Spatial accuracy in food-storing and nonstoring birds

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We compared the ability of coal tits, *Parus ater* (a food-storing species), great tits, *P. major*, and blue tits, *P. caeruleus* (two nonstoring species) to remember spatial locations in a spatial delayed-matching-to-sample task. Presentation of a single sample image on a touch screen was followed by a choice phase containing two, three or four images, in which the bird had to choose the original image. Storers made more correct choices than did nonstorers. Performance was affected by the proximity of the distractors: both groups performed less well when distractors were close to the sample although storers were less affected by proximity of distractors than were nonstorers. Both groups made correct decisions sooner than errors. We conclude that the accuracy of spatial memory in food-storing birds is greater than that of nonstorers.

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Many animals store food and recover it at a later time. Food-storing tit species scatter-hoard their food and appear to remember the locations of their caches (Cowie et al. 1981; Shettleworth & Krebs 1982; Sherry 1984). A capacious, long-lasting and organized spatial memory for these caches would seem necessary for efficient retrieval, while closely related nonstoring species would appear not to require such a highly specialized spatial memory.

There is now accumulating evidence that food-storing birds do possess advantages in their learning and spatial memory abilities over those of nonstoring birds. Olson (1991), for example, found that Clark's nutcrackers, *Nucifraga columbiana*, an extensive storer, outperformed both scrub jays, *Aphelocoma coerulescens*, an occasional storer, and pigeons, *Columba livia*, on an operant spatial delayed-nonmatch-to-sample procedure (DNMTS) as retention interval increased. In another DNMTS experiment by Olson (1991), birds had to respond to one, two or three images presented sequentially on a touch screen before making a choice between one of these images and another presented in a new location on the screen. Nutcrackers also outperformed the scrub jays and pigeons in this memory load task. In food-finding tasks, storers appear better able than nonstorers to discriminate between sites that had been seen to contain food and those that had been depleted (Krebs et al. 1990). There is evidence that food-storing birds are less affected than nonstorers by proactive interference. Clayton & Krebs (1994a) tested the ability of food-storing birds (marsh tits, *Parus palustris*, and jays, *Garrulus glandarius*) and

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nonstoring birds (blue tits, *P. caeruleus* and jackdaws, *Corvus monedula*) to return to locations where they had previously found food. The birds found the food equally well, but nonstorers were more likely than storers to return to locations that they had visited in the initial search phase, whether or not those locations contained food. Not only do storers appear to outperform nonstorers in various measures on spatial tasks, but they appear to attend to spatial cues in preference to colour/pattern cues in food relocation tasks, a preference not shown by nonstorers (Brodbeck 1994; Clayton & Krebs 1994b; but see Hurly & Healy 1996; Strasser & Bingman 1996; Vallortigara 1996). In addition, food-storing songbirds have a relatively larger hippocampus than do closely related nonstorers (Krebs et al. 1989; Sherry et al. 1989). Evidence from lesion studies has shown that an intact hippocampus is necessary for accurate retrieval of caches and for functioning spatial memory (e.g. Sherry & Vaccarino 1989; Hampton & Shettleworth 1996). Although storers appear to outperform nonstorers on spatial tasks, they do not outperform nonstorers on nonspatial tasks (e.g. Olson et al. 1995; Hampton & Shettleworth 1996).

Our aim in this experiment was to test whether food-storing birds have additional spatial memory advantages over closely related nonstorers. One way, in particular, in which the memory of food-storing birds may be specialized is the accuracy with which they remember the locations of their caches. Food caches are widely dispersed in discrete locations and marsh tits (food storers) are able to recover their own caches more reliably than hidden food placed only centimetres away (Cowie et al. 1981). Cowie et al. concluded that this accurate recovery
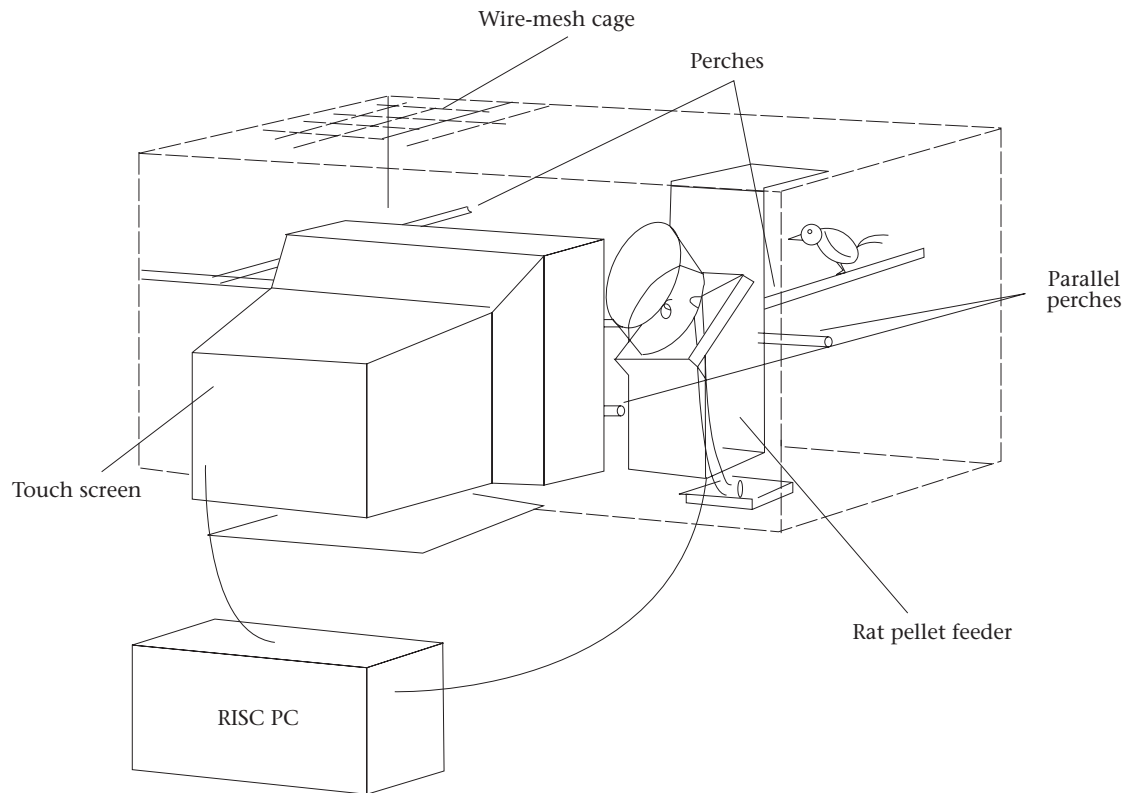
Figure 1. Apparatus, showing wire-mesh cage, touch screen, rat pellet feeder and perches.

was achieved either by memory for caches or by the marsh tits' preference for specific kinds of sites. In Cowie et al.'s experiment, in addition to the cache, food was hidden in sites at two distances from the original cache site: 'near' sites at 10 cm and 'far' sites at 100 cm. Birds were significantly more likely to remove their caches than the experimental seeds hidden 100 cm away but were almost as likely to find those hidden at 10 cm. However, as the cached seed nearly always disappeared first, it appeared that the birds were indeed accurate in remembering cache sites and subsequently found the extra seeds only by chance or by searching more carefully nearby.

To determine whether storers have a more accurate spatial memory than nonstorers, we carried out the following experiment. We used an operant delayed-match-to-sample procedure (DMTS) in which the birds (a food-storing species (coal tits) and two nonstoring species (blue tits and great tits, *P. major*)) were required to peck at an image in one of 20 locations on a touch screen. After a delay the birds had to choose the image in the original location, rather than images in distractor locations, in order to be rewarded. In some trials the distractor(s) was adjacent to the sample, and in others it was 'far' from the correct image. If a bird could remember the location of the sample image accurately it would be less likely to make errors to similar images, irrespective of their proximity or number. However, if accuracy of memory is limited, then birds should make more errors in those trials in which the distractor(s) is close to the sample image, than in those in which it is further away. We predicted that food storers would be more accurate in their choices than nonstorers.

METHODS

Subjects

We tested five storers (coal tits) and six nonstorers (three great tits, three blue tits). One coal tit and one great tit had previous experimental experience in a DNMTS task; the other birds were experimentally naïve. The birds were housed individually in cages (77 × 44 cm and 44 cm high) made of wire mesh with two parallel wooden perches running from the front to the back of the cage (Fig. 1) and were maintained on a 13.5:10.5 h light:dark cycle at 14–18°C (mean 16°C). They had access to water ad libitum and were fed a mixture of Orlux (commercial insectivorous bird food mix), a vitamin supplement, and peanuts, pine nut kernels, sunflower seeds and wax-moth, *Galleria mellonella*, larvae. On experimental days all birds had food removed at 0900 hours and fresh food returned at the end of an experimental session. Birds were tested for one session per day. Sessions began at 1000 hours and finished by 1900 hours. Since not all birds could be run simultaneously, those that were tested later in the day were fed small amounts of food until their session began. The maximum time that birds were without food was 3.5 h.

The birds were caught on private land, using mist nets held and used under BTO ringing permits, and were taken

and kept under an English Nature licence and Home Office licence. They were kept in captivity for different amounts of time but for at least 2 weeks before training began. For the first week, birds were fed an excess of food, before the diet was brought down to the same level as that of the other captive birds. Two birds, caught in June 1994, were released to the woodland in which they were caught in September 1996. Two others, caught in February 1997, were released in March 1999. One bird, caught in March 1996, died in captivity in May 1997. The other birds, caught in March 1996 or February 1997 are still in captivity, having been used in other experiments. Handling was kept to a minimum but all birds were caught every 2 months and were checked for moult and subcutaneous fat. Moult occurred normally and the birds were in good condition when released (fat levels in the tracheal pit were high and pectoral muscle was well developed). Our own capture/recapture data suggest good survival rates in released birds.

Apparatus

Images were generated on Intasolve touch screens using Arachnid software (Paul Fray Ltd, Cambridge, U.K.) running on Acorn RISC O/S computers. The computers were placed centrally in the room and the touch screens were mounted on movable trolleys which could be placed in front of any bird's cage. A sliding door in the front of each cage allowed the touch screen to be slotted into the cage wall. A removable standard rat pellet dispenser with a delivery tube to a tray in the bird's cage was attached to the front of the cage to one side of the touch screen. Two perches, 14 and 24 cm above the cage floor, positioned in front of the touch screen inside the cage, allowed all birds access to all the locations on the touch screen (see Fig. 1).

Protocol

We trained the birds to peck the touch screen by using a shaping procedure. Previous experience has shown that tits do not autoshape, so initially we taped a single wax-moth larva to the screen over a training image (a white square). In pecking at the larva the birds caused the white square to disappear and food (a small piece of peanut) to be delivered. We reduced the size of the larva until the birds pecked at the white square alone to gain the food reward. When the birds pecked at images in all possible locations for 3 consecutive days, training began on the spatial memory task.

The birds were trained in a DMTS task in which they were presented with a single white square (2×2 cm, the sample), in any one of 20 possible locations, in a 5×4 array, which they were required to peck at to gain a food reward. The screen measured 26.5×19.5 cm, and adjacent stimuli were separated by 3.5 cm horizontally and by 3 cm vertically. The locations of stimuli were generated randomly. The birds had to move away from the touch screen to collect the food. From pilot data we determined that the birds did not move back to the touch screen to eat the food; therefore they were not using body position

information to make choices. After a retention interval (RI) of 30 s, two visually identical images appeared, one in the original location and the other in one of the 19 remaining locations. To gain further reward the bird had to peck at the image in the original location (the choice phase). The stimuli extinguished only once the birds responded with a peck to one of them. An intertrial interval (ITI) of 80 s followed. RI and ITI were not visually discriminable since the screens were then blank. Training sessions were 20 trials long and there was one training session per day. The criterion for acquisition was either a mean performance of 75% correct over 5 days or, if the birds had not acquired the task after 40 days of training, 65% correct over 10 days. Once a bird reached one of the acquisition criteria it began the experiment.

For the experiment there were three session types consisting of the presentation of a single sample (as in training) but with one, two or three distractors in the choice phase (Fig. 2). Birds were each given a session of 15 trials per day. In any one session, trials contained the same number of distractors in the choice phase. The session type (number of distractors) alternated between days (order=2, 1, 3, 2, 1, 3 . . .). Birds were presented with 225 trials in each session type.

The mean proportion of correct choices for one, two and three distractor trials for each species were arcsine-square root transformed before analysis. This transformation is used to normalize proportion-correct data (Kirk 1995).

RESULTS

A two-way, mixed ANOVA on proportion-correct data (blue tits/great tits, session type) revealed no differences between the two species ($F_{1,4}=0.674$, $P=0.458$) so we combined the data from these species in the group 'nonstorers' in the remainder of the analyses.

Trials to Criterion

There was no difference between storers and nonstorers in the number of days taken to reach criterion (one-factor ANOVA: $F_{1,9}<1$, $P=0.498$). The mean time to criterion for storers $\pm$ SE was 51.6 ± 6.6 days (range 39–76 days) and for nonstorers 62.2 ± 12.4 days (range 26–114 days). Two of the storers reached the 75% criterion and three reached the 65% criterion. One nonstorer reached the 75% criterion and five reached the 65% criterion. Of the experienced birds, the coal tit reached the 75% criterion after 41 days and the great tit reached the 65% criterion after 62 days.

Performance

A mixed ANOVA (storers/nonstorers, session type) showed a marginally significant trend for storers to outperform nonstorers in the number of correct choices made ($F_{1,9}=5.044$, $P=0.051$). The number of correct choices decreased as the number of distractors increased
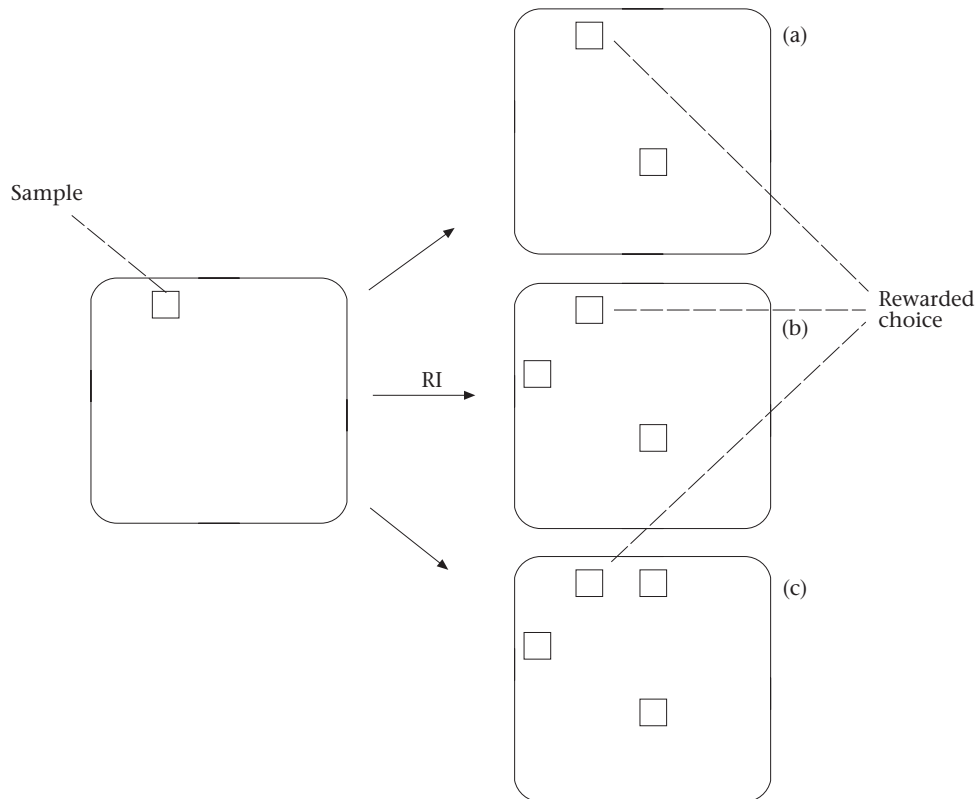
Figure 2. Schematic representation of the DMTS task. In the first phase of trials in all session types the birds were required to peck at a single sample image. After an RI of 30 s one of three choice types appeared: (a) the sample with one distractor image; (b) the sample with two distractor images; or (c) the sample with three distractor images. Responses to the image in the sample location were rewarded.

($F_{2,18}$=81.660, P<0.001; see Fig. 3a). There was no interaction between the main effects ($F_{2,18}$<1, P=0.640).

However, since the chance levels differed in each of the three treatments, the proportion correct is invalid as a performance score when comparing across session types. To make a valid comparison we equated the scores by transforming proportion-correct data into a sensitivity measurement (d'), the sensitivity to discriminate target and distractor locations, using signal detection theory (Macmillan & Creelman 1991). A direct comparison across the three session types using these sensitivity data (two-way, mixed ANOVA) revealed no significant difference between storers and nonstorers, but with a marginally significant trend for storers to outperform nonstorers ($F_{1,9}$=4.854, P=0.055). There was no change in performance as the number of distractors increased ($F_{2,18}$=3.069, P=0.071; see Fig. 3b) and there was no interaction between the main effects ($F_{2,18}$<1, P=0.719). If task difficulty increased with increasing numbers of distractors then we would expect the ability to discriminate between sample and distractor images (sensitivity) to decrease across session types. This was not the case.

Proximity of Distractors

Since the locations of the distractors occurred randomly, in some trials distractors were adjacent to the sample image, while in others they were all further away. We split the data into trials in which there was at least

one near distractor in the choice (3.0–4.5 cm from the sample, edge–edge) and trials in which all the distractors were further away (8.2–23.7 cm from the sample, edge–edge). There were different numbers of near and distant distractor trials occurring in each session type since the locations of the distractors were determined randomly. Therefore, there were proportionately more distant distractor trials in the one distractor session type (since the probability of only one distractor occurring near the sample is relatively low) and proportionately more near distractor trials in the three distractor session type (since the probability of at least one of the three distractors occurring near the sample is relatively high). Once these data were split into trials in which the distractors were either near to or far from the sample, the means derived contained different numbers of near and distant trials depending on the session type and even on an individual bird's trials. We used a three-way, mixed ANOVA (storers/nonstorers, session type, near/distant distractors) to examine the effect of proximity on performance. Overall, the main effects were accentuated: storers performed significantly better than nonstorers ($F_{1,9}$=6.760, P=0.029) and there was a significant increase in sensitivity across session types ($F_{2,18}$=8.148, P=0.003). What is more important to note here, however, is that the presence of a near distractor had a significant effect on the ability of both groups to make a correct choice when compared with performance in only distant distractor trials (Fig. 4; $F_{1,9}$=66.770, P<0.0001). Both groups were more likely to
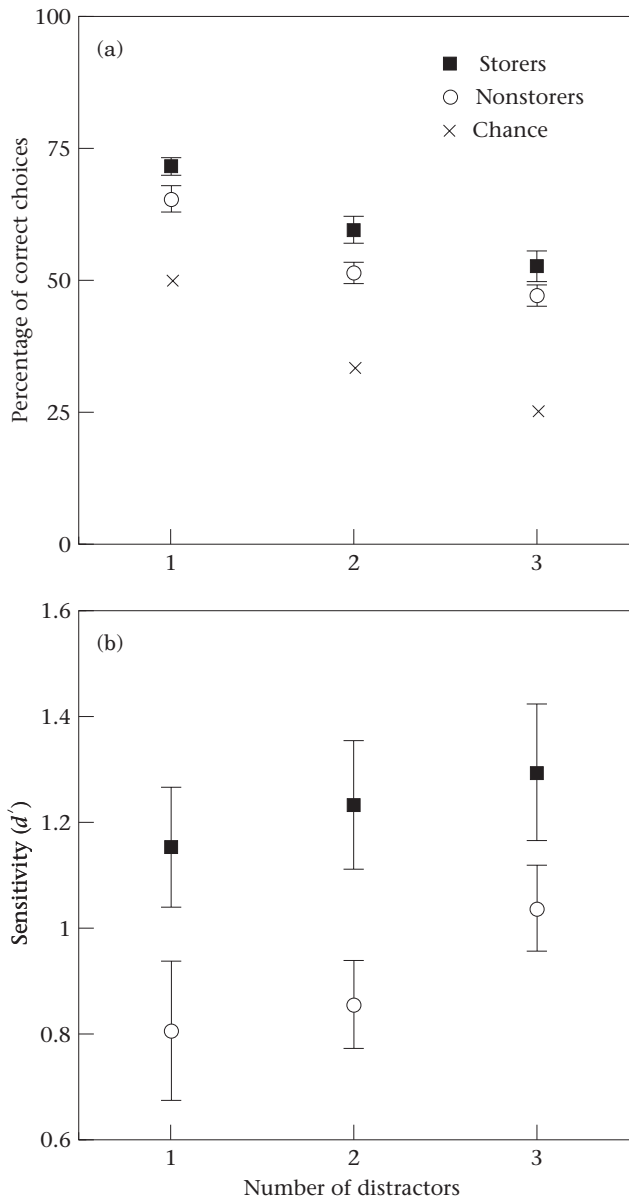
Figure 3. (a) Mean percentage of correct choices ±SE made by storers and nonstorers in each session type (one, two or three distractors). Chance levels are shown. (b) Discrimination sensitivity ±SE for storers and nonstorers in each session type.

Figure 4. Discrimination sensitivity ±SE of storers and nonstorers in trials with at least one near distractor, or with all distractors distant. Performance in each session type is shown (one, two or three distractors).

make an error if the distractor was close to the sample. The only significant interaction was between session type and the proximity of distractors ($F_{2,18}$=4.435, P=0.027; all other Fs<2.196, NS). While all sensitivities were roughly equal across session types in near distractor trials, in distant distractor trials, sensitivity was highest with three distractors and lowest with one. We investigated this significant interaction between performance across session types and the proximity of distractors, with two-way mixed ANOVAs (storers/nonstorers, session type) for near and distant distractor trials alone. In near distractor trials we found there was no change in sensitivity across session types ($F_{2,18}$=1.096, P=0.356) There was no significant difference between storers and nonstorers in their
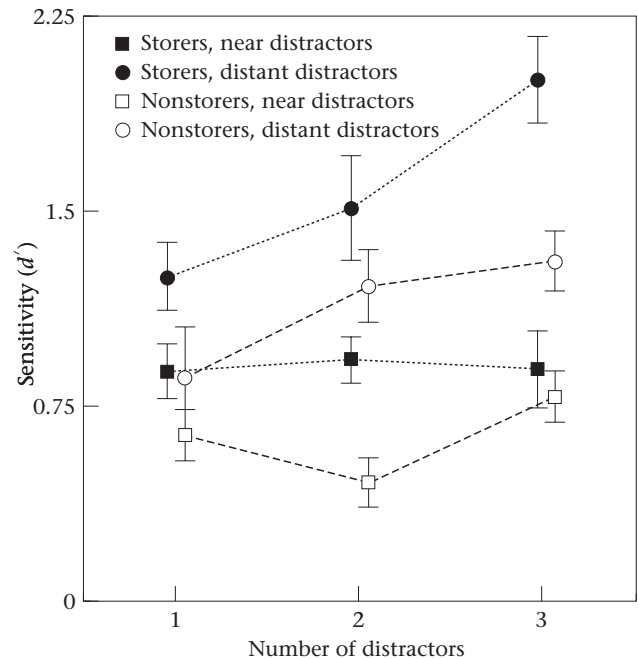
ability to choose the correct image, although there was a marginally significant trend for storers to outperform nonstorers ($F_{1,9}$=4.891, P=0.054), and no interaction between the main effects ($F_{2,18}$=1.804, P=0.193). Making the same comparison (two-way mixed ANOVA, storers/nonstorers, session type) with only distant distractor trials revealed that sensitivity increased across session types ($F_{2,18}$=8.374, P=0.003), and also that storers performed significantly better than nonstorers ($F_{1,9}$=6.059, P=0.036). There was no interaction between the main effects ($F_{2,18}$<1, P=0.392).

Latency to Peck

Although the ITI and RI were fixed between and within trials, during the sample and choice phases the birds were free to choose how long they took before responding to the stimuli. Data for response times were right skewed (the majority of response times were short while some were very long) and data for each bird were log transformed to normalize them. Using a three-way mixed ANOVA (storers/nonstorers, session type, correct/incorrect choice) we found that shorter latencies to peck after the RI (i.e. when a response to the choice was required) were associated with subsequent correct choices, and that longer latencies were associated with subsequent incorrect choices (Fig. 5; $F_{1,9}$=90.624, P<0.0001). There was no significant difference in the time taken by storers to respond to the choice compared with nonstorers, although there was a marginally significant trend for response times by storers to be longer than response times for nonstorers ($F_{1,9}$=5.087, P=0.051). The
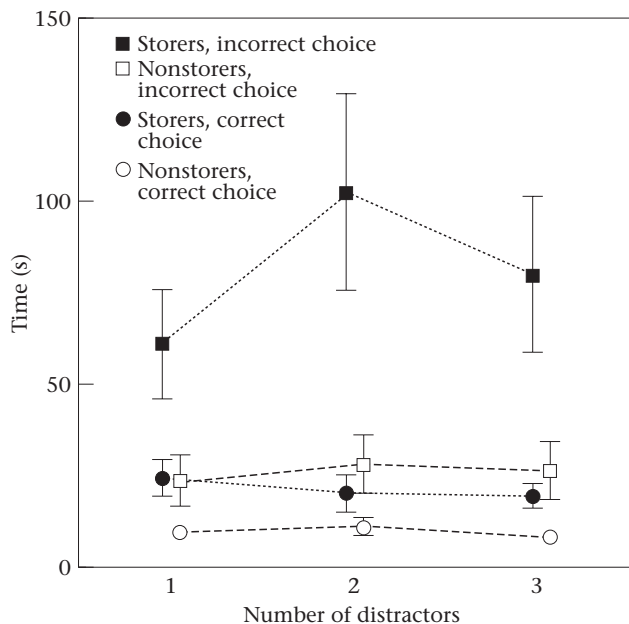
Figure 5. Mean times (antilog seconds) ±SE from the onset of the choice to the birds' response. Response times by storers and nonstorers in correct and incorrect trials are shown.

number of distractors appeared to have no effect on the time the birds took to make a choice ($F_{2,18}=0.288$, $P=0.753$). No interactions were significant ($Fs<4.31$, NS).

Shorter response times to the initial, sample image were associated with subsequent correct choices (in the later choice phase: $F_{1,9}=77.473$, $P<0.0001$). There was no difference between storers and nonstorers in response times ($F_{1,9}<1$, $P=0.944$). There was, however, a significant effect of the number of distractors in the subsequent choice ($F_{2,18}=5.709$, $P=0.012$). Although there was only one image in the sample phase, the birds responded more quickly in sessions with more distractors in the choice phase. None of the interactions between the main effects was significant ($Fs<1$, NS). It is not clear whether these effects are due to variation in motivation.

DISCUSSION

The results of this experiment are: (1) in a spatial DMTS task both storing and nonstoring tits performed better than chance after a retention interval of 30 s; (2) there was a trend for storers to outperform nonstorers; (3) performance did not change with increasing numbers of distractors; (4) the proximity of a distractor affected the performance of all birds, that is, the closer a distractor, the more errors the birds made; (5) the performance of storers was less affected by the proximity of distractors than that of nonstorers; and (6) all birds made correct choices more rapidly than they made errors.

Our results support our predictions that performance by the storers would be better than that of nonstorers and that storers would be less affected by the proximity of the distractor image(s), although the storers' superior performance over nonstorers just failed to reach significance.

This could be accounted for by the small sample sizes involved. Both groups made more errors when at least one distractor was near but there was a clear trend for storers to outperform nonstorers even in the near distractor trials. The limited field experiments, and more extensive field and laboratory observations, that have been carried out with food-storing animals have shown that cache recovery in a range of species is very accurate (e.g. Swanberg 1951; D. W. MacDonald 1976; Tomback 1980; Cowie et al. 1981; Stevens & Krebs 1986; Balda & Kamil 1989; I. M. V. MacDonald 1997). Whether this is due to accurate memory or to preference for specific types of cache site has not been fully established, although D. W. MacDonald's (1976) and I. M. V. MacDonald's (1997) observations would support the former. Hertz (1928) found that the proximity of distracting information affected jays in the same way as the proximity of the distractors in this experiment affected our birds. However, Hertz did not compare storers and nonstorers. Our results suggest that the spatial accuracy of the memory of food-storing tits is greater than that of the nonstorers. The storers' recall after a delay of 30 s appears to allow them to discriminate more accurately than the nonstorers between the sample and alternative locations, even though the difference was less conspicuous when the alternative location was as close as 3 cm (possibly a floor effect). Our results, although gained in a situation very different from that faced by a retrieving storer in the field, support the hypothesis that food-storing birds have a spatially accurate memory, which, in turn, supports the hypothesis that cache recovery in the field is based, at least in part, upon accurate memory for the locations of stored food. However, we are not able to determine whether the mechanism of this accurate recall is from storers encoding their memories more accurately than nonstorers, or because they lose accuracy at a slower rate than nonstorers (i.e. the rate of forgetting is slower in storers).

We also found that performance was not adversely affected by extra distractors in the choice phase. One possibility for successful retrieval in the field is that storers simply look in certain/preferred kinds of places. Although we did not present our birds with 'preferred' alternatives, our distractors were visually the same as the correct image, differing only in their location. And yet the visual similarity of the stimuli appears to have affected the birds' choice hardly at all. That food storers pay much more attention to spatial cues than to visual features is well documented: black-capped chickadees, *Poecile atricapillus*, jays and marsh tits all prefer to use spatial cues than visual features (Brodbeck 1994; Clayton & Krebs 1994b; Brodbeck & Shettleworth 1995). Nonstorers, on the other hand, appear to use both kinds of cue for returning to food locations. Not only did we then make this task more difficult for the nonstorers by forcing them to use spatial cues, we also presented them with a number of visually similar alternatives. However, while these may have contributed to error making by the nonstorers, this interpretation seems less likely as performance of both storers and nonstorers did not decline with an increasing number of distractors (Fig. 3b).

It is not possible to determine from this experiment whether the storers' greater ability to discriminate accurately between locations is due to their ability to encode spatial memories more precisely, or whether they are simply better able to retrieve the same memories as non-storers after a 30-s delay. In other words, is the spatial memory of storers encoded in greater resolution than that of nonstorers, as an adaptation to reduce memory interference, or is the resolution the same in storers and nonstorers but storers can remember for longer (and therefore retrieve the memory more accurately) than nonstorers? A number of noncomparative studies have examined accuracy in spatial navigation tasks, in which animals have to find hidden goals with respect to a landmark array (e.g. Spetch et al. 1992; Spetch & Mondloch 1993; Gould-Beierle & Kamil 1996). However, only a few have presented quantitative data on accuracy (Cheng 1990; Kamil & Jones 1997; Tommasi et al. 1997). Whether food-storing birds, at given landmark–goal distances, would show less error in searching than closely related nonstorers has yet to be tested. Such a comparison would enable us to determine whether food-storing birds do indeed encode their memory for space more precisely than do nonstorers. Although spatial discrimination tasks such as the one we used differ from spatial navigation tasks, we found that spatial accuracy is better in food-storers than it is in nonstorers. A comparative spatial navigation task between storers and nonstorers may enable us to determine more definitively whether this is the case.

Acknowledgments

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