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Memory for what, where, and when in the black-capped chickadee (*Poecile atricapillus*)

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Abstract Episodic memory is the ability to remember personally experienced past events (Tulving in Organization of memory. Academic Press, San Diego, pp. 381–403, 1972). In non-human animals, the behavioural criterion for episodic-like memory is remembering "what" occurred in conjunction with "when" and "where" (Clayton and Dickinson in Nature 395:272–274, 1998). We conducted tests for "what, where, and when" memory in a food-storing bird, the black-capped chickadee (*Poecile atricapillus*). In Experiment 1, chickadees found sunflower seeds and mealworms in concealed sites in their home cage. Birds later revisited these sites after either a short (3 h) or long (123 h) retention interval. Chickadees normally prefer mealworms, but at the long retention interval mealworms were degraded in taste and appearance. Chickadees showed some memory for what kind of food they had encountered and where, but no memory for when food had previously been found. Experiment 2 followed a similar procedure, except that chickadees searched for hidden sunflower seeds and mealworms in trees in an indoor aviary. These more natural conditions increased both the spatial scale of the task and the effort required to find food. In this experiment, birds showed evidence for all three components of what–where–when memory. Unlike some previous studies of episodic-like memory, birds' behaviour cannot be accounted for by differential memory strength for more recent events. The results show that memory for what, where, and when occurs in food-storing birds outside the corvid family, does not require food caching or retrieval, and that remembering "when" can depend on the nature of the task.

Keywords Episodic-like memory · Black-capped chickadee · Food storing · Caching · Hoarding

Introduction

The ability to remember personally experienced events was given the name episodic memory by Tulving (1972). More specifically, episodic memory refers to human autonoetic consciousness for personal past events remembered with details about what, where, and when they happened (Tulving 1985, 2002). Although Tulving (1983) argued that episodic memory was unique to humans, recent research has led to debate over whether or not animals have episodic memory. Positions have varied from the view that animals are "stuck in time" and experience a continuous present (Roberts 2002; Suddendorf and Corballis 1997, 2007) to the view that behavioural criteria are sufficient to identify episodic-like memory for past events in non-human animals (Clayton and Dickinson 1998; de Kort et al. 2005; Roberts 2006). There have been experimental tests of episodic-like memory in scrub jays (Clayton and Dickinson 1998, 1999; Clayton et al. 2001), magpies (Zinkivskay et al. 2009), pigeons (Skov-Rackette et al. 2006; Zentall et al. 2001, 2008), rats (Bird et al. 2003; Babb and Crystal 2005; Kart-Teke et al. 2006; Naqshbandi et al. 2007), mice (Dere et al. 2005a, b), meadow voles (Ferkin et al. 2008), gorillas (Schwartz et al. 2005), rhesus monkeys (Hampton et al. 2005; Hoffman et al. 2009), and Yucatan minipigs (Kouwenberg et al. 2009) with a range of results, some supporting and others refuting the idea that animals possess episodic or episodic-like memory. Episodic-like memory in

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animals is one aspect of the broader question of whether animals are capable of mental time travel, the ability to retrospect on past experience and to plan prospectively for the future (Busby and Suddendorf 2005; Suddendorf and Corballis 2007).

Clayton and Dickinson (1998) first reported that scrub jays (*Aphelocoma coerulescens*) possess episodic-like memory. In order to test non-verbal animals, Clayton and Dickinson identified three behavioural criteria in Tulving's (1972) definition of episodic memory. Tulving initially stated that episodic memory can be characterized as memory for a personally experienced past event—*what*—along with *where* and *when* the event occurred. In order to conclude that episodic memory had been observed, birds were required to demonstrate memory for the details of "what" had occurred, "where" it had taken place, and "when" in the past it had occurred. Scrub jays are food-storing corvids that cache both perishable and non-perishable food. Clayton and Dickinson (1998, 1999) allowed scrub jays to cache preferred but perishable wax worms and less preferred non-perishable peanuts in different locations in a sand-filled ice-cube tray. Memory was tested by presenting the jays with this tray again either 4 or 124 h after a caching episode. Peanuts were fresh after both delays, whereas mealworms were fresh after 4 h but degraded after124 h. In later trials, when the jays were re-exposed to the caching tray 4 h after caching worms, they searched at the worm locations before searching at the peanut locations. Conversely, if worms had been stored 124-h earlier, the jays visited peanut cache sites before worm sites. The differential search patterns after the two delays suggested the jays had learned about the change in palatability of the two foods over time and could recall not only where food of each type was located but also when the caching episode had taken place. Because only behavioural criteria were met, with no evidence of the autonoetic or conscious components of episodic memory possible in a scrub jay, this ability was called *episodic-like memory* (Clayton and Dickinson 1998). These birds have subsequently demonstrated quite sophisticated caching strategies, which take into account social aspects of caching events (Dally et al. 2005, 2006), and extend into the future as well (Correia et al. 2007).

As Zentall et al. (2001) pointed out, memory for what, where, and when is neither necessary nor sufficient evidence for episodic memory. Humans can have vivid episodic memory of an event with no memory for when and imperfect recall of where. We can, conversely, have accurate memory for the what, where, and when of events we did not personally experience, like the battle of Agincourt in 1415. The relation, if any, between memory for what, where, and when, in animals and episodic memory in humans remains unclear (see Roberts and Feeney 2009, for review). Whether animals can simultaneously recall the

"what", "where", and "when" of events, and if so, how, is nevertheless an important question in animal cognition. Consequently, we will not use the label, "episodic-like memory", but instead refer to the phenomenon as WWW memory.

Initial attempts to find WWW memory in animals using designs similar to that of Clayton and Dickinson (1998) were not successful. Tests with rats (Bird et al. 2003) and rhesus monkeys (Hampton et al. 2005) showed no evidence of WWW memory. Babb and Crystal (2005), however, devised a two-phase procedure using the radial-arm maze that did provide evidence for WWW memory in rats. In the first phase, rats visited four randomly chosen arms, three of which contained less preferred standard reward pellets and one of which contained a preferred chocolate reward. After either a 30-min or 4-h delay, rats were returned to the maze for a second phase in which all eight arms were available. After the short delay, the four arms that did not provide food during the first phase contained reward pellets. The previously baited arms, including the arm containing chocolate, were not replenished. Conditions after a long delay were identical except that the arm containing chocolate in Phase 1 was replenished with fresh chocolate. Rats made more visits and earlier visits to this arm after the long delay than after the short delay, suggesting they remembered what, where, and when for the previously encountered chocolate reward. Further results indicated that rats could use WWW memory in a flexible manner (Babb and Crystal 2005). When chocolate was paired with lithium chloride after rats had visited an arm containing chocolate, they subsequently showed a reduction in revisits to the chocolate location. The change in appetite for chocolate from preference to aversion caused rats to reduce visits to the location where chocolate had last been found. These results suggest that rats, like scrub jays, possess memory for the what, where, and when details of events. Naqshbandi et al. (2007) repeated Babb and Crystal's (2005) study but fixed the time of day at which the memory test occurred. Their results confirmed Babb and Crystal's (2005) findings and showed that circadian time of day was not the cue used by rats to solve the task, supporting the conclusion that rats possess WWW memory.

Using another food-storing corvid, the magpie (*Pica pica*), Zinkivskay et al. (2009) examined WWW memory for food items that differed in only a single property and not in food type. Previous tests of WWW memory used two types of food, a preferred food which degrades and a less preferred food which is always fresh. This means that animals only needed to learn about one food type (for example, the preferred food) and track the state of this food at different delays in order to behave appropriately at testing. In Zinkivskay et al.'s study, magpies were first given a caching phase in which they were allowed to store food

pellets in a substrate of wood shavings. The pellets consisted of scrambled egg and were dyed either red or blue. After either a short (4-h) or long (124-h) retention interval, magpies could retrieve previously stored pellets. The important manipulation for testing memory for what, where, and when was that pellets of one colour were replaced with inedible beads of the same colour, while pellets of the alternate colour were replaced with pellets containing fresh food. The inverse replacement occurred after the alternative retention interval. Magpies retrieved a larger proportion of edible compared to inedible items during test phases, indicating the birds had remembered what, where, and when for both foods even though the foods differed only in colour.

Scrub jays, magpies, and rats all store food and WWW memory in these animals may be a specialized ability that is useful to animals that cache and retrieve a variety of foods. Animals that cache different kinds of food and recover their caches at varying intervals may learn the perishability of these foods and remember when or how long ago they were cached. Foods that are likely to be degraded can be avoided, while those that are not can be recovered. If caching and recovering food at varying retention intervals favours WWW memory, we would expect to find WWW memory in birds unrelated to scrub jays and magpies that also cache and recover food. Black-capped chickadees cache a variety of foods in the wild and use spatial memory to retrieve their stored food at varying intervals after caching (Hitchcock and Sherry 1990; Sherry and Hoshooley 2007). In the present experiments we also examined whether caching behaviour is required for the formation of WWW memories in birds.

Experiment 1

Chickadees store both perishable insects and non-perishable seeds and remember the spatial locations of caches of different types of food, that is, "what" and "where" (Sherry 1984). Field experiments with close relatives of chickadees, marsh tits (*Poecile palustris*) and willow tits (*Poecile montanus*) show that food-storing parids retrieve their stored food anywhere from several hours to 50 days or more after storing it (Cowie et al. 1981; Brodin and Ekman 1994). In captivity, black-capped chickadees show good spatial memory for multiple locations (Crystal and Shettleworth 1994), and can remember the locations of caches for at least 28 days (Hitchcock and Sherry 1990). In the present study we test whether chickadees can remember food they have previously encountered but have not stored themselves, a task that allows comparison with non-storing animals. Tests specifically examined whether the birds could remember what, where and when about the food they had found.

Methods

Subjects

Subjects were six wild-caught experimentally naïve adult black-capped chickadees (*Poecile atricapillus*; see Smith 1993, for a detailed description of black-capped chickadees). Black-capped chickadees are sexually monomorphic, and we had no reason to expect that males and females would perform differently, so sex of the birds was not established through invasive means. Birds were captured in London and Elginfield, Ontario in October 2005. Chickadees are sedentary, year-round residents, forming flocks in the winter and mating pairs in the spring and summer. All birds used in this experiment were tested after hatch year, and so were at least 1 year old. The birds were maintained on a diet consisting of Mazuri® Diet (PMI Nutrition International LLC, Brentwood, MO, USA) mixed with raw hulled sunflower seeds and peanuts that was freely available in the home cage except for the 3.5 h prior to testing. These ingredients were all ground to a fine powder to prevent birds from caching food in their home cages outside test periods. Water was available at all times. Birds were individually housed and tested in their home cages. Birds were held in a common holding room with other chickadees in 71 cm × 36.5 cm × 42 cm cages arranged in racks of four. Birds were maintained on a 10/14 h light/dark cycle with light onset at 7 a.m. Birds were treated in accordance with the requirements of the University of Western Ontario Animal Use Subcommittee and the Canadian Council on Animal Care.

Materials

The experimental apparatus used in Experiment 1 consisted of 28 cm × 23 cm wooden boards 1.8 cm thick coated in a clear varnish. Twelve identical boards were used. Sixteen holes were drilled into each board. The holes were arranged in four equally spaced rows of four holes. Holes were 5 cm apart within and between rows. Each hole was 0.5 cm in diameter and 1 cm deep. Two pegs that protruded 0.5 cm from the board along both long sides were used to secure an opaque white Plexiglas cover plate (7.5 cm × 23 cm × 0.5 cm thick) over the holes. Two 5 × 2 cm pieces of Velcro secured to each of the long sides of the board were used to attach plastic, Lego-like blocks to the sides of the board. Blocks were opaque in solid colours of red, blue, green, yellow, and black.

All trials were recorded using a wireless video camera mounted inside the bird's cage that broadcast to a receiver and video recorder in an adjacent ante-room. Raw hulled sunflower seeds and small mealworms were used as food items on all trials.

Procedure

Birds were given 1–2 weeks to habituate to captivity following capture in the wild before habituation to experimental components was started. Birds first were presented with the experimental food items, then completed preference testing trials, followed by pretraining phases, and finally completed the experimental testing trials. Testing did not start until birds had been in the lab for approximately 1 month.

Preference testing: Tests were conducted to establish the birds' preferences for fresh mealworms versus sunflower seeds and for sunflower seeds versus degraded mealworms. Degraded mealworms were made unpalatable by first drying them for 2 days so they became discoloured, and then soaking them in a solution of Maria's Swedish Herbal Bitters, green food colouring, and quinine hemisulfate salt. Birds were presented with two dishes: one contained ten sunflower seeds, and the other contained ten half pieces of mealworm, either all fresh or all degraded. Birds were given two trials over 2 days for each comparison during which they had 10 min to freely consume the foods in the two dishes. The number of items taken from each dish was used as the preference measure. These tests established a 100% preference for fresh mealworms compared to sunflower seeds which fell to 17.7% choice of degraded mealworms compared to sunflower seeds.

Pretraining phase: Once birds were habituated to sunflower seeds and mealworms in preference testing, habituation to the experimental task commenced. To begin, birds were exposed to the experimental apparatus. Test boards were placed in the birds' home cages for 2 h at a time. Food was placed in the holes of the test boards and chickadees learned to find and remove food for consumption. Both foods were available, separately at first, and then simultaneously. Presentations with the food exposed continued until chickadees learned to reliably remove food from the test board. Next, the chickadees were trained on string pulling. The test boards were again presented to the chickadees for up to 2 h at a time in their home cages, but with knotted pieces of string places in the food holes, so that food items were no longer visible. All birds learned to pull the pieces of string out of the holes to access food over the course of a few days.

Testing: Experimental procedures were adapted from Clayton and Dickinson (1998, 1999). Trials during the experiment proper consisted of two phases. Phase 1 always began at 11.30 a.m. The powdered food diet was removed from the home cage at 9 a.m. before each trial. At the start of Phase 1 of a trial, the video camera was placed inside the cage and the wooden board placed on the floor of the cage

with the opaque cover plate over half the board exposing 8 of 16 possible food locations and preventing the bird from examining the covered holes. Each half of the board consisted of two adjacent rows of holes, the halves being divided at the midline of the board. Within each half, only one food type could be found and only four of the eight holes contained food. Each hole was covered by a string the bird had to remove. The birds were allowed to search the exposed side of the board for 5 min. The board was then removed from the cage and returned after 5 min whereupon birds were allowed to search the other side of the board for 5 min with the plate now covering the previously exposed side. During each of these inspection periods, the board was removed after 5 min had expired or after all food locations had been searched.

Phase 2 of trials always began at 2.30 p.m. The entire board was exposed at the start of the trial, with strings in every hole. Food items could be found in the holes in which they were located during Phase 1 of the trial. Birds were given 10 min to search the boards during Phase 2 of trials 1–7 and 7 min during Phase 2 of trials 8–10. The board was again removed after all food item holes had been inspected or the time limit had expired.

Throughout testing there were two trial types. Both phases of short retention interval (SRI) trials occurred in a single day, with a 3-h delay between Phase 1 and Phase 2. Food dishes were not returned to the chickadees until after completion of the entire trial so that the birds would not be satiated at the time of the second phase. In keeping with the Clayton and Dickinson procedure, sunflower seeds and mealworms were both palatable during Phase 2 of SRI trials. On long retention interval (LRI) trials, Phase 2 followed Phase 1 by 5 days and 3 h. In Phase 2 of LRI trials, sunflower seeds were still palatable, but mealworms were degraded. To prevent the birds from becoming satiated during the second phase of LRI test trials, food dishes were removed from the home cages 2.5 h before the start of Phase 2. The experiment consisted of 20 trials with each bird tested on 10 SRI and 10 LRI trials. Chickadees had the opportunity to learn after the first trial that food replenished at previously encountered sites, and could learn after the first LRI trial that worms degrade over time. Any information chickadees had about food replenishment after short and long intervals was thus acquired over the ten SRI and ten LRI trials.

The food exposed first, the side on which each food type was located and the holes containing food items were randomized and counterbalanced across trials. Trial type (SRI or LRI) was also randomized, with the condition that not more than three trials of a given type could occur sequentially. The coloured plastic blocks were attached to the sides of the apparatus at the start of every trial in a trial-unique configuration.

Results

The mean percent of trials in which the first search in Phase 2 was to the worm side is shown in Fig. 1a for SRI and LRI trials. While birds were observed to search for worms in their first choice more often during LRI trials ($M = 66.67$, $SD = 8.16$) than during SRI trials ($M = 55.00$, $SD = 20.74$), the difference was not significant (paired samples $t_6 = 1.34$, $P = 0.24$). Contrary to expectations if the birds remembered what, where, and when, birds were not affected by the retention interval and did not preferentially search for worms first on SRI trials when worms were fresh. A comparison of the birds' first search for worms to a chance score of 50% on SRI and LRI trials, showed that the birds searched for worms first significantly more often than expected by chance during LRI trials (one-sample $t_6 = 5.00$, $P = 0.004$) but not during SRI trials (one-sample $t_6 = 0.59$, $P = 0.58$).

Because there were four possible locations for each food type in this experiment, a paired samples t test was used to examine the percent of searches directed to the worm side in the first four choices of Phase 2. The percent of worm side searches made during SRI trials ($M = 64.95$, $SD = 9.31$) did not differ significantly from the percent included in the first four choices of LRI trials ($M = 61.67$, $SD = 9.04$), $t_6 = 0.60$, $P = 0.57$. Two one-sample t tests were used to compare mean values with the chance score of 50%. Birds included more worm sites in their first four visits than would be expected by chance at both the SRI, $t_6 = 3.93$, $P = 0.011$, and the LRI, $t_6 = 3.16$, $P = 0.025$.

Given the number of sites on the board, the number that contained food, the number of sites inspected in Phase 1, and the number of searches made by the birds in Phase 2, we could determine the expected number of food locations found by chance in Phase 2 using the hypergeometric distribution. Searches in Phase 2 were counted only up to a number equal to the number of food sites found in Phase 1 for each bird and trial individually on the grounds that beyond this number of searches, birds might actually be searching the board at random. A spatial accuracy score was calculated by subtracting the number of correct choices expected by chance from the number of correct choices observed. The mean spatial accuracy scores during all SRI and LRI trials of Experiment 1 are presented in Fig. 1b. A paired samples t test was used to compare the SRI and LRI scores. The accuracy of searches in SRI trials ($M = 1.04$, $SD = 0.45$) was greater than in LRI trials ($M = 0.52$, $SD = 0.16$), but this difference was not significant, $t_6 = 2.56$, $P = 0.051$. Spatial accuracy was further examined by comparing the accuracy scores during SRI trials and LRI trials, collapsed across food types, to the chance value of 0. After both retention intervals, birds demonstrated significantly greater spatial accuracy during testing than would be
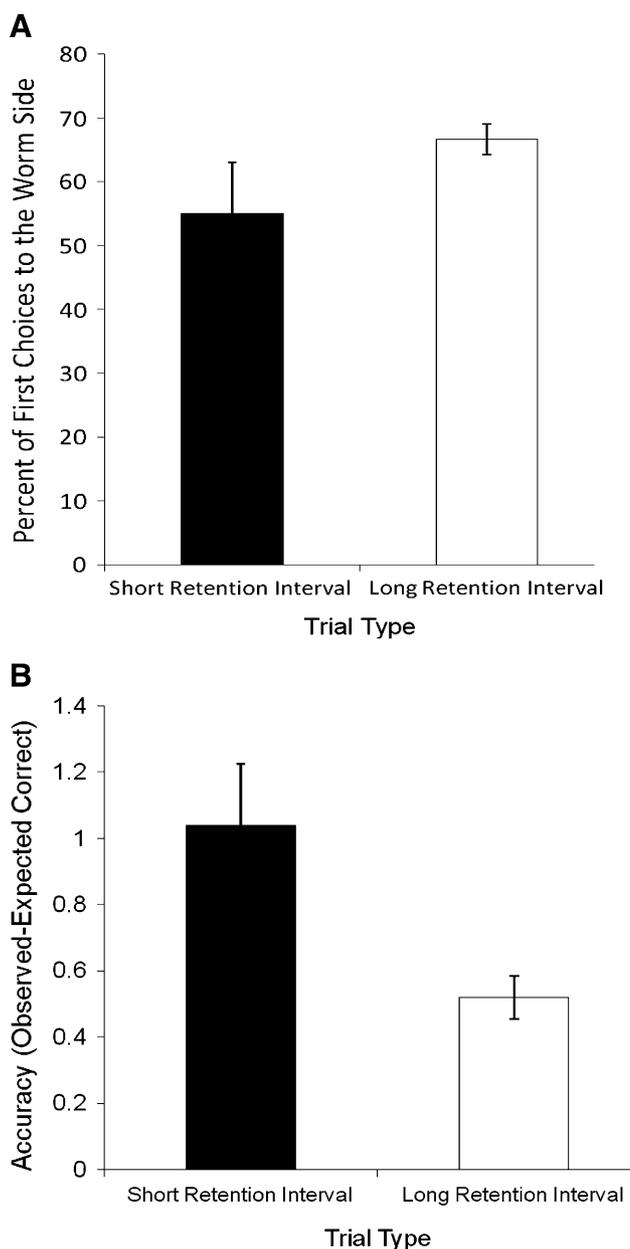
Fig. 1 The results of Experiment 1. **a** Percent of first choices in Phase 2 that were directed to the worm side of the test board. Shown are the mean number of trials on which the birds' first search in Phase 2 was on the worm side of the board as a percentage of the total number of trials. **b** Accuracy of search (observed number correct − expected number correct) in Phase 2. See text for calculation of expected number correct. All error bars = ±1 SEM

expected by chance: $t_6 = 5.60$, $P = 0.003$, for SRI trials; and $t_6 = 7.77$, $P = 0.001$, for LRI trials.

Discussion

The results of Experiment 1 showed black-capped chickadees did not exhibit WWW memory. Birds searched the worm side of the board first on both SRI and LRI trials, and

at a higher rate than expected by chance. There was thus no evidence that birds remembered when they had previously encountered worms and changed their behaviour on the LRI compared to the SRI. Birds did show the integrated "what" and "where" components of WWW memory. During Phase 2, birds preferred to search for worms first and included more worm sites in their first four choices. During Phase 2, birds also relocated food locations discovered in Phase 1 at a rate greater than chance. While birds were able to accurately remember what was found and where in this experiment, they did not show an ability to incorporate any information about when foods had previously been encountered in order to search for more palatable food. Importantly, while birds tended to search for mealworms during Phase 2 of LRI trials, they did not consume the unpalatable worms upon locating them.

It is unlikely that odour cues were used to relocate food items. If odour cues were available to the birds they should not only have shown very accurate search for food in known locations, but also accurate detection of food in unknown locations. Birds were considerably less than perfect at finding foods in hidden locations during Phase 1, tending to make more searches than necessary to locate the eight available food items. Furthermore, if birds could detect food odour cues, particularly the unpalatable bitter quinine used to degrade the worms in Phase 2, they should not have preferred to search for worms in Phase 2 of LRI trials as observed. This evidence suggests that the task does indeed assess memory rather than the direct detection of food by black-capped chickadees.

One explanation for the difference between these results and those of Clayton and Dickinson (1998) is that food-storing birds may not exhibit integrated memory for what, where, and when unless they are searching for food they have stored themselves. Rats exhibit WWW memory for food found on the radial maze (e.g., Babb and Crystal 2005; Naqshbandi et al. 2007) indicating that some animals have WWW memory for food they have encountered but not stored. Food-storing birds, however, may have to store food themselves in order to form WWW memories. Unfortunately, our chickadees were unwilling to cache food in the test boards reliably enough to allow us to look for differences in cache retrieval after short and long intervals in Phase 2.

Another reason chickadees may not have shown memory for what, where, and when in this experiment, however, involves the spatial scale of the testing apparatus. Chickadees stood directly on the board while searching in both Phase 1 and Phase 2. Little effort was required to move between food locations that were only 5 cm apart. Birds often searched in a directed fashion at a few holes before pulling out the strings at all the remaining holes very quickly. String pulling during the

latter stages of trials did not appear systematic and may have reflected the low cost of searching all holes on the board. While the first few directed searches may have been based on memory, subsequent searches may not have been. Once one item had been located, birds could potentially know "where", that is, on which side of the board food of that type was located. Birds may have, therefore, not relied on memory for when food was previously found because they could quickly investigate all food locations on the board at little cost. Birds in fact achieved high accuracy scores for worm locations without any indication they were influenced by whether mealworms were currently palatable. It is possible that chickadees may have remembered when foods were previously encountered, but were not motivated to recall and use this information because palatable sunflower seeds were only a few centimetres away from unpalatable mealworms.

Finally, the placement of the test board on the floor of the cage may also have influenced the behaviour of the chickadees. While scrub jays naturally store food on the ground (Vander Wall and Balda 1981), chickadees rarely do so, and instead forage and store food above ground in trees and shrubs (Smith 1993). We therefore modified the experimental apparatus in Experiment 2 to provide a larger and more natural foraging setting.

Experiment 2

The purpose of Experiment 2 was to explore the possibility that black-capped chickadees show WWW memory in a more natural foraging task. Because birds demonstrated "what" and "where" components of WWW memory in Experiment 1, the experimental design was not drastically modified. Testing was performed in a large aviary, a more natural environment that made searching for food more spatially and energetically demanding. Experiment 2 tested whether this environment would increase the likelihood that the birds would rely on integrated memory for when and where particular food types had been previously encountered.

Methods

Subjects

Subjects were nine wild-caught experimentally naïve adult black-capped chickadees captured in London and Elginfield, Ontario in October 2005, April 2007, and April 2008. The chickadees were maintained in the same manner as those in Experiment 1 but had not been trained or tested in Experiment 1.

Materials

Birds were observed in a 2.56 m × 3.9 m indoor aviary containing four artificial trees, each consisting of a branch approximately 1.8 m long with multiple smaller branches attached. Three of the branches were large pieces of Japanese maple, and the fourth was of an unknown type. Four holes measuring 0.5 cm in diameter and 1 cm deep were drilled into each tree. Hole locations were near natural perches on the tree from which the holes could be reached. Visits to holes were monitored in pretraining and if any holes were not visited or birds had difficulty inspecting them, perches (3 cm long 0.5 cm diameter dowel) were added to the branches. A coloured ring (white, yellow, orange, or red) was painted around the branch at each hole, with no two holes on any tree having the same coloured ring.

Trees were mounted upright in green plastic stands and the floor of the aviary was covered in Beta Chips™ (Northeastern Products Corp., Warrensburg, NY, USA) to a depth of 1 cm. One tree was placed in each corner of the aviary. To prevent access to certain holes, 16 3-cm wide strips of blue felt were cut to various lengths and wrapped around the branches to cover holes. Velcro was attached to the ends of the felt strips so they could be secured around the tree branches. The felt strips served the same purpose as the Plexiglas cover plates in Experiment 1.

Procedure

Pretraining: During the pretraining phase, chickadees were given a number of days to learn the components of the task. We did not conduct preference tests with the birds used for Experiment 2. Based on the results of preference testing for Experiment 1, which showed 100% choice of mealworms over sunflower seeds, it was assumed that the chickadees caught for Experiment 2 would similarly favour mealworms over sunflower seeds. Because testing was not done within the home cage for Experiment 2, birds were first given two 30-min sessions of individual flight in the test aviary to habituate them to the environment and artificial trees. No food was available during the flight sessions. Next, the chickadees were trained to locate visible food in the holes drilled in the artificial trees, just as was done for the testing boards in Experiment 1. Pretraining then proceeded to string-pulling behaviour. Pieces of string similar to those used in Experiment 1 were placed in the tree holes on each branch to conceal which locations contained food. Birds readily learned to pull string from the holes to locate hidden food items.

Testing: As in Experiment 1, there were two phases to each trial. Experiment 2 trials were carried out in as similar a fashion as possible to Experiment 1 trials. During Phase 1, the birds were only able to search in two trees at a time (as for halves of the board in Experiment 1). Two trees represent 8 of the possible 16 food locations. To maintain spatial separation of the food types, the aviary was divided into two equal halves at the midline from the experimenter's observation point, with two trees on each side of the midline. Within each set of two trees, only one possible food type could be found, and only four of the eight holes (two per tree) contained food. All holes were covered by knotted pieces of string. Chickadees were tested in the aviary individually. Food was removed from the birds' home cages approximately 2–3 h prior to testing so that birds were not satiated at the time of testing. At the start of Phase 1 of a trial, the blue felt strips were secured around one set of two trees. The chickadees were then moved from their home cages to the adjacent test aviary, released, and allowed to search for 5 min. The experimenter observed and recorded the birds' choices through a one-way window. After either 5 min or after all food items had been collected, the experimenter entered the testing aviary and switched the felt strips between the sets of trees such that the locations previously blocked were now exposed, and the holes exposed during the first 5 min were covered. Chickadees remained in the test room while the experimenter completed this switch, perched on branches, and then resumed foraging once the experimenter had exited. Birds again had up to 5 min to locate the food items. At the end of Phase 1, birds were returned to their home cages.

During Phase 2, all holes in all four trees were exposed, with a string in every hole. Food items could be found in the holes in which they were located during Phase 1 of the trial, regardless of whether the bird had retrieved the food or not during Phase 1. Birds were given 7 min to search the trees in this Phase of the experiment. Birds were removed from the testing aviary after either 7 min had elapsed or after all food items had been collected.

The same two trial types and delays used in Experiment 1 were used in Experiment 2 (SRI = 3 h, LRI = 123 h). The food exposed first, the set of trees in which each food type was located, and the holes in each tree containing food items were randomized and counterbalanced across trials. Trial type was also randomized, with the restriction that not more than three SRI or LRI trials could occur sequentially. The trees were switched between corners of the aviary and rotated between trials to create trial-unique configurations.

Results

The results of Experiment 2 showed that birds were more likely to search the worm side of the aviary first on SRI trials than on LRI trials, as expected if they used WWW memory to recall when worms had been found previously
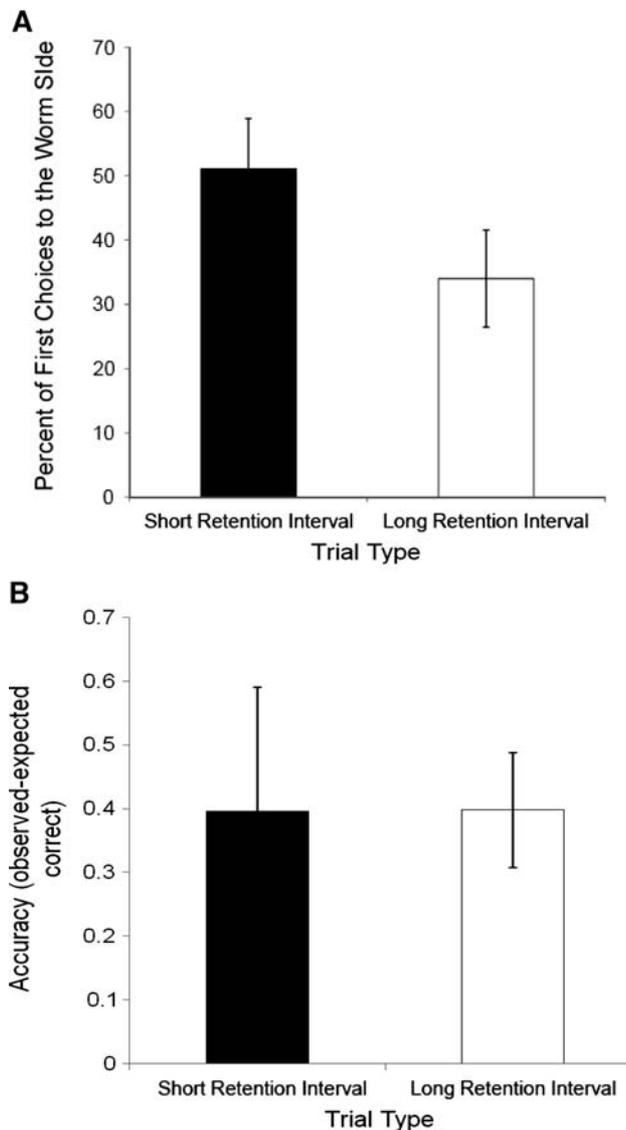
Fig. 2 The results of Experiment 2. **a** Percent of first choices in Phase 2 that were directed to the worm side of the aviary. Shown are the mean number of trials on which the birds' first search in Phase 2 was on the worm side of the aviary as a percentage of the total number of trials. **b** Accuracy of search (observed number correct − expected number correct) in Phase 2. See text for calculation of expected number correct. All error bars = ±1 SEM

(Fig. 2a). Birds searched the worm side first in Phase 2 significantly more often during SRI trials ($M = 53.33$, SD = 15.81) than during LRI trials ($M = 34.44$, SD = 15.09; paired samples $t_9 = 2.80$, $P = 0.023$). One-sample t tests compared the short and LRI percent to a chance score of 50%. Choice on SRI trials did not differ significantly from chance, $t_9 = 0.63$, $P = 0.55$, but birds chose the worm side first at a rate significantly below chance during LRI trials, $t_9 = 3.09$, $P = 0.015$.

More worm side searches were included in birds' first four choices during SRI trials ($M = 53.85$, SD = 12.51) than

during LRI trials ($M = 37.40$, SD = 14.82), paired sample $t_9 = 2.63$, $P = 0.03$. Two one-sample t tests compared mean values for each retention interval with the chance score of 50%. The percent of worm side searches observed in the first four SRI choices did not differ from chance, $t_9 = 0.92$, $P = 0.38$ but birds included fewer worm side searches in their first four choices than would be expected by chance during LRI trials, $t_9 = 2.55$, $P = 0.034$.

Accuracy of search was investigated using the hypergeometric distribution to generate accuracy expected by chance (Fig. 2b). As in Experiment 1, an accuracy score was obtained by subtracting the number of correct choices expected by chance from the number of correct choices observed. Birds were no more accurate during SRI trials ($M = 0.40$, SD = 0.39) than during LRI trials ($M = 0.40$, SD = 0.18). Two one-sample t tests were used to compare the accuracy scores for each retention interval against chance (0). Birds located food items at a greater rate than expected by chance at both retention intervals (SRI: $t_9 = 3.07$, $P = 0.015$; LRI: $t_9 = 6.51$, $P = 0.001$).

Discussion

In Experiment 2, birds behaved as if they remembered the what, where, and when properties of food they had previously encountered. Black-capped chickadees searched the worm side first more often on SRI trials when worms were fresh and palatable than they did on LRI trials when worms were degraded and unpalatable. Birds selected a greater proportion of worm locations in their first four choices in SRI compared to LRI trials. Both of these findings indicate memory for "when" food had been previously encountered. In the aviary environment, as in the home cage in Experiment 1, birds relocated food sites more accurately than expected by chance at both short and long delay intervals. Black-capped chickadees in Experiment 2 demonstrated "what", "when", and "where" memory for sites where they had previously found food.

General discussion

We found evidence for WWW memory in black-capped chickadees in one of two experiments. Birds showed no memory for "when" in tests conducted in their home cage, but in a large indoor aviary showed evidence of all three components of WWW memory. The latter more naturalistic version of the task was more energetically demanding and probably placed different cognitive demands on the birds. This finding is the first indication of WWW memory in a food-storing bird outside the corvid family (Clayton and Dickinson 1998; Zinkivskay et al. 2009) and also shows that food-storing is not necessary for the formation of

WWW memory in black-capped chickadees. In addition, the temporal design of the experiment, initially exposing both foods at approximately the same time, rules out the possibility that birds may have behaved differently at short and LRIs because food types differed in within-trial memory strength. Finally, our birds were wild caught and naïve in each experiment. Previous experience with the experimental conditions or with captivity is not necessary for the formation of WWW memory for what, where, and when in chickadees.

It was hypothesized that scrub jays and magpies may remember what, where, and when because of the selective advantage this trait confers on animals that rely on storing and retrieving food (Clayton and Dickinson 1998; Zinkivskay et al. 2009). An animal that caches foods that differ in perishability and recovers them after varying intervals would benefit from remembering when or how long ago they were cached. Animals could then flexibly adjust their retrieval schedule to retrieve perishable food before it degraded or even avoid items after they had degraded and become unpalatable. As expected by this hypothesis, we found that a food-storing bird unrelated to the corvids was also capable of remembering what, where, and when of food it had encountered.

The present results also indicate differences in the propensity to exhibit WWW memory between black-capped chickadees and scrub jays. Scrub jays show WWW memory when caching food in small trays in their home cage. Black-capped chickadees did not solve the what–where–when task in their home cage, but were successful when foraging in a large aviary. Scrub jays directed no first choices at all to the degraded worm locations after LRI trials, while black-capped chickadees did not completely inhibit searches to the worm side when worms were degraded and unpalatable. Scrub jays also showed an overwhelming preference for fresh worms, whereas black-capped chickadees' preference for worms was less strong.

A possible explanation for these differences may be that that degraded worms at the LRI produced a general depression in the value of worms to black-capped chickadees. Chickadees did not visit the worm side at a rate greater than chance during short delay trials even though preference tests in Experiment 1 showed chickadees had an exclusive preference for fresh mealworms compared to sunflower seeds. Worms were still fresh and palatable after 4 h at the SRI, but birds only sought them out as their first choice approximately 50% of the time. Neither scrub jays (Clayton and Dickinson 1998) nor rats (Babb and Crystal 2007; Naqshbandi et al. 2007) showed a decrease in their preference for worms, or cheese in the case of rats, after encountering these foods in a degraded state. However, while rats returned to the favoured location earlier when it was palatable versus degraded, they did not always return on their first choice as scrub jays did. Black-capped chickadees were also unable to entirely inhibit choices to the worm side at LRI. They choose the side containing degraded worms first on LRIs 66.6% of the time in Experiment 1 and 34.4% of the time in Experiment 2, even though preference tests had shown only 17.7% choice of degraded mealworms compared to sunflower seeds. Chickadees may therefore have generalized the state of worms encountered on SRI and LRI trials, with somewhat greater negative valuation of worms on LRI trials.

There were some methodological differences between the current study and those of Clayton and Dickinson (1998) which also might account for the differences in findings. Most important may be the fact that the present research used a found food design, whereas Clayton and Dickinson required their birds to cache food items themselves. Simply finding food in one location and attempting to relocate it later might be more prone to interference between trials compared to retrieving caches because birds can choose where they place their caches. Caching may also cause birds to observe the surroundings more carefully and remember better where an item was placed. The act of caching may additionally incorporate a time stamp for the event in memory, while finding a food item may not, particularly for animals that do not use temporally replenishing food resources. For animals that do exploit temporally replenishing foods, such as nectar feeding insects and hummingbirds, the "when" component of memory may be particularly important, and there is evidence that bumblebees (Boisvert and Sherry 2006; Boisvert et al. 2007) and hummingbirds (Henderson et al. 2006) can learn the intervals at which food replenishes.

There are a number of reasons the chickadees may have shown WWW memory in the aviary, but not in their home cage. One possibility is that the time and energy demands of the task in the home cage were not sufficient to induce the chickadees to use memory to solve the task. Birds could check all food holes in the home cage quickly without relying on memory. However, since chickadees were quite accurate in remembering where foods were located and what foods they were searching for, this argument would only apply to memory for when food was found.

Another possibility is that the naturalness of the task may explain the difference chickadees showed in behaviour between their home cage and the aviary, and might also explain the difference in behaviour in the home cage between chickadees and scrub jays. As was mentioned previously, the use of caching trays on the floor of the home cage may be ecologically appropriate for scrub jays, but inappropriate for chickadees. In the wild, scrub jays naturally cache food in the ground. Caching foods in sand in an ice cube tray is comparable to their natural caching behaviour. Chickadees, in contrast, do not search for food or

cache food on the ground, preferring instead to forage and store food in trees or shrubs above ground. A board on the floor of the home cage may not have been a good behavioural trigger for WWW memory in black-capped chickadees. Elevated, spatially dispersed food locations may have contributed to the expression of memory for what, where, and when in chickadees.

The design of the present experiment differed in an important way from Clayton and Dickinson (1998), resembling more closely the design used by Clayton and Dickinson (1999). Clayton and Dickinson (1998) separated caching of the two food types (waxworms and peanuts) in the first phase of their experiment. One caching event occurred 124 h before, and the other 5 h before testing. At testing, birds may thus have had differential memory strengths for the two food types, which could aid choice behaviour. If birds had strong memory for worms, this would indicate recent caching and palatable worms. If, on the other hand, birds had weak memory for worms, this would indicate a longer time since caching and unpalatable worms. Instead of relying on memory for when both foods had been cached, scrub jays could have simply searched for the food they remembered best. In the current study, we gave chickadees Phase 1 exposure to the locations of both food items 5 min apart. Birds were exposed to both food types either 3 or 123 h before Phase 2 testing. Our chickadees could not rely on difference in memory strength between the two food types to guide behaviour.

Differences in the natural history of chickadees and scrub jays may also contribute to the difference in behaviour observed. Chickadees show seasonal variability in their caching both in the wild (Brodin 2005; Hoshooley et al. 2007) and in the lab (MacDougall-Shackleton et al. 2003) and tend to cache food most during the colder months of the year when food is less abundant. Caching in the cold may refrigerate caches and prevent or slow degradation. Western scrub jays store many types of food all year round (de Kort and Clayton 2006) and may therefore be more affected by degradation of food during the time interval since caching and monitor the interval since caching more carefully than chickadees do.

The scrub jays tested by Clayton and Dickinson (1998, 1999) were hand reared, whereas the chickadees tested in the current research were wild caught. Hand reared and wild caught birds might be predicted to respond differently to food degradation, wild caught birds being less choosy, eating what is available, even if it is not in the most palatable condition. Their experience with degraded food in the wild might reduce the tendency to avoid degraded items at the LRIs. Behaviour on tests using the WWW paradigm may reflect experience with degraded food and the motivation to avoid unpalatable items.

The WWW test has only produced evidence for episodic-like memory in food-storing animals: chickadees in the present study; scrub jays (Clayton and Dickinson 1998, 1999); magpies (Zinkivskay et al. 2009); and rats (Babb and Crystal 2005; Naqshbandi et al. 2007). Tests for what–where–when memory have successfully been performed in pigeons (Skov-Rackette et al. 2006; Zentall et al. 2001, 2008) and rhesus monkeys (Hoffman et al. 2009), but these experiments are very different in nature. The temporal scale of events and retention intervals are much shorter in these studies, lasting only a few seconds in an operant chamber. In addition, the event to be remembered is the presentation of a stimulus rather than the availability of food per se. It is therefore difficult to compare the two types of WWW memory tests either in findings or what they indicate about the cognitive abilities of the animals. Tests of memory for what, where, and when on a time scale comparable to that used in the present study and by Clayton and Dickinson (1998, 1999) in animals that do not store food would be informative.

The current results show that chickadees did not show WWW memory when tested in their home cage but did when tested in a more natural and more demanding version of the task. We also found that in these food-storing birds, caching is not necessary for memory of what, where, and when. We did not, however, attempt to determine what mechanism the birds used to remember past events (Roberts et al. 2008) and in particular, what aspect of "when" is remembered. In the case of episodic memory in humans, "when" is usually understood to be a point in time. Tests of WWW memory in animals, however, allow for several different kinds of "when" (e.g., Friedman 1993). Animals could solve the what–where–when task by remembering a point in time but they could also solve it by remembering how long ago or the relative recency of two events (Church and Broadbent 1990). Further research is required to determine how the "when" of an event is remembered and how it is integrated with memory for the "what" and "where" of events.

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