

Black-Capped Chickadees (*Poecile atricapillus*) Anticipate Future Outcomes of Foraging Choices

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In 2 experiments we investigated the cognitive abilities of wild-caught black-capped chickadees (*Poecile atricapillus*) in future anticipation tasks. Chickadees were sensitive to anticipatory contrast effects over time horizons of 5, 10, and 30 min (Experiment 1). Chickadees also learned the order of events and anticipated that the quality of future foraging outcomes was contingent on current foraging choices. This behavior was demonstrated while foraging in a naturalistic aviary environment with a 30-min delay between the initial choice and the future outcome (Experiment 2). These results support the hypothesis that black-capped chickadees can cognitively travel in time both retrospectively and prospectively using episodic memory. This result shows the occurrence of anticipatory cognition in a noncorvid species of food-storing bird and supports the idea that cognitive time travel may have evolved in nonhuman animals in response to specific ecological selection pressures.

Keywords: future anticipation, mental time travel, anticipatory contrast, food storing

Within the declarative memory system, memory for personally experienced events, *episodic memory*, is distinguished from memory for facts about the world, *semantic memory* (Tulving, 1972). Mental time travel (MTT) is the ability to cognitively re-experience past events or to plan for future events and depends on both episodic and semantic memory (Schacter, Addis, & Buckner, 2008; Suddendorf & Corballis, 2007). Episodic memory in humans includes the property of *autonoetic consciousness* for personally experienced past events. The fundamental distinction of episodic memory is that it allows people to remember what, where, and when events happened along with a sense of reliving the episode (Tulving, 1985, 2002). Although Tulving (1983) argued that episodic memory is a uniquely human ability, there has been debate over whether nonhuman animals have a form of episodic memory. Although *autonoetic consciousness* cannot be accessed in animals, a number of recent experiments suggest that some animals can remember what, where, and when an event occurred. This ability has been called *what-where-when (WWW) memory* or *episodic-like memory* (Babb & Crystal, 2005; Clayton & Dickinson, 1998; de Kort, Dickinson, & Clayton, 2005; Roberts, 2002, 2006; Roberts & Feeney, 2009; Suddendorf & Corballis, 1997, 2007; Zinkivskay, Nazir & Smulders, 2009).

There has been ongoing research evaluating the episodic-like memory capabilities of nonhuman animals over the last decade (Babb & Crystal, 2005; Bird, Roberts, Abroms, Kit, & Crupi,

2003; Clayton & Dickinson, 1998, 1999b; Feeney, Roberts, & Sherry, 2009; Hampton, Hampstead, & Murray, 2005; Zinkivskay et al., 2009). More recently, theorists have begun to examine the importance of the episodic and semantic memory systems for future anticipation and planning (Atance & O'Neill, 2001; Buckner & Carroll, 2006; Correia, Dickinson, & Clayton, 2007; Raby, Alexis, Dickinson, & Clayton, 2007). Information stored in episodic and semantic memory may be used to generate elaborate mental scenarios describing the anticipated future, suggesting that MTT is a complex, constructive ability. Suddendorf and Corballis (2007) argued that the ability to use knowledge of past experiences to adaptively plan for the future provided the primary selection pressure for the evolution of brain structures responsible for human MTT. Schacter et al. (2008) subsequently advanced the constructive episodic simulation hypothesis, proposing that episodic memory and future simulation are based on common neural processes.

In nonhuman animals, Eichenbaum and Fortin (2009) demonstrated that rats can flexibly integrate memories to predict outcomes in novel situations. They argued based on neuropsychological and behavioral evidence that animals have the capacity for retrospective recollection and future prediction and that both abilities rely on the hippocampus in nonhuman animals, as is the case for human MTT. Although animal MTT may not be as elaborate or constructive as human MTT, the similarities in neural correlates suggest that animal MTT may be relatively complex in its own right. Raby and Clayton (2009) argued that even if animal MTT is qualitatively different from that of humans, the possibility for semantic propection—thoughts about the future without concurrent self-projections—is an overlooked area of research that has been hindered by a focus on human MTT.

Flaherty and Checke (1982) foreshadowed the recent interest in future planning and anticipation with an examination of anticipatory contrast, or the suppressed intake of a lesser value food at Time 1 in favor of a higher value food at Time 2. Results showed

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that rats receiving a 32% sucrose solution 5 min after access to a .15% saccharin solution greatly reduced intake of saccharin in favor of the future sucrose solution. The anticipatory contrast effect was observed whether solutions were presented in the same or different spatial locations. However, the effect was inversely related to the delay between saccharin and sucrose solution presentations, with greater anticipatory contrast over a 5-min horizon than over a 30-min horizon. Timberlake, Gawley, and Lucas (1987) similarly observed limited time horizons for rats' anticipation of future rewards in a spatial foraging test. Rats were only able to anticipate the availability of a future, richer patch for up to 16 min. Lucas, Timberlake, Gawley, and Drew (1990) later found that both the caloric and hedonic values of the future food modulate anticipatory contrast. These characteristics of the future food influence behavior over differing time courses, however, meaning that both the time horizon and specific foods used in experiments contribute to the contrast observed.

Clayton, Dickinson, and their colleagues (Raby et al., 2007) recently argued that if episodic-like memory and future planning are dependent on common processes and neural correlates, scrub jays, which show evidence of episodic-like memory, should possess the ability to cognitively anticipate future states. Raby et al. (2007) exposed scrub jays to the side compartments of a three-compartment chamber. Jays received breakfast in one side compartment and no food in the other. Birds were then presented with a bowl of cacheable food in the central compartment in the evening and were given free access to both side compartments for 30 min. Jays showed anticipation of future hunger by caching almost three times as many items in the no-breakfast compartment as in the breakfast compartment. In a second experiment, jays were given pine nuts in one compartment and kibble in the other during morning exposures. When presented with a bowl of cacheable items of both types of food in the evening, birds cached the items in anticipation of future consumption by caching each item in the compartment where it was typically not available in the morning. Future anticipation thus ensured the jays would have access to both pine nuts and kibble, no matter which compartment was baited for breakfast.

The Bischof-Köhler hypothesis states that animals are limited to the present in terms of need fulfillment and are unable to plan for a future need not currently experienced. One way to test this hypothesis is by prefeeding, because prefeeding leads to satiety for the food type that was prefed. Tests using the specific satiety effect demonstrated, in contrast to the Bischof-Köhler hypothesis, that scrub jays successfully planned for a future need state that was not presently experienced (Correia et al., 2007). Two groups of birds were given an opportunity to cache foods of two varieties. Caching was preceded and followed by prefeeding. One group was prefed the same type of food on both occasions (group same). A second group was prefed different foods before and after caching (group different). After the second prefeeding, birds were given access to their caches for a recovery period. The type of food that birds cached was the variable of interest in this design. As predicted by the future anticipation hypothesis, birds in the same group always cached the nonprefed food, whereas birds in the different group cached the food that was prefed before caching, rather than the food that was prefed immediately before cache recovery. The scrub jays were able to distinguish current motivation at caching from anticipated future motivation at recovery. Naqshbandi and

Roberts (2006) also obtained evidence against the Bischof-Köhler hypothesis in experiments with squirrel monkeys. The monkeys anticipated future thirst that was not experienced at the time of choice by choosing a smaller, less desirable quantity of food that led to earlier water replenishment, in preference to a larger, more desirable quantity of food that led to later water delivery.

Although evidence of episodic-like memory has not been forthcoming in experiments with nonhuman primates (Hampton et al., 2005), it has been reported that a chimpanzee cached stones for future use. Many of the stones were found around the ape's home compound or constructed by chipping pieces off of larger rocks and concrete in the compound (Osvath, 2009). Observations of this chimpanzee suggest that he anticipated a future need for the stones and stored them in an easily accessible location until the time at which they would be required (but see Roberts & Feeney, 2009). In another primate study, chimpanzees and orangutans were allowed to choose between four objects that could be used as functional tools (Osvath & Osvath, 2008). However, only one of these objects, a piece of hose, could be used to suck in a favored drink of fruit soup 70 min later in a different setting. To obtain the reward, apes had to anticipate the future availability of food and the need for the correct tool at that time. They also had to retain the correct tool during the delay and bring the tool with them on being granted access to the reward. The apes showed a highly significant preference for the hose and a highly significant tendency to later bring the hose to the reward room. These data suggest that the apes anticipated a future need for the tool to obtain their favored reward. These data indicate that retrospective WWW memory may not be universally linked to future anticipation in nonhuman animals. Alternatively, though, adequate tests of WWW memory for use with primates may not yet have been developed.

Scrub jays, magpies, and rats all store food and have all shown evidence of WWW memory. For these animals, WWW memory may be a specialized ability that allows animals to cache and retrieve a variety of foods. Animals that cache different types of perishable and nonperishable foods and recover their caches after varying intervals may learn about the rates of perishability of these foods and benefit from remembering when or how long ago foods were cached. Foods that have likely degraded during the storage interval can be avoided, whereas those that remain palatable can be recovered. WWW memory may thus be an adaptive ability that has evolved over time in food-storing animals. At the other end of the MTT spectrum, there is also an argument to make for future anticipation as an adaptive, evolved trait. Animals that revisit sources of food would benefit from anticipating when the food will next be available (Henderson, Hurly, Bateson, & Healy, 2006). It would be costly to waste time and energy foraging in a patch of food before the food has replenished or after it has spoiled. In support of this hypothesis, recent research has in fact begun to show that some animals that exhibit WWW memory for the past can also anticipate future events (Correia et al., 2007; Raby et al., 2007; Roberts, 2007).

Recently, black-capped chickadees have demonstrated memory for WWW details of events (Feeney et al., 2009). The ability observed in chickadees was in line with that of scrub jays (Clayton & Dickinson, 1998, 1999b) and magpies (Zinkivskay et al., 2009), two food-hoarding corvid species. In addition, scrub jays possess an ability to anticipate future events (Correia et al., 2007; Raby et al., 2007). We were thus interested in determining if black-capped

chickadees are similarly capable of prospective mental time travel. We conducted tests for future anticipation using two procedures, anticipatory contrast, and food patch replenishment.

Experiment 1

Experiment 1 tested future anticipation in black-capped chickadees using the anticipatory contrast paradigm (Flaherty & Checke, 1982). Birds were initially given a chance to freely consume sunflower seeds. Later, half the birds were allowed to freely consume pieces of mealworm. If chickadees can anticipate the availability of a preferred, higher value food (mealworms) in the near future, they should suppress intake of a lesser value food (sunflower seeds) to avoid satiation before the preferred food becomes available.

Method

Subjects. Twelve wild-caught black-capped chickadees (*Poecile atricapillus*) were used in Experiment 1. Chickadees are sedentary year-round residents, forming flocks in the winter and mating pairs in the spring and summer (Smith, 1993). Birds were caught in London, Canada, during April 2007 and April 2008. All birds used in this experiment were tested after hatch year, and so were at least 1 year old at the time of testing. The birds were maintained on a diet mix that was freely available in their home cages except for 2 to 4 light hours prior to testing. The mix consisted of Mazuri Diet (PMI Nutrition International, Brentwood, MO) with raw hulled sunflower seeds and blanched peanuts added. These components were all ground to a fine powder to prevent birds from caching foods in their cages during nontest periods. Water was freely available at all times. Each bird was housed and tested individually in a common cage room that held three additional chickadees. Cages measured 71 cm wide, 36.5 cm deep, and 42 cm high, and were arranged in racks of four. The birds were exposed to a constant 10:14-hr light–dark cycle with onset at 7 a.m.

Materials. Two food types were used in testing, sunflower seeds and small mealworms. Food items were presented to the birds in plastic dishes. During testing, 12 red dishes and 12 blue dishes were used, one of each color for each bird.

Procedure. Birds were initially divided into two groups, a control group ($n = 6$) and an experimental group ($n = 6$). There were approximately equal numbers of experienced and naïve birds in each group. Seven birds had prior experience with a previous specific satiety test. Chickadees were tested individually in their home cages between 9:00 and 10:00 a.m. Regular food dishes were removed between 4:00 and 5:00 p.m. the day before testing. The dark portion of the light–dark cycle began at 5 p.m. In the dark hours, chickadees roost and do not consume any food. The lights-on segment of the light–dark cycle resumed at 7 a.m. As such, birds were only food deprived for the morning light hours prior to testing and up to 1 light hr before lights off the previous evening.

Testing was carried out in three phases. All birds were first presented with a plastic dish containing 10 sunflower seeds and were allowed 5 min to consume seeds. After the 5-min access period, sunflower seed dishes were removed from the cages of all birds and a delay period ensued. During the three phases of testing, the delay period lasted 5 min, then 10 min, and finally 30 min.

Once the delay period elapsed, the experimental birds were given 5 min of access to a plastic dish containing 10 half pieces of mealworm. Control birds received no food at this time. On completion of the 5-min mealworm access period, the worm dishes were removed from the cages of the experimental birds. Regular food was returned 30 min to 1 hr after testing. To equate access to mealworms, control birds were given mealworms in the afternoon, after regular food had already been returned. The number of worms that control birds received was equal to the average number consumed by the experimental birds during testing. Birds were tested for 15 days using a 5-min delay, 10 days with a 10-min delay, and another 10 days at the 30-min delay.

Results

Group means for the three phases are presented in Figures 1a, 1b, and 1c, respectively. After Phase 1 of testing, one bird in the experimental group, Bird B, behaved very differently from the rest of the birds in that group. As shown in Figure 1b, the average bird in the experimental group consumed 3.2 sunflower seeds. Bird B consumed 4.30 sunflower seeds, almost 2 standard deviations ($SD = .58$) above the consumption of the other experimental birds. When Bird B is excluded from the experimental group, mean consumption by experimental birds is 3.0 sunflower seeds ($SD = .23$), making consumption by Bird B almost 6 standard deviations above the mean. Consequently, Bird B was removed from the analyses for Phases 2 and 3. Because only the experimental birds received worms in the future during testing, we predicted that these birds would consume fewer sunflower seeds than control birds if they were able to anticipate receiving a better food in the future. The curves shown in Figures 1a, 1b, and 1c all show that birds in the experimental group consumed fewer seeds than birds in the control group.

To ensure that data were analyzed for a period when birds had adjusted to each phase of testing, mean seeds consumed over the last three trials of each phase were used. Because the pattern of data was similar across all three phases, a 2 (group: control vs. experimental) \times 3 (phase: 5-min delay vs. 10-min delay vs. 30-min delay) analysis of variance (ANOVA) was run to see if there was an interaction between the effects of group and delay on seed consumption. Results of the split-plot ANOVA showed that there was an overall main effect of group on seed consumption, $F(1, 9) = 6.02, p = .04$, across all delay lengths. The control group consumed more seeds ($M = 4.72, SE = .64$) than the experimental group ($M = 2.96, SE = .16$). There was also a main effect of phase on seed consumption, $F(2, 18) = 3.49, p = .05$. Post hoc Tukey's tests indicated that there was a significant difference between consumption in Phases 1 and 2, with more seeds consumed during Phase 2 ($M = 4.15, SE = .49$) than during Phase 1 ($M = 3.57, SE = .40$), $q(3, 18) = 3.61, p = .05$. No other significant differences were observed between seed consumption rates of the 3 phases. There was no interaction between the effects of group and phase on seed consumption, $F(2, 18) = 0.10, p = .91$. The pattern of effects was consistent for all delays tested in the current experiment. This conclusion is confirmed by the fact that in the last three trials of the 5-, 10-, and 30-min phases individually, the difference in sunflower seed consumption by control and experimental birds was significant: $t(10) = 2.97, p = .014$, $t(9) = 2.35, p = .043$, and $t(9) = 2.80, p = .021$, respectively.

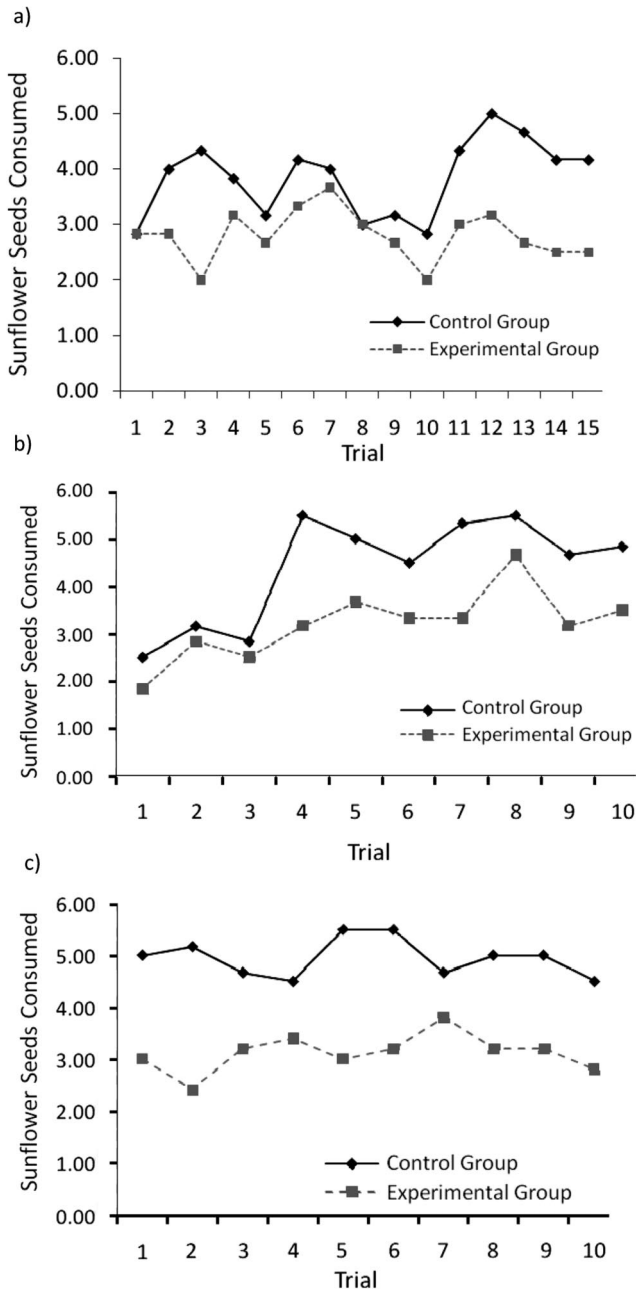


Figure 1. Sunflower seed consumption during Phases 1 (a), 2 (b), and 3 (c) of Experiment 1. Experimental birds received sunflower seeds followed after a delay by preferred mealworms. Control birds received sunflower seeds at the same time as experimental birds, but did not receive mealworms after the delay (mealworms were presented hours later in the home cage with regular ad lib food replenishment). Delays equaled 5 min in Phase 1, 10 min in Phase 2, and 30 min in Phase 3.

Discussion

Experiment 1 indicated that black-capped chickadees, like rats (Flaherty & Checke, 1982), can anticipate the future availability of a preferred food. Experimental birds readily suppressed intake of initially available sunflower seeds in favor of future mealworms.

These findings show that black-capped chickadees are able to anticipate the availability of a favored food 5 min into the future and will suppress consumption of a less preferred food in the present, even when in a food deprived state, to maximize intake of the preferred food that will only become available in the future.

Similarly, when the delay was extended to 10 min in Phase 2, chickadees still showed anticipation of future food availability. Throughout the 10 days of Phase 2 testing, experimental birds consumed fewer sunflower seeds than did control birds. Birds did increase consumption of seeds in Phase 2 as compared to Phase 1, but this was true of both groups. The difference between consumption by the two groups remained constant. Given that the regular ad lib diet was not returned to the birds until 30 min after testing each day, increasing the delay interval meant that birds had to wait longer for the return of their regular diet as well. It is therefore not surprising that birds would have to increase food intake slightly to ensure they were not hungry prior to being granted access to their regular food again. In essence, this can be seen as another form of anticipation—anticipation of the delay until the regular diet is returned to the home cage. There was no difference in seed consumption between Phases 2 and 3.

Finally, the results of Phase 3 mirror those of Phases 1 and 2. Experimental birds consumed fewer sunflower seeds over the course of testing than did control birds. In this case, black-capped chickadees were able to anticipate the future availability of a preferred food over a 30-min delay. Although it is possible that birds simply continued to display a learned, rewarded behavior from Phases 1 and 2, without anticipating the future over 30 min, this seems unlikely. If the chickadees in the experimental group could not anticipate the future availability of worms, there would be little reason to suppress intake of sunflower seeds. From the birds' perspective, without knowledge of the future food, they would be choosing between sunflower seeds now or nothing, and consumption of sunflower seeds should increase. Instead, the experimental group's seed consumption was fairly constant, with no noticeable increase in sunflower seed consumption that might suggest birds could not suppress seed intake in anticipation of future food that was delayed for 30 min.

Our results largely replicate the findings of Flaherty and Checke (1982). Chickadees, like rats, demonstrate anticipatory contrast between foods of differing incentive value. Flaherty and Checke argued that their results were not due to successive contrast. That is, suppression of saccharin at the beginning of trials was not caused by contrast with memory of sucrose from the previous trial. The authors pointed to two characteristics of the data to support their claim. First, the suppression of saccharin intake was larger with only a 5-min delay prior to sucrose delivery than was observed if rats had to endure a 30-min delay. Successive contrast between sucrose from the previous day and saccharin at the beginning of a trial should not be affected by the interval between saccharin and sucrose delivery within trials. Second, the between day interval for successive contrast would actually be slightly shorter for rats exposed to a 30-min within day separation between saccharin and sucrose than to a 5-min delay, so successive contrast would have enhanced saccharin intake suppression in the 30-min delay condition if successive contrast was driving the effects. Because the suppression was greater for the 5-min delay condition than for the 30-min delay condition, Flaherty and Checke concluded that their finding "supports the hypothesis that the reduced

saccharin intake is due to the anticipation of the impending sucrose rather than to the fact that sucrose was received 24 hr earlier" (p. 179). We argue a similar claim is valid for our chickadee results because the within-day interval did not affect the suppression of sunflower seed intake and the reduced across-day interval did not enhance the effect in the 30-min delay conditions of Phase 3. It is more likely that chickadees anticipated the within-day delivery of mealworms following sunflower seeds across 5-, 10-, and 30-min intervals.

Although Flaherty and Checke (1982) attributed anticipatory contrast to anticipation of a future reward, successive negative contrast is typically explained as a negative reaction to frustration generated by encountering a less preferred reward when a more preferred reward is expected. Further evidence that the effects found in Experiment 1 were not produced by successive negative contrast is found in a report by Papini (1997). When Papini trained pigeons to peck a key for 15 food pellets and then shifted them to a one-pellet reward, pigeons failed to show the successive negative contrast effect typically found in mammals. Pigeons' latency to respond for one pellet after receiving 15 pellets only gradually rose to the one-pellet level of a control group and did not overshoot the one-pellet level. This finding and others led Papini to conclude that the mechanisms responsible for successive contrast in mammals do not operate in birds.

Experiment 2

Experiment 2 was designed to test birds in a more naturalistic foraging environment. An aviary with artificial trees was used, with sets of trees designated as patches of food. In an initial phase, all food locations in the trees were baited with sunflower seeds. Depending on where birds searched in the initial phase, they would later have access to replenished sunflower seeds in the "seed patch," or newly available mealworms in the "worm patch." Birds had to avoid searching the mealworm patch in the first phase for worms to be available in the second phase. We examined both whether black-capped chickadees could anticipate when and where a preferred food (mealworms) would become available within the foraging environment, and whether they would behave in the initial phase in a way that guaranteed future availability of the preferred food.

Method

Subjects. Subjects were eight wild caught black-capped chickadees. Seven of the birds were previously involved in Experiment 1 as well as a retrospective memory task. One bird was experimentally naïve. Birds were captured in London, Canada, and were housed and maintained in the same fashion as in Experiment 1.

Materials. Birds were observed in a 2.56 m × 3.94 m indoor aviary containing four artificial trees. Each tree consisted of a main branch approximately 1.83 m long with multiple-smaller branches protruding from the main shaft. Three of the branches were large pieces of Japanese maple, and the fourth was of an unknown type of deciduous tree. Four holes measuring 0.5 cm in diameter and 1.0 cm deep were drilled into each tree. Food holes were located near natural perches on the tree from which birds could reach the holes. Perches (3 cm long, 0.5 cm diameter dowel) were added to the

branches near any holes that did not have a natural perch. A colored ring (white, yellow, orange, or red) was painted around the branch at each hole, with no two holes on any tree having the same colored ring. At each available hole, a piece of red yarn was tied around the branches, with approximately 10 cm excess. A knot was tied at the end of each piece of string. The 10 cm excess piece that extended from each branch allowed the knotted end to be placed inside the holes to prevent visual access to the food contained inside. For the purposes of the current experiment, green painters' tape was wrapped around two randomly selected food holes on each tree, so that only two holes would be available per tree during testing.

Trees were mounted upright in green plastic stands, and the floor of the aviary was covered in Beta Chips (North-Eastern Products Corp., Warrensburg, NY) to a depth of 1 cm. One tree was placed in each corner of the aviary. Tree locations and the holes that were accessible remained constant throughout testing but differed from the set-up used during training. Trees were assigned seed side or worm side designations according to the side of the room they were located on from the experimenter's perspective in the observation room. The foods available in the current experiment were raw hulled sunflower seeds and small mealworms.

Procedure. Chickadees were first habituated to the aviary testing room. Birds were given 30-min individual flight sessions in the aviary over 2 days. The artificial trees were in the room at this time, but were not baited. Next, the birds were taught how to pull strings to retrieve food items from the food holes. Wooden boards measuring 28 cm × 23 cm and 1.75 cm thick, with a 4 × 4 grid of holes, were placed inside the birds' individual home cages. At this time, all holes were baited with sunflower seeds. Birds were given free access to the boards for 1 day to retrieve the seeds. On the next day, boards were returned to the chickadees' cages, with only selected holes baited, and with knotted pieces of string inserted in the holes to prevent visual access to the seeds. Birds had to pull the strings out of the holes to search for food. Finally, birds were released back into the aviary for 30-min individual flight sessions with the trees baited and strings covering food in the holes. Chickadees received three sessions of aviary flight with trees baited.

The test trials occurred in two phases. During Phase 1, each hole in all four trees was baited with half a sunflower seed. Chickadees were transported by hand from their home cage to the aviary at the start of each trial. Birds were released into the aviary individually, and were given up to 5 min to locate and consume any four pieces of sunflower seed. On completion of Phase 1, birds were returned to their home cage for a 30-min delay period.

Phase 2 commenced at the completion of the delay period, when birds were again transported individually by hand from their home cage to the adjacent aviary. In Phase 2, locations where food had been found in Phase 1 were not replenished. Unsearched locations were replenished with either one piece of sunflower seed or half of a small mealworm. Whether sunflower seeds or mealworms were replenished depended on where the bird searched in Phase 1. If birds searched the seed side in Phase 1, and avoided foraging in the worm patch, they would find worms in the worm locations in Phase 2. If, on the other hand, birds could not inhibit searches to the worm side in Phase 1, these sites would not be replenished with worms in Phase 2 and chickadees would be left to collect sun-

flower seed pieces on the seed side of the aviary. That is, a typical trial would occur as follows. In Phase 1 all four artificial trees were baited with sunflower seeds. In Phase 2, sites that were searched in Phase 1 were not replenished. For the purpose of illustration, the left side of the arena could be designated the worm side and the right side of the arena, the seed side. In this hypothetical trial, during Phase 1 a bird might search three seed side locations on the right of the arena and one worm side location on the left. Consequently, in Phase 2, the three unsearched worm locations would be replenished with a piece of mealworm, while the one unsearched seed location would be replenished with a sunflower seed. This hypothetical bird would therefore have shown anticipation of future outcomes of foraging choices, by suppressing choice of the worm side in Phase 1 to obtain worms in Phase 2.

See Figure 2 for the experimental design. It is important to note that chickadees were permitted to search both worm and seed locations in Phase 1. Food availability in Phase 2 depended entirely on the specific locations selected, not on the side selected first in Phase 1, or the side searched most often in Phase 1. Phase

2 lasted for up to 5 min or until birds collected and consumed all available food items.

After every five test trials, two forced choice trials were given. On 1 day birds would be forced to search only holes on the worm side in Phase 1. During the second forced choice trial, the birds would be forced to search only the seed side in Phase 1. Birds were forced to search only one side of the room in Phase 1 on forced choice trials by placing a piece of tape over the holes in the trees on the opposite side of the room to block access to those holes. Order of the forced choice trials was counterbalanced. The non-forced side was baited in Phase 2 with the appropriate food (seeds on the seed side or worms on the worm side). Baiting in Phase 2 of forced trials could not be directly contingent on choices from Phase 1 in the same way as was true of free choice trials. Forced choice trials were designed to familiarize birds with the sequence of events and outcomes of choices as well as to disrupt position habits. However, birds generally always consumed all available food in Phase 1 of forced choice trials, having been food deprived beforehand, so a break from the typical experimental contingencies did not occur. In this way, we guaranteed that birds had experience with the contingencies associated with both search patterns throughout testing and reduced the likelihood that they would develop a position habit. The side of the aviary that was designated the worm side was counterbalanced across birds. Testing continued until birds showed an effect of anticipation or clear indication of a position habit.

Results

A within-subjects analysis was used to test whether birds could learn a causal link between behavioral choices in a sequence of events, and whether they could anticipate future food availability over a 30-min delay. The results supported the hypothesis of anticipation by black-capped chickadees, with four birds showing anticipation after only 10 days, while an additional two birds showed evidence after 15 days. Testing was terminated once birds had shown the anticipation effect. That is, testing lasted for 10 days for four of the birds and 15 days for two birds. Unfortunately, two birds showed no evidence of anticipation, instead forming position habits over time despite attempts to disrupt position habits with forced choice trials. One of these birds favored the left side of the room on 87% of trials, while the other favored the right side of the room on 87% of trials. These position habits were so strong that the two birds stopped responding on forced choice trials to the nonfavored side. The two birds that developed position habits were therefore not included in the statistical analysis of anticipatory ability. For the purpose of analysis, the data were divided into blocks of five trials to identify the first and last block of trials for each bird and to examine signs of learning that took place between these blocks.

The proportion of times that birds selected a worm side location first was examined to see if there were any differences across phases and blocks of trials. Anticipation would be indicated by birds suppressing visits to the worm side in Phase 1 to increase the availability of preferred worms in Phase 2. First choices are most indicative of learned discrimination between the two sides of the room because after the first choice, birds could know where each food was available and switch their search pattern accordingly. In Phase 1, birds would discover after a first choice to the worm side

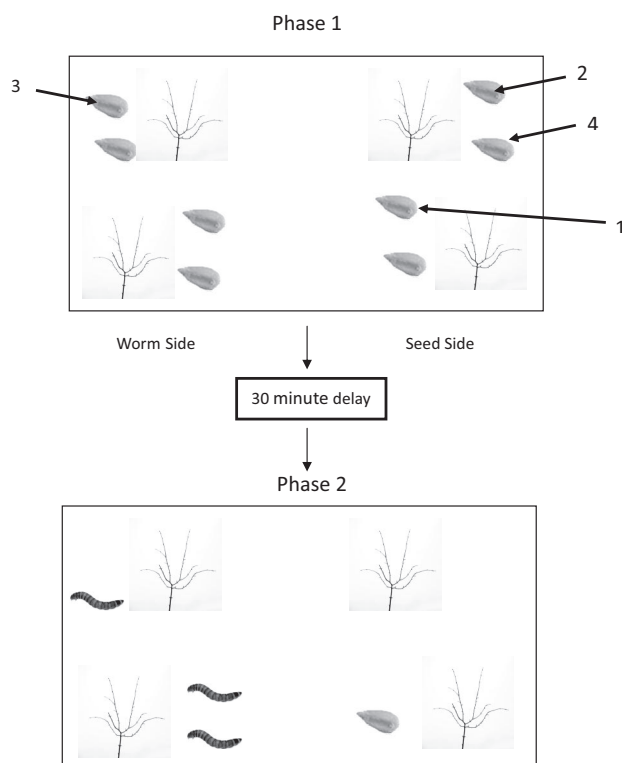


Figure 2. Design of Experiment 2. In Phase 1 all four artificial trees were baited with sunflower seeds. In Phase 2, sites that were searched in Phase 1 were not replenished. In this depiction, the left side of the arena is the “worm side” and the right side of the arena is the “seed side.” In this hypothetical trial, during Phase 1 the bird searched three seed side locations and one worm side location (numbers and arrows indicate order of tree visits). Consequently, in Phase 2, the three unsearched worm locations were replenished with a piece of mealworm, while the one unsearched seed location was replenished with a sunflower seed. This hypothetical bird would therefore have shown anticipation of future outcomes of foraging choices because it suppressed choice of the worm side in Phase 1 to obtain worms in Phase 2.

that worms were not yet available. In Phase 2, birds would learn after a first choice to a baited hole on the worm side that worms were available. Similarly, after a choice to a baited location on the seed side in Phase 2, birds would find that they had not selected the worm side, and could switch to searching the other side of the aviary. We examined learning between the first and last block of trials to see if birds responded to the outcome of events by the end of testing compared to the initial trials when they were still naïve.

Proportions were calculated by summing the number of times the worm side was selected first and then dividing the sum by the number of trials in the block (five trials). A 2 (block: first five trials vs. last five trials) \times 2 (phase: Phase 1 vs. Phase 2) repeated-measures ANOVA was used to analyze the data. Results demonstrated a significant interaction of block and phase, $F(1, 5) = 8.90$, $p < .04$. As can be seen in Figure 3a, by the end of testing (last block) birds suppressed visits to the worm side locations in their first choice of Phase 1 compared to first block behavior. Birds also increased their first choices to the worm side in Phase 2 between the first and last blocks of trials.

Paired t tests determined that there was no significant difference between the proportions of first choices directed to the worm side during Phase 1 ($M = 0.47$, $SE = 0.13$) and Phase 2 ($M = 0.65$, $SE = 0.12$) within the first block of trials, $t(5) = 2.17$, $p = .08$. In contrast, during the last block of trials, the proportion of first choices directed to the worm side was significantly suppressed in Phase 1 ($M = 0.23$, $SE = 0.10$) compared to Phase 2 ($M = 0.85$, $SE = 0.08$), $t(6) = 9.43$, $p < .001$. In addition, the proportion of first choice visits directed to the worm side in Phase 1 was compared to chance (0.5) for both the first and last blocks of trials. There was no difference from chance in the first block, $t(5) = .25$, $p = .81$. However, supporting the idea that our chickadees learned to anticipate future availability of mealworms, the proportion of first choices of worms in Phase 1 of the last block of trials was significantly lower than chance expectation, $t(5) = 2.79$, $p = .04$. The contrast between the proportion of first choices of the worm side in Phase 1 of the first and last blocks also approached significance in a paired-samples t test, $t(5) = 2.45$, $p = .06$. Thus, following the initial learning period in the first block of trials, chickadees anticipated worm availability in Phase 2 and suppressed their choices of the worm side in Phase 1. In the last block of trials, birds directed 90% of their first choices to the worm side in Phase 2, and only chose the worm side first 20% of the time in Phase 1.

We also analyzed the percent of the first four choices that were directed to the worm side in each phase across blocks (Figure 3b). This analysis was aimed at determining how successfully the birds were able to maximize the availability of worms in Phase 2. The first four choices were examined because birds could make only four choices in Phase 1, leaving four baited sites available in Phase 2. The fewer worm sites a bird chose in Phase 1, the more worm sites the bird would find baited in Phase 2. A 2 (block: first five trials vs. last five trials) \times 2 (phase: Phase 1 vs. Phase 2) repeated-measures ANOVA was used to analyze the data. The analysis revealed a significant interaction between blocks and phase of testing on the percentage choice of worm side locations in the first four choices, $F(1, 5) = 10.00$, $p = .03$ (see Figure 3b). Paired t tests indicated that for the first block of trials there was no significant difference in percentage choice of worm side locations between Phase 1 ($M = 47.2$, $SE = 15.2$) and Phase 2 ($M = 61.8$,

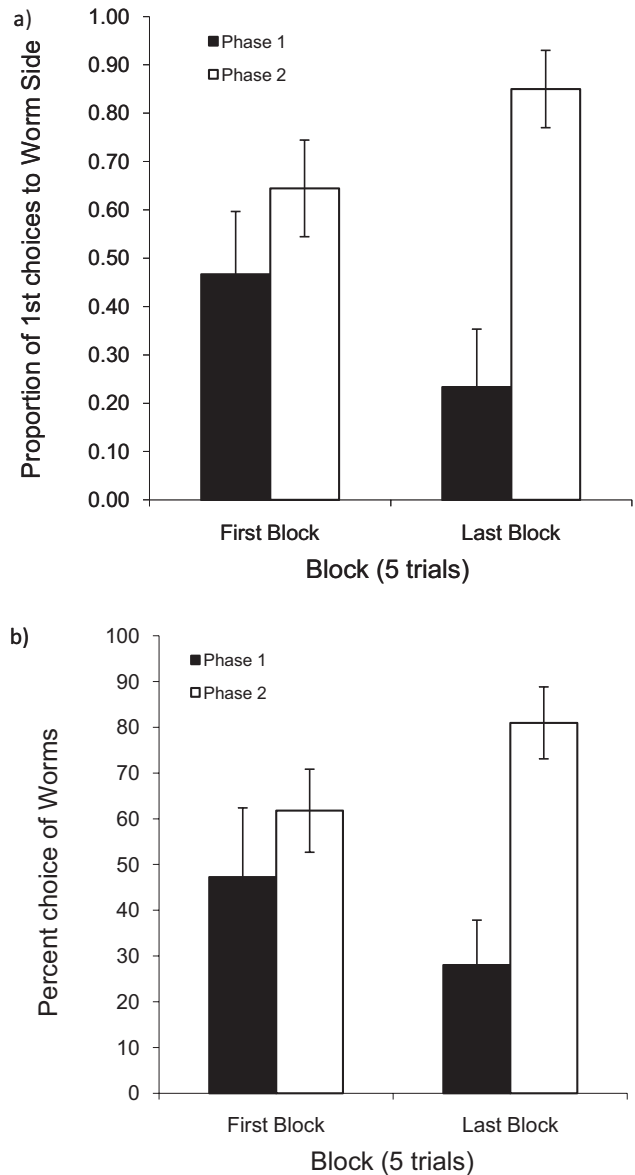


Figure 3. Proportion of first choices to the mealworm side of the aviary (a) and percentage of all choices to the mealworm side (b) after a 30-min delay in Experiment 2. Error bars represent SEM.

$SE = 9.8$), $t(5) = .98$, $p = .37$. In contrast, during the last block of trials, the percentage of searches directed to the worm side in the first four choices was significantly larger in Phase 2 ($M = 81.0$, $SE = 7.9$) than in Phase 1 ($M = 28.0$, $SE = 9.1$), $t(5) = 14.42$, $p < .001$.

Finally, we also compared percentage choice of worm side locations to chance (50.00%) for both the first and last block of trials during Phases 1 and 2. The percentage choice of worms during the first block of Phase 1 and Phase 2 did not differ from chance, $t(5) = .18$, $p = .86$ and $t(5) = 1.2$, $p = .28$. During the last block of trials, the percentage choice of worms during Phase 2 exceeded chance predictions, $t(5) = 3.94$, $p = .01$. Birds selected more worm side locations within the four Phase 2 choices than

would be expected by chance. In Phase 1, percentage choice of worms did not differ from chance, but approached significance, $t(5) = 2.42, p = .06$. Even though birds only directed approximately one of four choices to the worm side (28%), the result failed to differ from chance. An examination of individual choices indicates that this finding is likely driven by a single bird, which was not able to inhibit searching worm side locations below 50% during Phase 1. However, the bird did reduce choice of worm side locations in Phase 1 from 93% in the first block, to 60% in the last block. Thus, the bird does show evidence of learning the task, but may simply have been unable to reduce choices to the worm side below 50%, or may have required an additional block of trials to do so. If that bird is removed from the analysis, we find that chickadees directed fewer choices to the worm side during Phase 1 of the last block of trials (21.6) than is predicted by chance, $t(4) = 3.59, p = .02$.

Discussion

The pattern of results in Experiment 2 is consistent with the hypothesis that black-capped chickadees are able to anticipate future food delivery in a naturalistic foraging situation. Chickadees responses to the sequence of events in the experiment suggest they understood that future outcomes (Phase 2) depended on present behavior (Phase 1). These results agree with those reported in Experiment 1, and are consistent with previous findings showing that chickadees learn to store foods only in locations where caches remain intact for later recovery and will avoid locations that are always pilfered (Hampton & Sherry, 1994). Similar learning ability has been observed in scrub jays (de Kort, Correia, Alexis, Dickinson, & Clayton, 2007).

Although the findings of Experiment 2 may be interpreted as evidence of future planning in chickadees, the possibility that they arise from a process that does not involve MTT should be considered. The successive negative contrast effect was considered as an alternative account of the findings in Experiment 1 and may also be considered as an explanation of the findings from the second experiment. Successive negative contrast is held to arise from a frustration response that occurs when an expected reward is replaced by one of less quantity or quality. The frustration response blocks or reduces operant or consummatory behavior that would otherwise occur. It could be argued that chickadees learned to expect worms on the worm side of the aviary after encountering worms there in Phase 2 of the previous trial and were then frustrated by encountering seeds on the next Phase 1 visit to that side. Frustration would then lead chickadees to avoid the worm side and forage for seeds on the nonworm side.

The frustration account may be problematic in light of Papini's (1997) suggestion, based on his pigeon studies, that birds may not experience frustration and thus do not show successive negative contrast. Beyond this concern, the pattern of findings observed in Experiment 2 may not be completely consistent with a frustration account. Consummatory successive negative contrast typically shows a pattern of initial reduction in consummatory behavior after first encounter with a reward of lesser quality than expected, followed by a recovery over a few trials to the baseline level of consummatory behavior (Norris, Daniel, & Papini, 2008). By contrast, chickadees preference for the nonworm side in Phase 1 was more marked in the last block of five trials than in the first

block of five trials. In addition, it is not clear how a basic frustration account would explain why chickadees learned to avoid the worm side in Phase 1, but go to it first in Phase 2. Somehow, chickadees' frustration response would have to be conditional on the Phase 1 trial but not the Phase 2 trial; such an assumption would suggest that chickadees were aware of the different rewards occurring on the worm side in different phases.

Still, the possibility that chickadee's differential preference for the worm side of the aviary in Phases 1 and 2 arose from a process other than anticipation of future worms cannot be ruled out completely by these findings. An important control experiment that should be carried out is one in which the contingency between Phase 1 visits and Phase 2 availability of worms is eliminated. In such an experiment, chickadees would find a full supply of worms on the worm side in Phase 2, regardless of the number of seeds taken from each side in Phase 1. Indifferent choice between sides in Phase 1 would suggest that the contingency was necessary for chickadees to learn a preference for the nonworm side in Phase 1.

We should also consider the possibility that anticipatory contrast, observed in Experiment 1, could explain the results of Experiment 2. Focusing on just the worm side of the aviary for the moment, we see that seeds are presented at Time 1 and that worms are presented at Time 2. It is possible that anticipatory contrast could have caused our chickadees to inhibit consumption of seeds in worm side locations during Phase 1 in favor of later worm delivery in Phase 2. This is essentially the mechanism observed in Experiment 1. However, there is an important difference between Experiments 1 and 2 that weakens the argument that anticipatory contrast could explain the results. In Experiment 1, food delivery at Time 2 was not contingent on choices made at Time 1. Rather, satiety at Time 2 was contingent on consumption during Time 1. Worms were always delivered to chickadees at Time 2 in Experiment 1. The task for food-deprived birds in the experimental group of Experiment 1 was to inhibit the drive to consume lesser valued food at Time 1 to avoid experiencing satiety when the preferred food was delivered at Time 2. In Experiment 2, on the other hand, food delivery at Time 2 was directly contingent on choices made at Time 1. Birds could not simply inhibit consumption of sunflower seeds entirely. If chickadees made no choices during Time 1, the trial would be considered a mistrial, and Time 2 would not occur, meaning no worms would be delivered. Instead, birds had to consume sunflower seeds during Time 1, but on a particular side of the aviary if they were to obtain worms at Time 2. Anticipatory contrast, as explained by Flaherty and Checke (1982), does not explain the ability of chickadees to avoid a particular patch of food, rather than simply inhibiting choice of a lesser valued food.

The chickadees' pattern of performance is further remarkable when primary and secondary reinforcers are considered. The primary reinforcers delivered in the experiment were the worms available in Phase 2. These reinforcers should have conditioned birds to favor the worm side of the testing arena. Secondary reinforcement occurs when cues associated with reward acquire rewarding value. Secondary reinforcers in the current experiment would be features of the trees, walls, and floor on the worm and seed sides of the aviary. Because the worms were preferred primary reinforcers, the secondary reinforcers for the worm locations should be stronger than secondary reinforcers for seed locations, and thus these secondary reinforcers associated with the worms

should have conditioned the birds to favor the worm side locations. Instead, birds inhibited choices of the worm side in Phase 1, increasing visits to the worm side during Phase 2 instead. However, the worm side of the testing aviary is the side that would have the stronger primary and secondary reinforcing value because it was the side associated with the preferred food. This association would hold regardless of the phase of testing. The choice pattern that was displayed suggests that birds were aware of which side would have nonvisited holes replenished with worms 30 min in the future.

Our pattern of findings argues against a strictly conditional learning interpretation, in which animals learn to search for food where they were last rewarded. In the current experiment, the birds had to make the opposite choice in Phase 1 to get the highly rewarding food in Phase 2, rather than return to where they had just received a highly favored reward at the end of the previous trial. There is some evidence of conditional learning over long delays with rats (e.g., Lett, 1975, 1977a), but the findings are controversial (Lett 1977b; Roberts, 1976, 1977). We do not think conditional learning provides a parsimonious explanation of why birds were more likely to return to the less preferred side of the aviary at the start of the next trial after receiving worms on the preferred side in the previous trial.

Another possibility is that chickadees learned a serial order of when and where sunflower seeds and worms were available within the test arena and by the second block of trials were able to make foraging choices based on those two events. More important, however, it was not the case that worms were always available in Phase 2. Worm replenishment in Phase 2 was dependent on the birds not searching those sites in Phase 1. Thus, to be able to suppress searches to future worm sites in Phase 1, birds had to learn a serial order and associate choice of a favored location in Phase 1 with future unavailability of the favored food item in Phase 2. This explanation appears to be more parsimonious than the hypothesis that chickadees learned a fixed serial sequence of behaviors that involved switching from one side of the aviary to the other.

As can be seen in the percentage choice data, black-capped chickadees did not completely inhibit searches to the worm side during Phase 1. The 28% choice of future worm sites in the first four searches of Phase 1 in the final block of testing is indicative of suppression compared to the first block of testing (approximately 47%) but does not show complete inhibition by the birds. On average, approximately one of the four possible Phase 1 choices was directed to a worm side location by the chickadees during Phase 1 of Block 2. This tendency in chickadees mirrors findings in a retrospective task with chickadees (Feeney et al., 2009). In that study, chickadees were unable to completely inhibit searches to the worm side during Phase 2 of a WWW task after a 5-day delay, by which point worms were degraded and unpalatable. It may be that chickadees value worms enough to occasionally check their availability and palatability. Chickadees' overall behavioral pattern, however, indicates both retrospective and prospective cognitive abilities in the two sets of studies.

General Discussion

In two experiments we investigated the prospective cognitive abilities of wild-caught black-capped chickadees. Experiments 1 and 2 clearly supported the hypothesis that black-capped chickadees, a food-storing bird capable of retrospective WWW memory

(Feeney et al., 2009), would also show anticipation of future events. We found evidence suggesting that black-capped chickadees can anticipate a forthcoming event at least 30 min into the future. This is the first evidence of possible future anticipation in a bird outside the corvid family. Our birds demonstrated behavior suggesting anticipation of future events in both home cage and naturalistic aviary testing, and in two different paradigms, indicating that the behavioral outcomes do not depend on idiosyncratic features of the tasks. As well, the design of these tasks ruled out the notion that caching is necessary for anticipatory behavior.

Experiment 1 revealed that black-capped chickadees showed evidence of anticipation in the form of anticipatory contrast. As found by Flaherty and Checke (1982) and Timberlake et al. (1987) in rats, our results indicate that chickadees inhibit intake of a less preferred food in favor of a future favored food. Chickadees exhibited the contrast effect when the preferred food was delayed at least 30 min, while rats tended to perform worse as the delay increased beyond 16 min (Timberlake et al., 1987). An important difference between our findings and those of Flaherty and Checke (1982) involves the foods used. Flaherty and Checke first provided rats with saccharin solution, a nonnutritive food, and subsequently allowed the animals to access a sucrose solution that was both favored and nutritive. Because we used sunflower seeds and mealworms, both foods in our study had nutritive quality. The fact that chickadees showed anticipatory contrast between two nutritive items rather than between nutritive and nonnutritive foods suggests that anticipation may be a sophisticated and robust capacity. Birds and other animals may use anticipatory contrast to ensure a balanced intake of multiple foods. This is supported by the fact that chickadees did not completely neglect sunflower seeds, but instead reduced intake to avoid satiation when the mealworms were later provided.

Experiment 2 involved a more complex design than Experiment 1 in a naturalistic foraging environment. Black-capped chickadees behaved as if they anticipated future events by modifying their current foraging choices. During Phase 1, chickadees had to search in the location opposite that where their favored food would later be found, to gain later access to their favored food. This design contingency rules out the possibility of simple conditioning because the favored food (worms) location should have higher conditioned secondary reinforcing value than the less favored food (seeds) location. Experiment 2 was also more naturalistic than Experiment 1 in terms of both foraging behavior and the apparatus used. These properties of the experiment suggest that the behavior we observed in black-capped chickadees is not an artifact of laboratory experimentation but likely occurs in birds in the wild as well.

The research we presented supports the idea of an evolutionary hypothesis of selection for retrospective and prospective cognitive abilities in food-storing animals (Clayton & Dickinson, 1998; Feeney et al., 2009; Zinkivskay et al., 2009). Because none of the tasks we used required the animals to cache and retrieve food, which was also the case for the retrospective tasks we employed in examining WWW memory in chickadees (Feeney et al., 2009), our results suggest that future anticipation in these birds does not depend on the act of food caching. In addition, our methods of testing for WWW memory and future anticipation can readily be used with nonstoring birds to test the hypothesis that MTT is dependent on the evolution of food storing behavior.

The mechanism black-capped chickadees employ to achieve future directed behavior was not established by these experiments. Roberts et al. (2008) removed the confound between the two cues for retrospective MTT and found that rats identified past events based on how long ago they occurred, not when they occurred within a temporal framework (circadian time of day). A similar distinction between when and how long from now can be made for future prospection. Events could be anticipated in terms of the exact future time at which they will occur, or as occurring after an interval between the present and future event. The procedures we and other researchers have used in future anticipation tasks confound when and how long from now. It should be possible to determine by experiment which property of future time animals anticipate. Knowing which cues animals rely on to retrospect to the past and plan for the future will allow for better comparison with human MTT abilities. At the same time, it will be important to discover the neural correlates of prospection and retrospection in chickadees as well as other animals (Eichenbaum & Fortin, 2009; Fortin, Wright, & Eichenbaum, 2004). This research represents the first evidence that a noncorvid species of food-storing bird may anticipate the future and take appropriate action. Our work also further supports the idea that nonhuman animals are capable of MTT. The study of MTT in animals may help identify evolutionary homologies and evolutionary convergence between animals and humans in the cognitive processes involved in MTT.

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f. Total Distribution (Sum of 15c and 15e)	746	636
g. Copies not Distributed (See instructions to Publishers #4 (page #3))	121	164
h. Total (Sum of 15f and g)	867	800
i. Percent Paid (15c divided by 15f times 100)	98%	97%

16. Publication of Statement of Ownership
 If the publication is a general publication, publication of this statement is required. Will be printed in the **January 2011** issue of this publication. Publication not required.

17. Signature and Title of Publisher, Business Manager, or Owner
Barbara Spruill
 Dir. Service Center Operations
 Date: **10/8/2010**

I certify that all information furnished on this form is true and complete. I understand that anyone who furnishes false or misleading information on this form or who omits material or information requested on the form may be subject to criminal sanctions (including fines and imprisonment) and/or civil sanctions (including civil penalties).

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