the recovery phase of the experiment the bird could gain access to the hole's contents. The window had a small hole (3 mm diameter) in the lower right hand corner (see below). A piece of black cloth (3 \times 3.5 cm) was stapled to the block above the hole so as to cover both the hole and most of the window. It was held in place by a piece of Velcro attached to the block below the hole. This piece of cloth could be lifted easily by both species. Each block had a perch 0.9 cm in diameter \times 5.5 cm long 4 cm below the central hole. The blocks were arranged on seven of the nine artificial 'trees' randomly placed around the room. The trees were cut saplings set into concrete bases or plastic umbrella stands. Arranged at various heights on the trees were perches, 10 cm long, onto which the blocks could be positioned. The blocks were placed

Table I. Summary of data ($\bar{X} \pm SE$) collected from experiments 1 and 2

	Experiment 1		Experiment 2	
	Coal tits	Great tits	Coal tits	Great tits
No. of trials	15.00 \pm 0.00	15.00 \pm 0.00	18.17 \pm 3.98	17.71 \pm 3.69
No. of holes visited in phase 1	4.50 \pm 0.50	3.75 \pm 0.63	14.61 \pm 3.98	14.68 \pm 3.80
Duration of phase 1 (min)	2.28 \pm 2.37	1.88 \pm 1.95	3.55 \pm 3.98	4.69 \pm 3.53
No. of holes visited in phase 2	2.25 \pm 0.25	3.25 \pm 0.25	21.81 \pm 7.85	20.79 \pm 8.31
Duration of phase 2 (min)	2.02 \pm 1.63	1.27 \pm 1.01	5.80 \pm 3.34	6.71 \pm 4.27
No. of seeds seen in phase 2	1.00 \pm 0.00	1.00 \pm 0.00	5.05 \pm 1.50	4.52 \pm 1.35
Retention interval (min)	34.40 \pm 7.42	34.13 \pm 8.09	130.44 \pm 16.46	132.97 \pm 18.46

at different heights and pointing in different directions. Visual cues were provided in the form of large coloured cardboard symbols on three of the walls (not the wall containing the trapdoors). In the centre of the room was a wooden perch 30 cm high.

Training

For the duration of the experiment food bowls were removed from the birds' living cages at dusk or shortly afterwards (1700–1800 hours, GMT). Following testing the birds were given a fresh portion of the maintenance diet. As dawn was at about 0700 hours and the birds were tested about 3 h later, this meant that after their overnight fast the birds had only the peanuts they ate in the experiment during the first 3 or 4 h of daylight. Under this feeding regime the birds were trained to come into the room and lift the pieces of cloth on the blocks in search of pieces of peanut placed in the large (0.5 cm) holes. During initial training all seven sites contained pieces of peanut, but later only one site was rewarded. The birds required between 15 and 18 days of training and the criterion performance for proceeding to the next stage was for the bird to visit the block containing a piece of peanut within 5 min.

Window-shopping trials

Window-shopping trials were conducted on the same schedule as training except that the trials were divided into two phases approximately 30 min apart. One trial was conducted each day. In the first phase only one block contained a piece of peanut (average weight = 62 mg). Each hole was covered by a plastic window through which the peanut was visible but not accessible. The hole containing the peanut also had a smaller piece of peanut (average

weight = 7.8 mg) pressed into the small hole in the window where the bird could pull it out. When a bird lifted the cloth it would remove and eat the piece of peanut. The occurrence of 'window-shopping' was recorded when the bird visited a site and lifted the cloth. Each block contained the peanut once for the first 7 days, in random order. This order was maintained for subsequent trials.

In the first phase of the trial the bird was allowed into the room to window-shop until it located the single site containing a peanut. All of the sites inspected and the length of time taken for the bird to locate the site with a piece of peanut were recorded. The birds were given no food between the two phases of the trial.

The bird was allowed back into the room 30 min later for the second, recovery, phase of the trial. The phase lasted until the bird visited the rewarded site or until 5 min had elapsed, whichever came sooner. The birds almost always visited the rewarded site within 5 min. All of the windows were now open but the black cloths were again pressed down leaving the holes accessible but not visible. The site where the bird had found a piece of peanut in the first phase was the only site to contain a peanut in this phase. As we had shown in previous work, using the same experimental design, that the birds did not locate the seed in phase 2 by responding to direct cues (e.g. sight, smell; Shettleworth & Krebs 1986), we did not run these controls in the present experiments.

A summary of the data collected from this experiment is shown in Table I.

Results and Discussion

Number of visits to find the seed

The simplest comparison of performance comes from examining the number of visits to find the

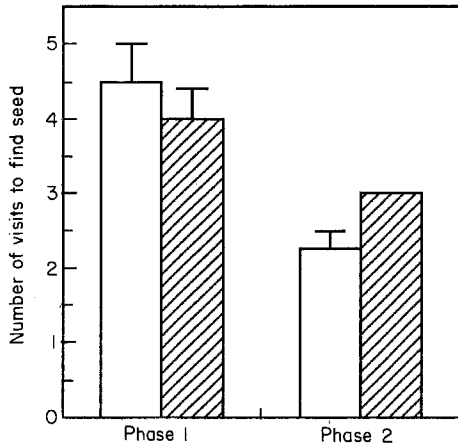


Figure 1. Experiment 1. The number of visits to find the seed in phases 1 and 2 (means of individual bird medians + se; great tits in phase 2 have a standard error of zero). □: Coal tit; ▨: great tit.

peanut in phase 1 and phase 2 of the experiment. In phase 1 the birds are searching for a piece of peanut placed randomly in one of seven sites, so they should need on average to visit 4.0 sites (assuming no revisiting) to find the peanut. In phase 2 the birds have the possibility of using their experience in phase 1 to direct their search, and might therefore be expected to visit fewer than 4.0 sites before finding the seed. Therefore one way to examine the performance of each species is to see if it is significantly above chance. A more direct comparison of the two species is to examine the number of different sites visited by each species to find the seed in phase 2.

Both coal tits and great tits performed significantly above the chance level of 4.0 in phase 2 (using individual bird medians as data points for coal tits, $t=7.0$, $df=3$, $P<0.01$, two-tailed, one sample t -test; for great tits all four birds had a median of 3.0). Examining the performance of individual birds based on the 15 trials revealed that three coal tits and one great tit were above chance (based on the median \pm 95% confidence intervals of 15 trials per bird).

In phase 1 there was no significant difference between coal tits and great tits in the number of visits needed to find the seed ($t=0.775$, $df=6$, $P=0.468$), but in phase 2 the coal tits visited significantly fewer different sites before they found the seed ($t=3.0$, $df=6$, $P=0.024$; Fig. 1). The performance in phase 2 is further analysed in Fig. 2. In phase 1 a site could fall into one of three exclusive and exhaustive categories: found to contain a

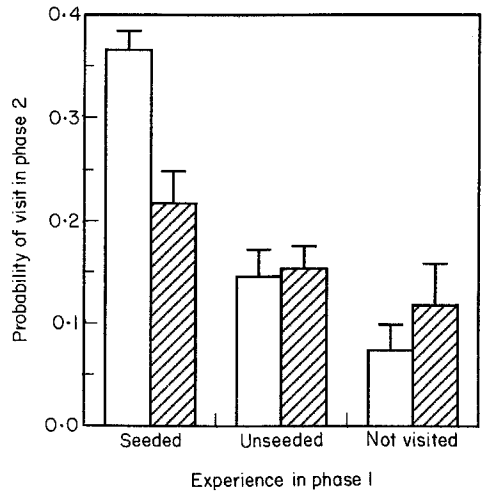


Figure 2. Experiment 1. The probability of visiting a site on the first look in phase 2, in relation to experience of that site in phase 1 (means of individual bird means + se). □: Coal tit; ▨: great tit. See text for further details.

peanut (s = seeded); visited and found to contain no peanut (u = unseeded); and not visited (n = non-visited). $P(v|s)$ is the probability of visiting a seeded site on the first look in phase 2 (averaged across all trials); $P(v|u)$ and $P(v|n)$ are the probabilities of visiting unseeded and non-visited sites, respectively. These probabilities were estimated from the data by calculating the proportion of times each event occurred for each bird. For example if the site with the seed was visited on the first look on 10 out of the 15 trials, $P(v|s)$ would be estimated as $10/15=0.67$.

The data summarized in Fig. 2 were angular transformed and analysed with a split-plot ANOVA with species as the plots and experience in phase 1 as a fixed effect within plots. This showed a significant effect of experience in phase 1 ($F_{2,12}=13.494$, $P<0.001$) and of species ($F_{1,6}=43.007$, $P<0.001$). (The species \times experience interaction was not significant: $F_{2,12}=2.84$, $P<0.10$.) Inspection of Fig. 2 suggests that the difference between species arose mainly because coal tits are more likely to return to seeded sites than are great tits. Multiple comparisons of $P(v|s)$, $P(v|u)$ and $P(v|n)$ within each species were made using Tukey's significant difference test and $\alpha=0.05$. These showed that for coal tits $P(v|s)$ was greater than $P(v|n)$ whilst for great tits there were no significant differences between classes.

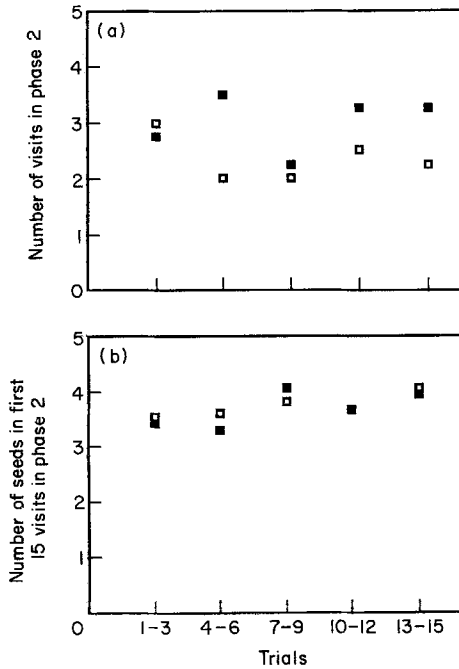


Figure 3. (a) Experiment 1. The performance of the two species (mean values of individual bird medians) over the first 15 trials of the experiment, grouped into three-trial blocks. (b) Experiment 2. The performance of the two species (number of seeds averaged across species) over the first 15 trials of the experiment, grouped into three-trial blocks. □: Coal tit; ■: great tit.

Effect of experience

One possible explanation of the results reported above (Fig. 1) is that coal tits learned the task more rapidly than great tits. However, over the course of the experiment neither coal tits nor great tits showed any evidence of improvement in performance, at least as measured by the number of looks to find the seed in phase 2 (Fig. 3a).

Effect of location of seed on previous trials

In phase 1, coal tits were significantly more likely to go to sites that had been rewarded in the preceding three trials than to sites used in earlier trials (paired *t*-test, $P < 0.02$), while great tits showed no such trend (paired *t*-test, $P > 0.05$; Fig. 4). This indicates that there may also be a difference between the species in the extent to which experience in preceding trials affects performance in later trials (i.e. in long-term retention of memory from one trial to the

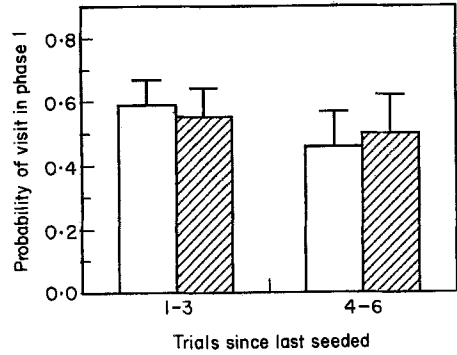


Figure 4. Experiment 1. The effect of past experience. The probability of visiting a site in phase 1 as a function of whether the site was rewarded in a previous trial during the three preceding trials or on trials 4-6 preceding the reference trial (means of individual bird means + SE. □: Coal tit; ▨: great tit).

next, producing so-called proactive interference; Wright et al. 1986).

Other differences between the species

So far we have interpreted the differences in performance between species in terms of differences in memory, but other factors might also account for the results. In experiment 3 we consider the possible effects of reward size and deprivation on performance. Within the present experiment there were no significant differences between the species in the number of holes visited in phase 1 (Fig. 1), in the time taken to visit the holes, or the retention interval (Table I). Another factor that could in principle influence performance is site preference: if, for example, great tits restricted their visits to a few preferred sites this might decrease performance in phase 2 in trials when these sites were not the rewarded one. Preference was analysed by calculating the number of holes that were visited on 0, 1, . . . *n* trials during phase 1 (thus a bird with strong preferences would visit some holes on a high proportion of trials and others not at all). This analysis revealed that although each individual showed significant preferences (chi-squared test) there were no significant differences between the means for coal tits and great tits ($\chi^2 = 3.8$, $df = 6$, NS).

To summarize, in phase 2 of experiment 1 coal tits performed slightly but significantly better than great tits (Fig. 1). It still remains to be shown, however, that this difference between the species is not caused by differences in factors other than memory (see experiment 3 and Discussion).

EXPERIMENT 2

In experiment 2 our aim was to test whether the difference observed in experiment 1 would be exaggerated when we increased the difficulty of the task. Instead of searching for a single seed hidden in one of seven sites, the birds were allowed to search for seven hidden seeds behind the windows in a total of 60 sites. The experiment was run with eight coal tits and seven great tits. The overall design of experiment 2 was similar to that of experiment 1: in phase 1 of a trial the bird was allowed to search for hidden seeds behind windows, and in phase 2 it was allowed back into the room to search for the seeds seen in phase 1, these now being accessible but hidden behind the cloth flaps.

Methods

Subjects

The subjects were seven great tits and eight coal tits (two of which had previously been used in other experiments, but none was used in experiment 1) caught in deciduous woodland near Stanton St John, Oxfordshire. The birds lived in natural day-length in individual outdoor living cages measuring 1.5 m wide \times 6 m long \times 2.5 m high. Diet and general maintenance was as described in experiment 1.

Experimental environment

The birds were tested in a room 3.75 \times 3.9 \times 2.4 m high which was connected to each of the outdoor living cages by a trapdoor. The 3.75-m wall with the trapdoors had a door with a smoked one-way Plexiglas window through which the birds could be observed in the experimental room.

In the experimental room were 60 wooden blocks of the type used in experiment 1. The blocks were arranged around the room on two of the walls and on nine artificial trees randomly placed around the room. The blocks were placed pointing in different directions to make it more difficult for the birds to move up or down to all the blocks of one tree before moving on to the next tree. The blocks placed on the walls were also positioned so as to minimize systematic search patterns. In the centre of the room there was a bowl of water and a wooden perch 30 cm high.

Training

The birds were trained in the same way as described in experiment 1 except there were 60

blocks in the experimental room and during training all 60 sites contained pieces of peanut. The birds required between 7 and 11 days of training. The criterion performance for going on to the next stage was when within a training session the bird visited seven blocks within 10 min.

Window-shopping trials

Window-shopping trials were run with half of the 60 holes blocked. The purpose of this procedure was to attempt to eliminate the tendency of the birds to visit the same sites every day. Thirty holes were selected at random and were covered by a white 1-cm sticker (these were not removed for phase 2). The remaining 30 holes contained pieces of peanut. The holes were then covered by the plastic window through which the sticker or peanut was visible but not accessible. The first phase was the same as in experiment 1 except that the bird was allowed into the room to window-shop until it had located seven sites containing a piece of peanut or until 10 min had elapsed, whichever came sooner. All inspected sites were recorded. When the bird had returned to its home cage it was given three or four small pieces of peanut.

Two hours later the bird was readmitted to the experimental room for the recovery phase of the trial. In this phase all of the windows were open, the cloths again pressed down onto the Velcro and only the seven sites where the bird had seen a peanut during window-shopping in phase 1 contained a piece of peanut. This phase of the experiment lasted until the bird had visited all seven seeded sites or until 10 min had elapsed, whichever came sooner. The number of trials and their durations are indicated in Table I.

Results and Discussion

The analyses of this experiment were based on the first 15 holes visited in phase 2. This number of visits was chosen because it gave an equal amount of data per trial, whilst including trials in which phase 2 sessions contained the fewest visits.

Number of seeds found in the first 15 visits

There was no significant difference between the two species in the number of seeds found after 15 visits (coal tits: $\bar{X} \pm \text{SE} = 3.86 \pm 1.35$; great tits: 3.7 ± 1.47). As in experiment 1, there was no strong evidence of an improvement in performance with time (Fig. 3b); coal tits appear to show a slight

increase, but this is not significant (rank correlation, $P > 0.10$).

Probability of visiting sites containing seeds

As in experiment 1, we compared the transformed probabilities of visiting three classes of site in phase 2 ($P(v|s)$, $P(v|n)$ and $P(v|u)$). Before calculating the values of $P(v|s)$ etc., the sites were divided into 'high' and 'low' preference categories on the basis of the number of trials on which each site was visited during phase 1 of each trial (Shettleworth & Krebs 1986). High preference sites were those visited on 30% of trials or more and low preference sites were visited on fewer than 30% of trials. This division was chosen so that approximately equal numbers of sites fell into the two categories.

The classes of site were less well discriminated than in experiment 1 (as might be expected from the greater complexity of the task; Fig. 5). The data in Fig. 5 were subjected to a split plot ANOVA with species as plots and experience in phase 1 as a fixed effect. The data for high and low preference were included as repeated measures. There was a significant effect of species ($F_{1,13} = 14.409$, $P < 0.01$), of experience in phase 1 ($F_{5,65} = 44.691$, $P < 0.001$) and of an interaction between species and experience in phase 1 ($F_{5,65} = 12.845$, $P < 0.001$). When the data for high and low preference holes were analysed separately in split plot ANOVAs, the interaction term was significant for high preference holes ($F_{2,26} = 55.353$, $P < 0.001$) but not for low preference holes ($F_{2,26} = 0.641$, $P = 0.535$). Thus coal tits and great tits differ in their discrimination of the three classes of site, at least in high preference holes.

Multiple comparisons using Tukey's significant difference test showed that for high preference holes coal tits discriminated between all three classes of site, visiting seeded sites more than unseeded or non-visited sites and non-visited sites more than unseeded sites, but great tits did not discriminate between seeded and unseeded, visiting both more than non-visited sites. Great tits showed a similar pattern for low preference holes (seeded the same as unseeded, both greater than non-visited). Coal tits discriminated between seeded and non-visited but not between seeded and unseeded sites or between unseeded and non-visited sites.

Other differences between the species

The two species did not differ in the mean number of sites visited in phase 1, the time taken

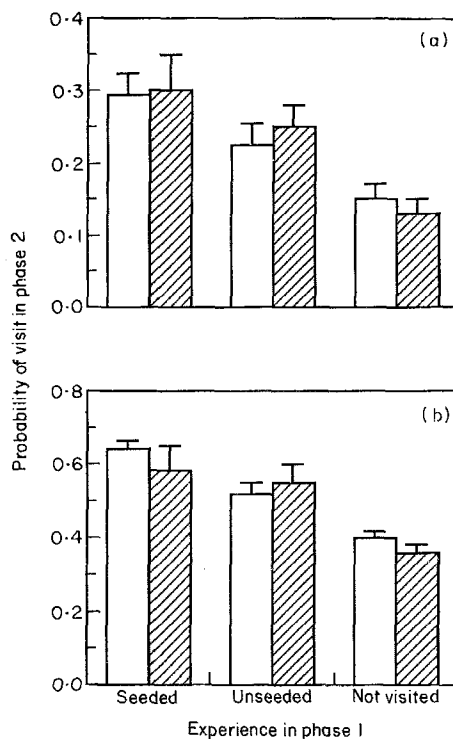


Figure 5. Experiment 2. The probability of visiting a site in phase 2 in relation to experience of that site in phase 1 (a) for low preference holes; (b) for high preference holes. Details as for Fig. 2a.

to visit sites in phase 1 or the retention interval (Table I).

In conclusion, the patterns revealed by comparison of the probability of visiting sites that were seen in phase 1 to contain a seed, to contain no seed, or were not visited, showed that coal tits appear to be better than great tits at discriminating between visited sites that contained a seed and those that contained no seed. We had predicted that the difference between species observed in experiment 1 would be emphasized in experiment 2. This was not true for the overall success in finding seeds as measured by the number of seeds found in 15 looks. However, this is a relatively weak measure of performance in experiment 2, where the possibility of finding seeds by visiting preferred sites is greater than in experiment 1 because there are more sites available. The other measure of performance, namely discrimination of different classes of site, showed a significant difference between species in experiment 2 but not in experiment 1.

Table II. Summary of experiment 3 (\bar{X} from three birds \pm SE)

	Low reward/ high deprivation	Low reward/ low deprivation	High reward/ high deprivation	High reward/ low deprivation
No. of trials	15	15	15	15
No. of holes visited in phase 1	15.5 \pm 4.0	14.8 \pm 4.3	15.9 \pm 2.7	15.4 \pm 3.4
No. of seeds seen in phase 1	6.9 \pm 0.8	6.7 \pm 1.0	7.1 \pm 0.6	7.1 \pm 0.4
Duration of phase 1 (min)	3.9 \pm 2.8	4.1 \pm 2.6	3.2 \pm 1.5	2.9 \pm 1.7
No. of holes visited in phase 2	21.1 \pm 6.6	17.9 \pm 3.2	19.3 \pm 4.6	16.7 \pm 2.4
No. of seeds seen in phase 2	4.5 \pm 1.3	3.3 \pm 1.2	3.9 \pm 1.3	3.9 \pm 1.1
Duration of phase 2 (min)	3.8 \pm 2.4	4.4 \pm 2.0	6.1 \pm 2.3	7.6 \pm 3.4
Retention interval (min)	127.6 \pm 16.5	124.4 \pm 13.7	127.9 \pm 21.4	121.8 \pm 16.5

EXPERIMENT 3

Differences between species in performance in experiments 1 and 2 could be due to factors other than differences in memory (Bitterman 1975; Macphail 1982). We have already considered the effect of differences in the number of sites visited and time taken to visit sites in phase 1. In this experiment we examine the effect of two factors that might be expected to influence motivation to search for food: reward size and level of deprivation. In experiments 1 and 2 we used the same reward size and deprivation for the two species. However, the weight of a great tit is almost twice that of a coal tit (19 g versus 10 g), so if reward size and deprivation level scales with body size it could be argued that the species experienced different levels of these factors in experiments 1 and 2. Metabolic rate of passerines increases approximately with $W^{0.73}$, where W = body mass (Schmidt-Nielsen 1984). Relative to its requirements, the reward of about 60 mg used in experiments 1 and 2 was therefore smaller for a great tit than for a coal tit. Similarly, because of its higher absolute requirement, a deprivation period of a fixed time would result in a greater deficit for the larger species, although here it could be argued that the picture is complicated by the amount of reserves carried as fat in relation to metabolic rate. In short, great tits may have performed less well because of interspecific differences in motivation. Therefore we investigated whether or not performance of great tits in the same set-up as experiment 2 would be influenced by reward size or level of deprivation.

Although it would be ideal to compare the two species across a range of values of these two factors, we analysed their effect only on the great tit in the complex window-shopping task. The logic of this is

that if (as it turns out) reward size and deprivation with the range tested have little effect on performance of one species, they are less likely to account for the differences between species.

Methods

Subjects

The subjects were four of the great tits used in experiment 2. This experiment was run after these four birds had completed experiment 2.

Procedure

The birds were maintained as described in experiment 1. This experiment was run to examine the effects of reward and deprivation on the birds' performance in the recovery phase of a trial. The layout of the experimental room was the same as in experiment 2 but the size of the pieces of peanut behind the windows was varied between treatments. The piece of peanut behind the window could be 'large' (average weight = 142 mg) or 'small' (average weight = 18 mg). Following phase 1 the birds were given either no peanut or four pieces of peanut (average weight = 38 mg each): these two conditions correspond to 'high' and 'low' deprivation, respectively. The experiment was designed as a factorial experiment with 5 days of each treatment to allow a test of the main effects of bird, deprivation and reward size as well as the interaction between them; however, the birds began to moult part way through the experiment and so the design was not completed. Therefore the analysis was done just for main effects. Four birds were each tested with three of the four conditions.

A summary of the data collected from this experiment is shown in Table II.

Results and Discussion

The angular transformed values of $P(v|s)$, $P(v|u)$ and $P(v|n)$ were calculated for the first 15 visits of each trial (in this case high and low preference sites were combined; Fig. 6). Paired t -tests were used to compare the performance of each bird in $P(v|s)$, $P(v|u)$ and $P(v|n)$ across the experimental conditions. There was no significant difference in either $P(v|s)$ or $P(v|u)$ across the four conditions. In one comparison, that of low deprivation/small reward and high deprivation/large reward, $P(v|n)$ differed significantly ($P < 0.05$): the value was higher in the former than in the latter treatment. The explanation of this effect is not clear and may be a chance result in a large number of comparisons. Thus, under the range of conditions studied here, two motivational variables, seed size and deprivation level, did not have a significant effect on the probability of returning to sites where a seed had been seen. This helps to support the view that the differences between coal tits and great tits observed in experiments 1 and 2 did not arise as a result of differences in motivation.

GENERAL DISCUSSION

The main results of our experiments are as follows. (1) Coal tits (a storing species) performed slightly better than great tits (a non-storer) in a spatial memory task in which the bird was required to return in phase 2 of a trial to the site where it had seen a seed 30 min earlier in phase 1 (experiment 1). (2) In a more complex task in which there were seven sites with seeds out of a total of 60 sites, and the retention interval was 2 h, there was a difference between the species in their discrimination of sites visited in phase 1 that did and did not contain a seed. (3) Motivational variables (reward size and deprivation) did not appear to have an effect on returning to seeded sites.

Relationship Between Window-shopping and Storing

In contrast to many previous comparative studies of memory and learning (see Introduction), in this study we have attempted to identify on the basis of the ecology of two species a particular difference in memory that could be predicted a priori. The experimental task was designed to incorporate some of the features of food-storing memory: a site is visited

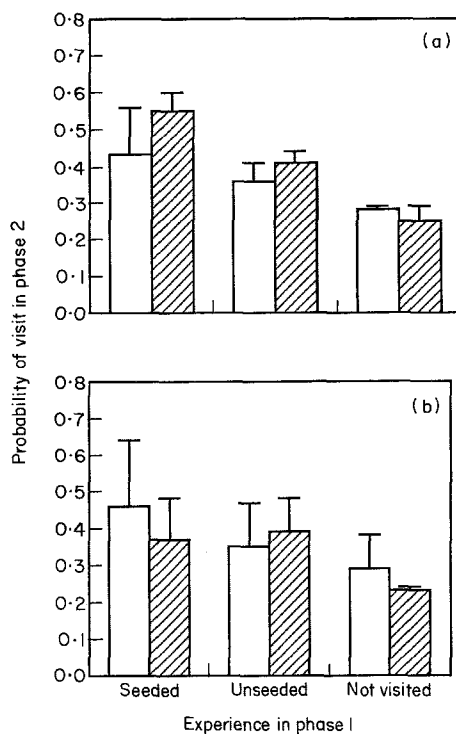


Figure 6. Experiment 3. The probability of visiting a site in phase 2 in relation to experience of that site in phase 1 for (a) low deprivation and (b) high deprivation conditions and different reward sizes (means of individual bird means \pm SE). \square : Small reward; ▨ : large reward.

once and food is placed in it, some aspect of the site is memorized during this single visit, and the bird returns to the site once some time later to collect its hoard. The main difference between storing and window-shopping is that in the latter case the bird does not place the food in the site itself; the similarities include the fact that memory is based on a single trial and that it is in some sense spatial.

However, the differences we have observed between a storing and a non-storing species are small. This could be because there are in fact only small or subtle differences, or because the task we studied did not reveal the differences. In this context it is worth noting that although window-shopping resembles food-storing in the ways outlined above, as previously shown (Shettleworth & Krebs 1986), food-storing tits do not perform as well in remembering the locations of window-shopped food as they do with stored food. This difference appears to be attributable to the presence of the window rather than to the fact that the seeds

are encountered and not stored, since without the window, performance does not differ between storing and encountering seeds at least at retention intervals of 2 h (Shettleworth & Krebs 1986; Shettleworth et al., in press). This suggests that the current experiments do not reveal the full spatial memory capacity of the food-storer. Therefore it could be that the very small differences we have observed would be amplified if the storers were tested in a task that reveals their full memory capacity.

Alternative Interpretations

In experiment 3 and in the comparisons summarized in Table I, we considered whether factors other than differences in memory might account for the differences in performance in experiments 1 and 2. Here we consider other possible interpretations. One possibility is that great tits are more thwarted than coal tits by observing a seed behind a window. If differences in tendency to visit a site with a seed in phase 2 reflect differences in motivation rather than differences in memory, then the balance of positive reinforcement (the seed) and negative reinforcement (the window) could be different for the two species. Whilst this might account for a lower value of $P(v|s)$ in great tits, it does not readily account for the difference between the species in their discrimination of unseeded and non-visited sites in experiment 2 (great tits discriminate less well than coal tits).

A second possibility is that the difference between the species is not a result of memory but a result of perceptual discrimination. Coal tits might inspect sites they visit during phase 1 more thoroughly than do great tits (this might be a tendency that is deployed normally during storing food) and therefore have more cues with which to discriminate seeded and unseeded sites in phase 2. The data from the present experiments cannot distinguish this possibility from the interpretation that the difference is one of memory.

Comparisons Based on Other Memory Tasks

Hilton (summarized in Krebs, in press; Krebs et al., in press) compared the spatial memory of storing and non-storing tits in two tasks. In an analogue of the radial maze developed by Olton & Samuelson (1976), non-storing blue tits, *P. caeruleus*, and great tits performed with greater accuracy than storers (coal tits and marsh tits, *P. palustris*) at

a retention interval of 30 s between forced and free choice, but the former showed a steeper decline in performance with increasing retention interval, suggesting that in this task storers have a more persistent memory. In another comparison of the same four species on a simple spatial discrimination (the birds were trained over a series of trials to go to six out of 64 sites), the storing species tended to do worse than the non-storers. Thus there is no consistent pattern of storing species performing better than non-storers across a range of memory tasks. Further work is necessary to define the conditions under which storers do better (Balda & Kamil 1989, Krebs, in press; Krebs et al., in press).

It should also be apparent that although we have referred to the differences observed in experiments 1 and 2 as being associated with food-storing, this conclusion is based on only one pair of species, a storer and a non-storer. Therefore, before concluding that the small differences we observed here are related to storing, we need to collect data on other storing and non-storing species.

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