Mechanisms of What-Where-When Memory in Black-Capped Chickadees (*Poecile atricapillus*): Do Chickadees Remember "When"?

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Integrated what-where-when memory, sometimes called 'episodic-like' memory, has been shown to occur in a number of animals, including food-storing birds and rodents. It is not always clear in these studies, however, what aspect of "when" is remembered. We examined memory for what, where, and when in black-capped chickadees *Poecile atricapillus* in a procedure designed to dissociate memory for elapsed time (how long ago) from memory for a point in time, the sense of "when" implied in most discussions of episodic or episodic-like memory. Chickadees searched for food in multiple trials that each involved a two-phase procedure. In Phase 1, birds found preferred mealworms in half the sites on one side of an aviary and less preferred sunflower seeds in half the sites on the other side of the aviary. In Phase 2, following a retention interval, birds searched in the aviary with fresh sunflower seeds placed in the sites that held seeds in Phase 1 but either fresh or degraded mealworms in the sites that held mealworms in Phase 1. Whether a site held fresh or degraded worms depended on either when during the day Phase 1 had occurred (Group When), how long ago Phase 1 had occurred (Group HLA), or both (Group When + HLA). Chickadees in all three groups were able to discriminate where and when palatable worms were to be found, but there were temporal limitations on the use of HLA and When + HLA cues that were not found for the use of When cues.

Keywords: WWW memory, mental time travel, episodic-like memory, when cues, how-long-ago cues, time perception

Episodic memory refers to the ability to remember a personal past event (what event took place) in conjunction with where and when the event occurred. It has been argued that episodic memory is found only in humans (Roberts, 2002; Suddendorf & Corballis, 1997, 2007; Tulving, 1985, 2002). In humans, episodic memory refers to autonoetic consciousness for personal past events, that is, the feeling of consciously and introspectively reexperiencing details of remembered events (Tulving, 1985, 2002). However, research with scrub jays and rats has led to a decade-long debate over whether episodic memory is uniquely human (e.g., Babb & Crystal, 2005, 2006a; Clayton & Dickinson, 1998, 1999; Suddendorf & Corballis, 1997, 2007).

Clayton and Dickinson (1998) identified three behavioral criteria in Tulving's (1972) original conceptualization of episodic memory which they operationally defined for use in nonverbal tests of episodic-like memory in animals. Tulving initially referred to episodic memory as memory for a personally experienced past event (*what*), along with *where* and *when* the event occurred. Thus, in nonverbal analogs to self-report measures, nonhuman animals have to make choices that demonstrate memory for the details of "what" occurred, "where" it took place, and "when" in the past the event occurred. Clayton and Dickinson (1998, 1999) demonstrated that after caching food, scrub jays were more likely to retrieve preferred wax worms first if they had been cached only 4 hr previously, but searched for less-preferred peanuts if worms had been cached 124 hr previously, an interval that caused perishable worms to degrade. The shift in preference, correlated with retention interval, suggested the jays could recall not only where food of each type was located, but also when the caching episode had taken place. Because conscious autonoetic recollection cannot be demonstrated in animals, the ability of nonhuman animals to make choices based on behavioral what-where-when criteria was described as *episodic-like* or *WWW* memory. These results have recently been corroborated in a second food-storing corvid, the magpie (Zinkivskay, Nazir, & Smulders, 2009), and in food-storing black-capped chickadees, members of the parid family (Feeney, Roberts, & Sherry, 2009).

Similar results have been found with rats on the eight-arm radial maze (Babb & Crystal, 2005, 2006b; Naqshbandi, Feeney, McKenzie, & Roberts, 2007; Roberts et al., 2008). During an initial study trial, rats visited four randomly chosen arms, with nonpreferred food pellets placed on three arms and a highly preferred food (chocolate or cheese) placed on a fourth arm. Rats were returned to the maze for a test trial after one of two intervals of time (30 min or 4 hr), with pellets placed on the arms not visited on the study trial and the preferred food replenished on its original arm after 4 hr but not after 30 min. Rats made early

visits to the arm that contained the preferred food after 4 hr but not after 30 min. Thus, rats remembered the location (where) of the arm containing the preferred food (what) and the point in time when it had initially been encountered (when). Further research has extended these findings to show that rats can remember food locations across days (Roberts et al., 2008) and can transfer appropriate choices to novel preferred foods (Babb & Crystal, 2005, 2006a).

Although the discovery that nonhuman animals could remember when an event happened was important, Roberts (2002) and Roberts et al. (2008) cautioned against the conclusion that animals actually remembered a point in time. Memory for when suggests that nonhuman animals are using mental time travel (MTT) to locate a past event within a temporal framework of hours and days. An alternative proposition is that nonhuman animals keep track of how much time has elapsed since an event like caching or encountering a particular food item at a particular place. Without proper contingencies in place, results that indicate memory for "when" cannot distinguish the use of a temporal framework strategy from the use of an elapsed time strategy.

Human beings have at their disposal at least three different mechanisms of memory for time (Friedman, 1993). *Distance-based* cues involve evaluating the passage of time between encoding and retrieval. Information obtained from distance-based processes estimates elapsed time. *Location-based* cues do not rely on the age of a memory, but rather on information associated with the time of encoding. Information about the time of encoding is later retrieved when episodic memory is invoked (Friedman, 1993). Finally, *Relative Time of Occurrence* cues involve the connections between temporally contiguous events, that is, the serial order of events (Friedman, 1993). Serial pattern ordering in nonhuman animals (Hulse & Dorsky, 1979; Merritt, MacLean, Jaffe & Brannon, 2007; Wallace & Fountain, 2002) may result from a process resembling memory for relative temporal occurrence in humans.

Although it may appear reasonable to conclude that nonhuman animals possess location-based memory for "when" (Babb & Crystal, 2005; Clayton & Dickinson, 1998), this may not be the mechanism underlying WWW memory. Instead, nonhuman animals might use a distance-based process of keeping track of elapsed time using an accumulator or circadian timer (Church & Broadbent, 1990; Crystal, 2006; Gibbon, 1991). If this is the case, then WWW memory in animals may be qualitatively different from human episodic memory, which allows people to place past events in an absolute mentally represented temporal dimension (Friedman, 2005). Even honeybees have demonstrated integrated WWW memory (Pahl, Zhu, Pix, Tautz, & Zhang, 2007). Pahl et al. hypothesized that bees use circadian timing and called this ability *circadian timed episodic-like memory.* Interval timing, temporal frameworks, and circadian timing are not equivalent cognitive mechanisms. Although controls for circadian time-of-day cues have been used in experiments with scrub jays (Clayton & Dickinson, 1998) and rats (Babb& Crystal, 2006b; Naqshbandi et al., 2007), controls for discrimination based on elapsed time (how long ago) have not been used.

To distinguish between the possible mechanisms of "when" and 'how long ago,' Roberts et al. (2008) performed an experiment with rats on the 8-arm radial maze. Both the time of day and how long ago a preferred reward was encountered were varied systematically. Reliance on distance-based information in human memory

is akin to the how-long-ago mechanism in rats. Location-based memory strategies can similarly be equated with a "when" mechanism. Different groups of rats in the Roberts et al. experiment could use when, how long ago, or both as cues for the replenishment of the preferred reward. In this way, the location-based and distance-based temporal memory cues were dissociated. Within a single day, rats successfully used memory of how long ago a preferred reward had been encountered to collect fresh replenished rewards and avoid degraded rewards. Rats given only absolute time (clock time) as a cue to a previous encounter with a favored food did not succeed in the task. Similar results occurred in a subsequent experiment that extended the retention interval to two days. The findings of these two experiments indicated that rats were not sensitive to when during the day they first discovered preferred food on an arm of the radial maze. By contrast, rats were able to use elapsed time, that is, how long ago the preferred food was found, to determine whether it would be found replenished or degraded at testing.

The important conclusion from Roberts et al.'s (2008) study is that rats do not need to remember the time at which food was encountered either within a day or between days in order to show the "when" component of WWW memory. The inability of rats to use knowledge of when in a temporal framework a past event occurred weakens the argument that WWW memory in rats is similar to episodic memory in humans. While humans can recall when an event occurred within a past temporal framework of hours, days, or years (Friedman, 1993, 2005), rats appear to remember only how much time has gone by since a past event. Recently, WWW memory using a when cue was demonstrated in rats (Zhou & Crystal, 2009), but in that study how long ago cues were eliminated rather than made irrelevant. There are currently no other tests of preferred timing mechanisms for MTT in nonhuman animals.

Black-capped chickadees (*Poecile atricapillus*) store both perishable insects and nonperishable seeds and remember the spatial locations of caches of different types of food (Sherry, 1984; Sherry & Hoshooley, 2007). In captivity, black-capped chickadees demonstrate accurate spatial memory for multiple food stores (Crystal & Shettleworth, 1994) and can remember the locations of caches for at least 28 days (Hitchcock & Sherry, 1990). Previously, we demonstrated that black-capped chickadees showed WWW memory for food they had found (Feeney, Roberts, & Sherry, 2009) and can accurately anticipate future outcomes of foraging choices (Feeney, Roberts, & Sherry, 2011). However, the results of those studies did not identify the mechanism black-capped chickadees use to represent time. It could be that chickadees perform in a manner similar to rats, overwhelmingly preferring to rely on elapsed intervals (Roberts et al., 2008) unless forced to use a temporal framework (Zhou & Crystal, 2009). Because chickadees scatter hoard food items throughout their habitat, while rats larder hoard food in their burrows, chickadees may have developed more sophisticated means of remembering the temporal properties of caching and foraging episodes than have rats.

In the research reported here, we investigated the temporal process used by black-capped chickadees in a WWW memory task. Three groups of black-capped chickadees were tested for their ability to make return visits to a favored food location. In a between-groups design, the cues that indicated whether a preferred food found on an initial trial would be replenished or degraded on

a test trial were how-long-ago cues only, when cues only, or both how-long-ago and when cues.

Method

Animals

Subjects were 30 wild-caught black-capped chickadees (*Poecile atricapillus*) captured in London, ON in 2008 and 2009. All were adults of unknown sex. Birds were housed in $40.5 \times 30.5 \times 30.5$ cm individual cages in a $2.39 \times 2.87 \times 2.79$ m holding room on a 10:14 hr light–dark cycle with light onset at 7:30 a.m. Birds were maintained on a mixture of ground Mazuri diet, sunflower seeds, and peanuts with water available ad lib.

Materials

The experiment was carried out in a large, three-part testing suite. Birds were observed in a $2.79 \times 2.87 \times 2.79$ m aviary flight area, located between the holding room and an observation room ($1.93 \times 2.87 \times 2.79$ m). Small doors (20×20 cm), one for each of the 16 holding cages, could be remotely opened from the observation area to allow individual birds into the flight area. A one-way observation window (1.17×1.80 m) between the observation room and the flight area allowed trials to be observed and data recorded without disturbing the birds.

The aviary contained four artificial trees consisting of a branch approximately 1.8 m long with multiple smaller branches mounted upright in a green plastic stand. Four holes, each measuring 0.5 cm in diameter and 1 cm deep, were drilled into each tree. Holes were positioned near natural perches on the tree and food was provided in these holes during observation sessions. Birds' visits to holes were monitored in pretraining. 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 near the hole. 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 color. One tree was placed in each of the four corners of the aviary. To prevent visual access to the contents of holes, short pieces of red string were knotted at one end and tied to the branches next to food holes. Knotted ends were placed in the holes to conceal whether a hole held food. Strips of green painter's masking tape were placed around branches to block access to certain holes. Raw hulled sunflower seeds and small mealworms were used as food in all trials.
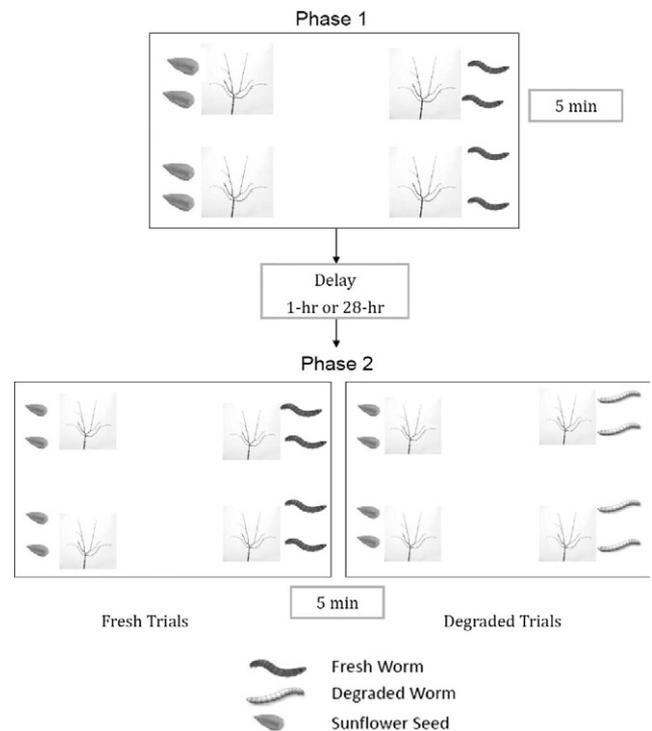
Procedure

Habituation.   Birds were housed in holding cages for 1 month before experimental testing began. Food and water were always available ad libitum. Flight training commenced after the first week of habituation. All birds were given three 30-min sessions of free flight in the testing room to familiarize them with the environment. Holding cage doors were left open to allow birds to fly between the testing room and their home cages.

Foraging training.   Birds were given additional training trials to ensure they were adept at retrieving food from the artificial trees. Birds were food deprived up to 2 hr before these training sessions to ensure they were motivated to collect food. First, food

was placed so that it was visible in the holes in trees and birds were given 20 min to collect and consume food. On two days trees were baited with seeds and on two days trees were baited with worms. The orders of seed (A) and worm (B) days were ABBA, BAAB, ABAB, and BABA and varied between birds. Next, the red strings attached to the trees were placed in the holes to conceal the presence of food and birds were given 15-min sessions in which they learned to pull strings to obtain the food items. String-pulling behavior was acquired in 6 to 10 sessions. Any birds that did not learn the behavior were given an extended afternoon and overnight session in the aviary flight room with food in holes and strings in place.

Testing.   Chickadees were randomly assigned to three groups of eight birds each: Group "When," Group "How Long Ago (HLA)," and Group "When + How Long Ago (When + HLA)." Each group of eight birds was further subdivided into two subgroups of four birds, allowing us to counterbalance temporal contingencies across groups.

Each test trial consisted of two phases, as shown in Figure 1. During Phase 1, eight of the 16 food holes were available, two holes per tree (randomly selected for each trial). The remaining holes on each tree were made unavailable by covering them with

Figure 1. Phase 1 and Phase 2 procedures. One side of the aviary was randomly designated on each trial to be the seed side in Phase 1, the other to be the worm side. Two of the four holes on each tree were baited with either seeds or worms. Unbaited holes were blocked with masking tape. After a retention interval, birds were reintroduced to the aviary for Phase 2. Seeds were replenished at the locations where they were previously encountered in Phase 1. Fresh worms were replenished at their Phase 1 sites on fresh-worm trials; on degraded-worm trials, degraded worms were placed in the holes where birds had found fresh worms in Phase 1. Phase 1 and Phase 2 each lasted for 5 min or less.

strips of masking tape. For each trial, trees on one side of the aviary were designated as the seed trees and trees on the other side of the aviary were designated the worm trees. Baited food holes in the seed trees contained a single raw hulled sunflower seed. Baited holes in the worm trees contained half a small mealworm. Items were placed into the food holes prior to the release of birds into the aviary, and the knotted ends of the strings were inserted into the holes to cover the food items. Food side designations were counterbalanced across trials. To start a trial for individual birds, the home cage door was raised releasing the bird into the aviary flight room. Chickadees were allowed to forage in the aviary for 5 min. Phase 1 terminated when all available food had been retrieved or 5 min had elapsed. At the termination of Phase 1, the aviary flight room light was turned off, the holding cage door was opened, the bird flew back to its lighted holding cage and the holding cage door was closed. Chickadees returned to the aviary flight room to complete Phase 2 after one of two retention intervals, a short retention interval of 1 hr or a long retention interval of 28 hr. Birds remained in their home cages in the cage room during the delay between phases.

During Phase 2, in which the same eight food holes were accessible, fresh sunflower seeds were always replenished at the seed locations. Mealworms could be replaced at Phase 1 locations in either a fresh or degraded state, depending on the group and the time of testing. Mealworms were degraded by drying sacrificed worms and then soaking them in a solution of quinine hemisulfate salt (Sigma Pharmaceuticals Ltd., St. Louis, MO) and Maria's Swedish Bitters (Flora Manufacturing, Burnaby BC).

The exact trial types and replenishment designations used throughout testing varied by group and subgroup (See Figure 2). For Group When, the time of day at which Phase 1 occurred predicted the quality of the mealworms that would be found at worm sites in Phase 2. Thus, for Subgroup When-9 a.m., fresh mealworms were always replenished at Phase 1 worm sites when Phase 1 occurred at 9 a.m., and degraded mealworms were placed at Phase 1 worm sites when Phase 1 occurred at 12 p.m. For Subgroup When-12 p.m., fresh mealworms were always replenished at Phase 1 worm sites when Phase 1 occurred at 12 p.m., and degraded mealworms were placed at Phase 1 worm sites when Phase 1 occurred at 9 a.m. Although Phase 2 retention tests were given on different trials 1 hr and 28 hr after Phase 1 occurred, the length of the delay was an irrelevant cue to the quality of worms to be found in Phase 2.

Whether birds from Group HLA encountered fresh or degraded mealworms depended on the interval between Phase 1 and Phase 2. Subgroup HLA-1 hr always had fresh mealworms replenished at Phase 1 worm sites after a 1-hr delay before Phase 2 and always had degraded mealworms placed in Phase 1 worm sites after a 28-hr delay. Subgroup HLA-28 hr always had fresh mealworms replenished at Phase 1 worm sites after a 28-hr delay before Phase 2 and always had degraded mealworms placed in Phase 1 worm sites after a 1-hr delay. Although Phase 1 commenced at 9 a.m. on half the trials and at 12 p.m. on half the trials, only the length of the delay between Phase 1 and Phase 2 predicted whether fresh or degraded mealworms would be found during the Phase 2 retention test.

Group When + HLA was tested under the standard conditions used in previous WWW or episodic-like memory studies with birds and rats. That is, the time of Phase 1 and the retention
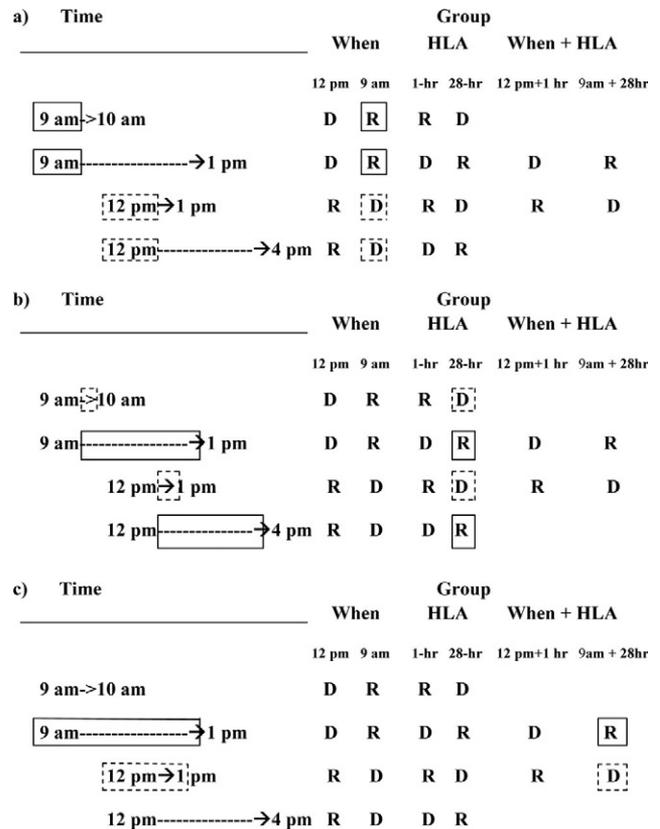

Figure 2. The conditions used with each group and its subgroups are shown in three panels, with Phase 1 and Phase 2 times and retention intervals on the left and the Phase 2 worm condition (R = Replenished; D = Degraded) on the right. The manipulated variable in each group is boxed on the left, with the Phase 2 worm condition in one subgroup boxed on the right. Temporal conditions enclosed by solid boxes signal replenished mealworms, and temporal conditions enclosed by dashed-line boxes signal degraded mealworms. Panel *a* boxes the Phase 1 times manipulated in Group When. Panel *b* boxes the retention intervals manipulated in Group HLA. Panel *c* boxes the Phase 1 times and retention intervals used in Group When + HLA.

interval were confounded so that either could be used to predict the quality of the mealworms found at Phase 1 worm sites in Phase 2. For When + HLA Subgroup (9 a.m. + 28 hr), fresh mealworms were always replenished at Phase 1 worm sites when Phase 1 occurred at 9 a.m. and the delay until Phase 2 was 28 hr and degraded mealworms were placed at Phase 1 worm sites when Phase 1 occurred at 12 p.m. and the delay until Phase 2 was 1 hr. For When + HLA Subgroup (12 p.m. + 1 hr), fresh worms were always replenished at Phase 1 worm sites when Phase 1 occurred at 12 p.m. and the delay until Phase 2 was 1 hr and degraded worms were always placed at Phase 1 worm sites when Phase 1 occurred at 9 a.m. and the delay was 28 hr.

All three groups were tested for 20 trials, five trials at each combination of Phase 1 time and delay for When and HLA subgroups and 10 trials each at 9 a.m. + 28 hr and12 p.m. + 1 hr for When + HLA subgroups. Chickadees were tested on one trial per day with trials that involved the 28-hr delay requiring two days. Days on which each Phase 1 and Phase 2 pairing were tested

were pseudorandomized with no more than three replenished or degraded trials consecutively.

All measurements of birds' behavior in this experiment were recorded by a single experimenter (M.C.F.). A single observer was used because chickadees' choices were nonambiguous. The four trees were placed in the corners of the room, allowing the experimenter to easily see which tree a bird visited. Within trees, the holes in branches where food was hidden were each marked with a different colored ring. Finally, each hole that was used for the various phases of test trials had a knotted string in it that birds had to remove in order to search the hole for food. Removal of the string was quite visible and allowed a clear record of the location chosen.

Results

Three birds developed position habits during the course of the experiment. At the start of a trial, these birds tended to visit the tree in the flight room closest to their home cage. Therefore, birds exhibiting a position habit were not influenced by trial-specific contingencies, and their data were not included in the analyses. As a consequence, data are presented and analyzed for four birds in subgroups When-12 p.m., HLA-1 hr, and When + HLA 12 p.m. + 1 hr. All other subgroups contained five birds. Thus, a total of 27 chickadees were included in the final analyses. All statistical tests were considered significant when $p < .05$.

Initial Choices in Phase 2

We examined birds' first choices in Phase 2 to find out how When and How-Long-Ago contingencies influenced food searching behavior. Because all of the holes in trees were covered with a piece of knotted string at the start of Phase 2, birds had to remember where food was found in Phase 1 in order to obtain fresh rather than degraded worms. Because the trees on each side of the aviary contained only worms or only seeds, birds did not have to rely on memory for type of food locations after their first choice to find each kind of food. That is, birds could pursue a strategy of staying on the same side when a fresh worm was found and switching to the other side when a degraded worm was found. The proportion of trials in which the first choice of Phase 2 was directed to the worm side is depicted in Figure 3a for the three groups. The means show that birds in each group made more first visits to the worm side when worms were fresh than when they were degraded.

The data shown in Figure 3a were analyzed by a 3 × 2 analysis of variance (ANOVA) containing the factors Group (When vs. HLA vs. When + HLA) and Trial Type (Fresh Worms vs. Degraded Worms). The effect of group was not significant, $F(2, 24) = .14$, $p = .87$, but a strong effect of trial type was found, $F(1, 24) = 45.38$, $p < .001$. This significant effect of trial type shows that birds in all three groups searched first on the worm side of the flight room more often on fresh worm trials than on degraded worm trials. The Group × Trial Type Interaction was not significant, $F(2, 24) = 3.17$, $p = .06$, but an examination of Figure 3a indicates that the difference between fresh- and degraded-worm trials was greater in Group When than in Group HLA and Group When + HLA.
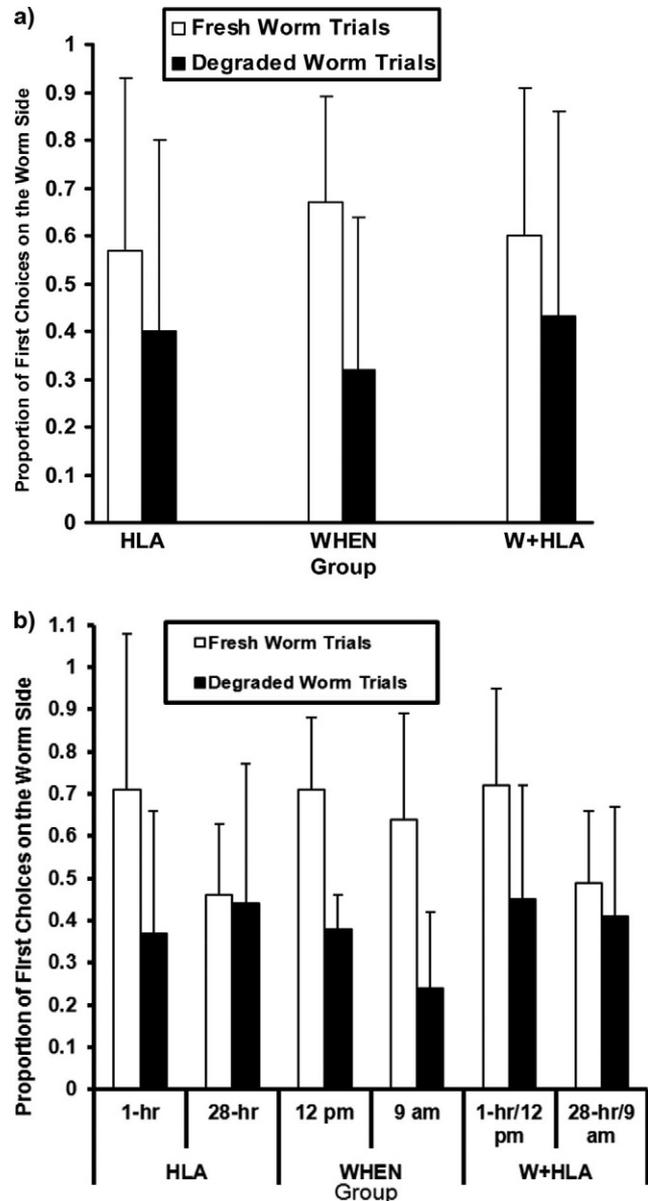

Figure 3. The proportion of first choices in Phase 2 that were directed to the fresh and degraded worm side locations are shown for all birds in Groups When, HLA, and When + HLA (a), and for each subgroup within each of these three groups (b). Error bars are 95% confidence intervals. HLA = how long ago.

The source of this weaker effect of trial type in Group HLA and Group When + HLA than in Group When was explored by examining the first-choice data for each subgroup separately as shown in Figure 3b. These data suggest that a strong effect of trial type appeared in both of the subgroups of Group When. When the data were collapsed across the Group When subgroups, significantly more choices were directed to the fresh worm side than to the degraded worm side, $t(8) = 6.13$, $p < .001$. This effect was observed for both subgroups individually. More fresh worm sites than degraded worm sites were visited initially by Subgroup

9 a.m., $t(4) = 3.83$, $p = .019$ and by Subgroup 12 p.m., $t(3) = 7.55$, $p = .005$.

Examination of Group HLA subgroups (Figure 3b) indicates a different pattern. The effect of trial type is more pronounced in the 1-hr retention interval subgroup than in the 28-hr retention interval subgroup. When data from the subgroups were combined, the proportion of first visits to fresh worm sites was significantly higher than the proportion of first visits to degraded worm sites, $t(8) = 3.06$, $p < .016$. This same effect was significant when data from just Subgroup 1-hr were tested, $t(3) = 3.52$, $p = .04$, but was nonsignificant when data from just Subgroup 28-hr were tested, $t(4) = 1.41$, $p = .23$.

The same pattern appears in the data shown in Figure 3b for the When + HLA subgroups. The pooled data from both subgroups yielded significantly more first choices of fresh worms than degraded worms, $t(8) = 2.62$, $p = .03$. When the subgroups were analyzed separately, significantly more initial choices of fresh worms than of degraded worms were found in Subgroup 12 p.m. + 1 hr, $t(3) = 3.55$, $p = .04$, but not in Subgroup 9 a.m. + 28 hr, $t(4) = .20$, $p = .85$.

Number of Fresh and Degraded Worms Collected per Trial

In Phase 2, each of the trees on one side of the flight room contained two worms and each of the trees on the other side of the aviary contained two sunflower seeds. Chickadees' success at foraging for fresh worms in Phase 2 was analyzed by counting the number of worm sites visited in the first four choices. These data are shown in Figures 4a and 4b as the proportion of fresh and degraded worm sites visited. Figure 4a shows the overall proportions for each group. All three groups visited more fresh worm sites than degraded worm sites in the first four visits, with Group When showing a slightly larger effect than Group HLA and Group When + HLA.

The data in Figure 4a were subjected to a Group × Trial Type ANOVA that revealed no effect of group, $F(2, 24) = .003$, $p = .99$, but showed a highly significant effect of trial type, $F(1, 24) = 85.90$, $p < .001$. The Group × Trial Type Interaction was not significant, $F(2, 24) = 2.61$, $p = .09$.

Figure 4b shows the proportion of worm sites visited in the first four choices for each subgroup. The data from the combined subgroups of Group When yielded a significant effect of trial type, $t(8) = 6.61$, $p < .001$. Tests for the effect of trial type were also significant for Subgroup 9 a.m., $t = 3.61$, $p = .023$ and for Subgroup 12 p.m., $t(3) = 10.34$, $p = .002$.

Data from the combined subgroups of Group HLA shown in Figure 4b revealed that the proportion of fresh worm sites visited was significantly higher than the proportion of degraded worm sites visited, $t(8) = 5.61$, $p < .001$. This difference was also significant in Subgroup 28-hr, $t(4) = 5.19$, $p = .01$, but fell short of significance in Subgroup 1-hr, $t(3) = 2.69$, $p = .07$.

An analysis of the data from the pooled subgroups of Group When + HLA showed significantly more fresh worms taken than degraded worms, $t(8) = 4.08$, $p = .004$. When the effect of trial type was analyzed for each subgroup, it was found that the fresh worm advantage was significant for Subgroup 12 p.m. + 1 hr, $t(3) = 4.14$, $p = .03$, but not for Subgroup 9 a.m. + 28 hr, $t(3) = 2.16$, $p = .10$.
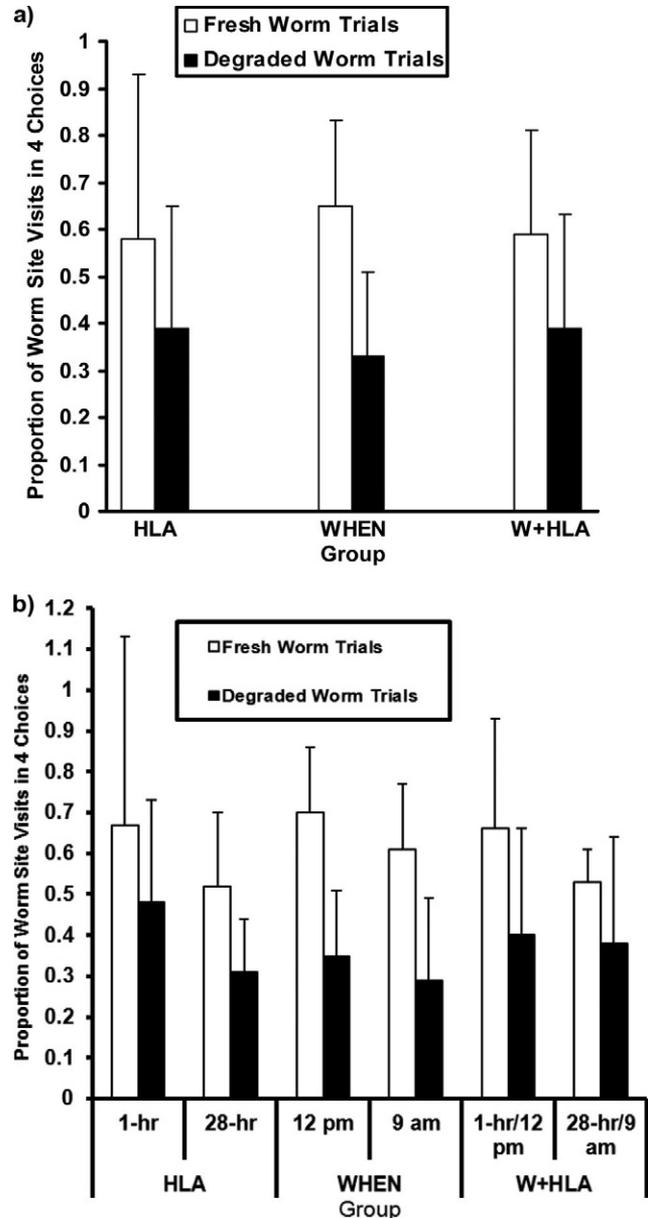

Figure 4. The proportion of the first four choices in Phase 2 that were directed to fresh and degraded worm side locations are shown for all birds in Groups When, HLA, and When + HLA (a), and for each subgroup within each of these three groups (b). Error bars are 95% confidence intervals. HLA = how long ago.

Discussion

The analyses of proportion of fresh and degraded worm sites visited in the first four choices mirrored that for the analysis of first site choice in Groups When and When + HLA. That is, there was an overall preference for fresh worm sites in Group When that appeared in both subgroups 9 a.m. and 12 p.m. In Group When + HLA, there was also an overall preference for fresh worm sites, but the effect was more apparent in Subgroup 12 p.m. + 1 hr than in Subgroup 9 a.m. + 28 hr. The first site visit data and the total

worms collected in the first four visits data did not agree in Group HLA. Although chickadees showed a stronger preference for initial visits to fresh worm sites in Subgroup 1-hr than in Subgroup 28-hr, they visited a significantly higher percentage of fresh worm sites in the first four choices in Subgroup 28-hr but not in Subgroup 1-hr. It should be kept in mind that the initial choice data are a better measure of memory because total worms taken in the first four choices may represent, in addition to memory, a strategy of staying on the worm side of the aviary once a fresh worm was found or switching to the opposite side of the aviary once a degraded worm was found.

The results show that black-capped chickadees have WWW memory for past events. Group When + HLA could use both the time of day when Phase 1 occurred and the retention interval between Phase 1 and Phase 2 as cues to indicate whether fresh or degraded worms would be available in Phase 2. The overall findings were similar to those from previous experiments with scrub jays (Clayton & Dickinson, 1998, 1999) and rats (Babb & Crystal, 2005, 2006b). They also replicated our previous findings of WWW memory in black-capped chickadees (Feeney et al., 2009, Experiment 2). Of more interest was the finding that both Group When and Group HLA showed significantly more initial visits to fresh worm sites than to degraded worm sites. Group When could use only the time of day when Phase 1 occurred as a cue, and Group HLA could use only the length of the retention interval between phases as a cue. The finding that both groups' overall data showed clear discrimination between fresh-worm and degraded-worm trials indicates that chickadees can use both time of day and elapsed time as cues to indicate the state of worms in Phase 2. This experiment provides the first demonstration of these abilities in a bird, more specifically in food-storing black-capped chickadees. It would be of interest to find out if other birds or other food-storing birds can also use unconfounded when and how-long-ago cues.

More detailed analysis of the subgroups used in these experiments revealed some limitations on the use of temporal cues by the birds. Chickadees in Subgroup 9 a.m. and Subgroup 12 p.m. of Group When were able to successfully use both times of day to indicate when worms would be fresh or degraded. However, a clear difference between subgroups appeared in Group HLA. Subgroup 1-hr successfully discriminated between fresh-worm and degraded-worm trials, but Subgroup 28-hr did not. The same pattern appeared in Group When + HLA. Even though this group could use both Phase 1 time and the retention interval as cues, they discriminated between fresh and degraded worm trials only in Subgroup 12 p.m. + 1hr and not in Subgroup 9 a.m. + 28 hr.

Why did chickadees show little discrimination between fresh and degraded worm trials when the retention interval was 28 hr? This behavior may be traced to the natural history of black-capped chickadees. In their natural environment, birds normally retrieve much of the food they have stored within a few days (Brodin, 1992; Cowie, Krebs, & Sherry, 1981; Stevens & Krebs, 1986), though some stored food is retrieved after much longer intervals (Brodin & Ekman, 1994). Foods left for longer periods of time either decay or are taken by conspecific and nonconspecific cache pilferers. An efficient strategy would be to return to cached food or to found food sources after short retention intervals but not to bother searching for them after longer retention intervals. The birds tested in this experiment may have used this strategy and avoided returning to fresh worm locations where food had been found 28 hr earlier. Birds tested in this experiment were wild-caught and may have had ample opportunity to learn from experience that food items cached or found at a particular location may be gone after intervals of a day or longer.

How do the mechanisms responsible for WWW memory in black-capped chickadees compare with those responsible for WWW memory in rats? Roberts et al. (2008) found that rats tested on a radial maze were most successful at foraging for replenished rather than pilfered foods when given access to elapsed time as a cue to the time of occurrence of a past event. In contrast, chickadees in the present experiment showed WWW memory most readily if it was based on when an event occurred in a temporal (circadian) framework. Thus the mechanisms of MTT used by chickadees and rats may differ. This possibility is supported by the fact that chickadees given HLA cues were successful only if worms degraded in an ecologically likely fashion (fresh worms after 1 hr and degraded worms after 28 hr), while performance in rats was not limited by this constraint. The HLA group tested by Roberts et al. (2008) showed equivalent discrimination between replenished and pilfered reward trials at short and long retention intervals. Rats showed little discrimination, however, when the cues were based on the time of day that Phase 1 occurred.

The suggestion that birds are more sensitive to time of day cues than rats is supported by other evidence. Rats can readily keep track of elapsed time intervals, possibly by the use of internal accumulators (Gibbon, 1991), the animal's own behavior (Killeen & Fetterman, 1988) or circadian oscillators (Church & Broadbent, 1990; Crystal, 2006). By contrast, rats do not perform well on time-place foraging tests. McDonald, Hong, Ray, and Ralph (2002) failed to find evidence for a "time of day stamp" in tests of place memory using a Morris water maze, aversive and appetitive context memory, and stimulus-response habits on a radial maze. Under a range of testing conditions, rats regularly exhibit difficulty with memory related to time of day (Carr & Wilkie, 1999; Means, Ginn, Arolofo, & Pence, 2000; Means, Arolofo, Ginn, Pence, & Watson, 2000; Pizzo & Crystal, 2004).

Birds, in contrast, show good accuracy in time-place foraging tasks. In laboratory studies, garden warblers learned when to visit feeding sites that provided food at different times of day, anticipating the next available site once the previous site had depleted (Biebach, Gordijn, & Krebs, 1988; Biebach, Krebs, & Falk, 1994). Field studies also show that foraging pigeons, seagulls, starlings, and crows flock to outdoor locations where people gather to eat in order to collect dropped scraps of food (Wilkie et al., 1996). More important, the birds anticipated the typical peak time of human numbers and available food at these sites even on weekends and holidays. Scavengers' visits thus were predicted most accurately by time of day rather than by the number of people at the site. Many species of bird are adept at using information about daily temporal cycles in food availability to forage successfully.

Additionally, there may be an important difference in the birds' and rats' use of time cues stemming from their daily cycles. Chickadees are a diurnal species that is active and forages from sunrise to sunset. Rats are nocturnal animals that wake at dusk, forage during the night, and return to burrows at dawn. Chickadees and rats may be more sensitive to time of day and the passage of time at different points in the circadian cycle. The fact that nocturnal rats are typically tested during human diurnal waking

hours—the rat's natural nocturnal resting phase—may hinder the ability of rats to use appropriate temporal cues in WWW memory tests when limited to a single cue type.

A final difference between rats and chickadees is that rats are central-place foragers and larder hoarders while chickadees are scatter hoarders. Rats travel outward from a central burrow to locate food in numerous patches throughout their habitat. Foods that are small are consumed in the patch, but larger items that take more time to consume and may leave the forager vulnerable to predation are carried back to the central burrow. It has been shown that rats use this strategy on a radial maze, treating the arms as patches and the center platform of the maze as a central hoarding place (Phelps & Roberts, 1989). Rats also rely on a "win-shift" foraging strategy. Once a patch has been depleted, they shift to a new patch and do not return to the depleted patch over a long interval during which it may become replenished. Rats exploring a radial maze behave in this fashion, either refusing to reenter previously visited arms or doing so only after visiting all the other arms on the maze (Roberts, 1992). The fact that rats prefer to use elapsed time cues in radial maze WWW memory tests (Roberts et al., 2008) is in line rats' preferred foraging and timing strategies. Interval timers or internal accumulators could easily signal to the rat the elapsed time since a patch or arm of the radial maze has been visited. An HLA task that requires subjects to use elapsed time to discriminate between replenished and pilfered food trials may then be easily learned by rats.

Black-capped chickadees are nonmigratory year-round residents in North America. Consequently, they have to adapt to cold winter climates with reduced food availability. To combat the scarcity of food, chickadees store and retrieve food (Sherry, 1984). As scatter hoarders, chickadees store many thousands of food items in their environment, remember these cache locations, and later retrieve the food items (Brodin & Ekman, 1994; Cowie, Krebs, & Sherry, 1981; Hitchcock & Sherry, 1990). With reduced daylight hours during the fall and winter, chickadees need to consume enough food prior to dusk to have sufficient energy stores to survive the long nights. Chickadees may have developed a sensitivity to circadian cycles that allows them to track daylight hours in order to store sufficient energy for their long overnight fast on winter nights. Our current finding that chickadees perform best in WWW memory tests when using absolute time of day cues may be an expression of the adaptive value of a circadian time sense.

How does WWW memory and its underlying mechanisms relate to episodic memory in humans? Humans rely on a distance-based, or HLA, strategy if accuracy for the temporal quality of event information is not crucial and if extreme temporal distances are compared (Friedman, 1993). As well, humans are more likely to give distance-based than location-based estimates of the timing of episodic memories if asked to produce either the date of an event or how many days ago it occurred. In some respects, then, rats' preference for HLA cues is more akin to human tendencies than is chickadees' preference for when cues. On the other hand, humans are able to use both cues, and chickadees likewise seem better able to use both types of cues than rats. It may be difficult to compare WWW memory in nonhuman animals conclusively with episodic memory in humans if the mechanisms controlling WWW memory in nonhuman animals and the factors driving the evolution of these mechanisms do not always pertain to human use of episodic memory. For example, human episodic memory within a temporal framework often involves symbolic linguistic encoding that is not possible in animals.

Different mechanisms for processing temporal perspective in WWW memory may explain why attempts to replicate Clayton and Dickinson's (1998, 1999) scrub-jay findings in other species (rats: Bird, Roberts, Abroms, Kit, & Crupi, 2004; monkeys: Hampton, Hampstead, & Murray, 2005) initially failed. If MTT develops in different ways for different underlying functions in different species, it may not be possible to model MTT across species with a single standard test. An important next step may be identifying ultimate and proximate causes of behaviors controlled by past and future episodic events in nonhuman animals. Such information could then be used to develop tests of MTT for different nonhuman animals that are ecologically valid and thus would allow us to better test the possibility that a species has retrospective or prospective MTT abilities.

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