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Interaction of memory systems is controlled by context in both food-storing and non-storing birds

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Abstract
Animals and humans have multiple memory systems. While both black-capped chickadees (*Poecile atricapillus*) and dark-eyed juncos (*Junco hyemalis*) are under selective pressure to remember reliable long-term spatial locations (habit memory), chickadees must additionally quickly form and rapidly update spatial memory for unique cache sites (one-trial memory). We conducted a series of three experiments in which we assessed the degree to which habit and one-trial memory were expressed in both species as a function of training context. In Experiment 1, birds failed to demonstrate habits on probe trials after being trained in the context of a biased Match-to-Sample task in which the same high-frequency target was always correct. In Experiment 2, habit strongly controlled performance when habits were learned as Discriminations, defining a specific training context. In Experiment 3, context no longer defined when to express habits and habit and one-trial memory competed for control of behavior. Across all experiments, birds preferentially used the memory system at test that was consistent with the context in which it was acquired. Although the memory adaptations that allow chickadees to successfully recover cached food might predispose them to favor one-trial memory, we found no species differences in the weighting of habit and one-trial memory. In the experiments here, context was a powerful factor controlling the interaction of memory systems.

Keywords Chickadee · Process dissociation paradigm · Habit · One-trial memory

Introduction

Memory is composed of multiple systems. Different types of memory are characterized by different functional properties and supported by distinct neural substrates (Sherry & Schacter, 1987; Squire & Zola-Morgan, 1991). A key distinction between systems is that some are subject to cognitive control and some are automatic. Working memory can be monitored and controlled, is highly flexible, is quick to update, and is vulnerable to interference and competing cognitive load. In contrast, *habit memory* is distilled from repeatedly-performed actions or repeatedly=encountered stimuli. Habit memory is automatic, inflexible, slow to update, and highly robust against interference and competing cognitive load.

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Working memory and habit memory often represent redundant information. For example, if you go to the bathroom to brush your teeth before bed, your behavior is likely controlled both by working memory for your current goal of brushing your teeth and the habit of always going to the bathroom to brush your teeth before bed. These redundant pieces of information can cooperate to control your behavior: both types of memory indicate that you should go to the bathroom to brush your teeth. Other times working memory and habit memory encode different information and compete for control of behavior. When two memory systems compete, resolution of the conflict may be determined by extent of training (Hassett & Hampton, 2017; Packard & McGaugh, 1996; Poldrack & Packard, 2003), the match between the training context and the testing context (Roberts, 2019; Roberts et al., 2016a, b), ecology and evolutionary history of the animal (Hampton et al., 1998; Rosati et al., 2014; Wittig et al., 2016), or some combination of these factors.

Cognition is shaped by both the long- and the short-term demands of the environment in which it has occurred. Therefore, species may differ in ability or strategy for solving specific cognitive tasks (Audet et al., 2018; Balda et al.,

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1996; Rosati et al., 2014; Sherry & Strang, 2015). Black-capped chickadees (*Poecile atricapillus*) and dark-eyed juncos (*Junco hyemalis*) are both small passerine birds that over-winter in southern Ontario, where they face cold temperatures and food scarcity. Chickadees and juncos both face predation risk that must be managed while foraging (Lima, 1985, 1988), both forage in flocks with a dominance hierarchy (Fretwell, 1969; Smith, 1976), and the two species have overlapping diets, which include seeds in colder months (Lima, 1988; Odum, 1942). A major difference between these two species is that chickadees cache food and use memory to recover these caches (Sherry & Vaccarino, 1989), whereas juncos do not.

The performance of food-storing black-capped chickadees recovering cached food shows many properties of working memory, such as rapid updating (Barrett & Sherry, 2012; Sherry, 1984), but also manifests other properties, like long duration (Hitchcock & Sherry, 1990; Roth et al., 2012b), which are unlike working memory. Because memory for cached food is not a perfect match with traditional conceptualizations of working memory, but may also not match well with concepts in human memory such as episodic memory either, we here refer to the type of memory associated with cache recovery as "one-trial memory." This term helps capture the features of these memories that make them like working memory while allowing us to avoid premature attachment with previously defined memory systems.

Because chickadees need to remember the locations of cached food they may be predisposed to use one-trial memory more than habit memory. Juncos may rely more on habit memory. We hypothesize this difference occurs because chickadees store hundreds of items in unique locations each day, each of which they experience only briefly, and which they remember with high spatial fidelity (Sherry, 1989). Because scatter-hoarding birds do not re-use cache sites (Sherry et al., 1981), a given cache site is empty, and there is no value in revisiting it once its contents have been retrieved. In contrast to what is often true for other animals, for a chickadee retrieving caches, it is not fruitful to return to a cache site that has been recently paired with food and subsequently depleted, because that site no longer contains food. Memory for cached food must therefore be frequently and flexibly updated. Thus, chickadee behavior may be more strongly controlled by one-trial memory than is the behavior of juncos. Such specialization could reflect both short-term pressures related to experience and learning (Clayton & Krebs, 1994; Patel et al., 1997) and long-term selective pressures (Roth et al., 2010, 2012a).

In contrast, stronger reliance on less flexible, gradually acquired habits can be a very successful strategy for non-caching birds that depend on repeatedly locating the same food patches, or food patches with the same properties across time. Thus, junco behavior may be more strongly controlled by habit memory. Because chickadees also must forage for food to eat immediately or cache, they also need to form habits; however, in recovering caches, chickadees face an additional demand on one-trial memory that juncos do not. Although memory for caches could reflect a specialization uniquely expressed in the context of natural foraging, there is some evidence from laboratory experiments that chickadees may rely more on one-trial memory in other tasks as well, as described below.

Some evidence from the laboratory suggests that chickadees and juncos may solve the same memory tasks with different weightings of memory systems. For example, juncos were more accurate than chickadees in continuous spatial alternation, a task that may be solved by a habitual motor pattern, whereas chickadees were more accurate than juncos on spatial non-Match-to-Sample task, which encourages reliance on one-trial memory (Hampton & Shettleworth, 1996b). On a task where chickadees and juncos were required to remember lists of stimuli, chickadees and juncos showed patterns of errors consistent with different types of memory (Hampton et al., 1998). Chickadees tended to make familiarity-based errors, indicating that one-trial memory more strongly controlled their performance. Juncos made more novelty-based errors, indicating that associative strength more strongly controlled performance. As a result of this difference in strategy chickadees showed a drop in accuracy with longer lists, a pattern not found in juncos. After a manipulation of reinforcement forced both species to rely on one-trial memory, chickadees outperformed juncos.

When two types of memory are in operation, situational demands can also determine which memory system is most strongly expressed. For example, animals may shift between reliance on one-trial memory and on habit depending on whether conditions are stable or rapidly changing, as tested experimentally in serial reversal tasks (Hassett & Hampton, 2017). Factors that influence emotional state, like stress or the administration of an anxiogenic drug, can increase reliance on habit (reviewed in Packard & Goodman, 2013). Task demands like the competing cognitive load of a secondary task (Basile & Hampton, 2013) or intervening items to be remembered (Basile & Hampton, 2010) can attenuate working memory more than familiarity, and working memory but not familiarity, can come under cognitive control as evidenced by their differential susceptibility to directed forgetting (Brown & Hampton, 2020).

Context is one specific situational demand that may affect weightings of different memory systems. Roberts et al. (2016a, b) found an effect of learned context on the relative weightings of one-trial memory and habit memory in pigeons performing two competing memory tasks: Match-to-Sample and Discrimination learning that used overlapping stimulus sets. First, they established the independence of one-trial memory trained in Match-to-Sample, and habit

trained in Discrimination tests by testing them in competition with one another. In a subsequent experiment, the memory tasks were each trained in a distinctive context that used ambient light to cue the type of test that would follow. The context of the ambient light protected one-trial memory performance from competition from habit memory. Thus, if a type of memory is trained in a certain context, subjects may differentially express the memory system associated with that context when tested in that context.

The *process dissociation paradigm* (PDP) can assess the independent contributions of one-trial memory and habit because it allows for simultaneous measurement of the influence of multiple memory systems in a single task (Guitar & Roberts, 2015; Jacoby, 1991; Roberts et al., 2015, 2016a, b; Tu & Hampton, 2013; Tu et al., 2011). Studies of monkeys that use PDP have been based on a modified *delayed Match-to-Sample task* (DMTS), which typically depends on one-trial memory (Tu & Hampton, 2013; Tu et al., 2011). After initial training on DMTS, certain images were selected to be "high-frequency" images, which appeared as the sample more frequently during study and were therefore disproportionately reinforced at test. Monkeys gradually developed a habit that biased them toward selecting the disproportionately reinforced images, whether or not such an image appeared as a sample on a given trial. On Congruent trials the habit and one-trial memory acted in concert, and called for the same response, because the correct choice was a high-frequency sample image. On Incongruent probe trials, the sample was not the high-frequency item. Thus, the test display included both a low-frequency image seen at study and a high-frequency image not seen at study, pitting one-trial memory and habit against one another. Scores describing the strength of habit and one-trial memory were then calculated. In primates, one-trial memory and habit can be doubly dissociated by PDP, with one-trial memory, but not habit, reduced by long delay intervals and habit, but not one-trial memory, affected by reinforcement history (Tu & Hampton, 2013). Similar dissociations have also been described in rats (Guitar & Roberts, 2015) and pigeons (Roberts et al., 2015).

In the current study, we tested chickadees and dark-eyed juncos on a series of spatial memory experiments to assess their reliance on one-trial memory and habit in a process dissociation paradigm. We hypothesized that if chickadee food caching has led to selection for one-trial memory, then chickadees would rely relatively more on one-trial memory compared to non-caching juncos. If this is the case, we would expect chickadee matching performance to generate higher one-trial memory scores compared to that of juncos. By contrast, if the degree to which memory performance is controlled by one-trial memory and habit is primarily determined by situational variables, then one-trial and habit memory scores will be affected equally by task demands regardless of species.

General method

Subjects

Five wild-caught black-capped chickadees (*Poecile atricapillus*) and five dark-eyed juncos (*Junco hyemalis*) were used. Chickadees and juncos were captured by Potter trap and mist nest, respectively, on or near the Western University campus. All birds were adult after-hatch-year birds and sex was not determined. All procedures were carried out under Western University Animal Care protocol 2015-019 and conformed to Canadian Council on Animal Care guidelines.

Each bird was identified with a unique combination of two colored Darvic color bands (Avinet) placed on the same leg. A 12-mm 125-kHz RFID (radio frequency identification) tag (GiS mbH, Lenningen Germany) was attached to the pair of color bands. Each RFID tag had a unique hexadecimal code that could be read automatically to identify birds.

Housing and maintenance

Birds were held individually in one of four outdoor aviaries on the roof of the Advanced Facility for Avian Research at Western University. Each aviary contained branches or shrubs as perches, a wooden overnight shelter, and a touchscreen apparatus. Aviaries varied in size from 2.8 l × 1.2 *w* × 2.3 h to 3.2 l × 2.4 *w* × 2.3 h m. Birds could hear and see other birds in the aviaries and free-living birds outside the aviaries. Birds had ad libitum access to water (heated in winter to prevent freezing). Chickadees had ad libitum access to powdered nutritionally complete Mazuri Small Bird Diet (PMI Nutrition International, Brentwood MO) and were provided with powdered sunflower seed from approximately 1 h before sunset to approximately 8:30 a.m. the following day. Food was powdered to prevent chickadees from making food caches. Juncos were provided with powdered nutritionally complete Mazuri Small Bird Diet mixed with powdered sunflower seed from approximately 1 h before sunset to approximately 8:30 a.m. the following day and were provided with budgie seed mix from approximately 1 h before sunset until dark. Juncos also had ad libitum access to grit. Chickadee and junco diets and maintenance differed slightly, as described, because of different nutritional and energetic requirements of these species. Birds were tested year round.

Touchscreen apparatus

Cognitive testing systems consisted of a touchscreen and laptop computer (Hewlett-Packard, Palo Alto, CA, USA) apparatus that was housed in an all-weather enclosure (Fig. 1). Three horizontal perches attached in front of the

touchscreen at 0, 10 and 18 cm above the bottom of the screen allowed birds to reach any part of the screen. A 7-cm diameter platform or "porch" 20 cm in front of the touchscreen contained an antenna (GiS mbH, Lenningen Germany), which read birds RFID tags to initiate trials. The location of the porch ensured birds could see stimuli presented anywhere on the 15-in. color LCD touchscreen (Elo, Menlo Park, CA, USA). Access to the hopper food delivery system (custom built) was provided through a 1 cm diameter opening in another platform 7 cm in front of and 7 cm below the touchscreen that also contained an RFID antenna that read the bird's RFID tag and confirmed its identification. Infrared beam-break sensors at the opening to the food hopper detected the bird's pecks to the hopper and were used to control the duration of hopper access. The hopper provided powdered black oil sunflower seed. The enclosure stood on a post such that the bottom of the touchscreen was 1.3 m above the aviary floor. Programs written in Visual Basic (Microsoft Corporation) running on the laptop computer displayed stimuli on the touchscreen and recorded RFID detections, infrared beam breaks, and the bird's responses on the touchscreen. Birds could freely come and go from the apparatus and the program resumed running when they returned and were detected by either RFID antenna. Birds were typically tested daily in their home aviaries for the duration of each experiment. Training sessions were monitored for criterion performance; probe sessions were controlled by the computer such that the session ended when birds had completed the desired number of trials.

Statistical analysis

Proportions were arcsine transformed before statistical analysis to better approximate the normality assumption underlying parametric statistics (Keppel & Wickens, 2004, p.155).

For Experiments 2 and 3, we compared Congruent probe trials, in which habit and one-trial memory call for the same test response, with Incongruent probe trials, which pit habit and one-trial memory against one another. We used the proportion of these trials on which birds selected a high-frequency sample location that had been disproportionately reinforced during training to generate PDP scores (Jacoby, 1991; Tu & Hampton, 2013; Tu et al., 2011). The resulting PDP scores could be used to assess the contributions of one-trial memory and habit to memory performance and to compare the relative reliance on one-trial memory and habit across species.

Information on the calculation of PDP scores can be found in the Online Supplemental Material (OSM).

Procedure

Training. Birds were shaped in a series of stages to participate in memory tests. Birds were initially attracted with peanut butter placed on the apparatus. This was followed by a training program that provided food reward for landing in either of the antenna fields or pecking the touchscreen. A subsequent program reinforced landing on the porch, pecking an image on the touchscreen and going to the food hopper, followed by a further program that imposed an FR2 requirement for pecks to the touchscreen. Following a rewarded response to the screen, the hopper was raised and remained raised for 1 s after the infrared beam detected the first peck to the hopper.

Experiment 1

Method

Birds learned three tasks: Discrimination, Match-to-Sample, and Biased Matching.

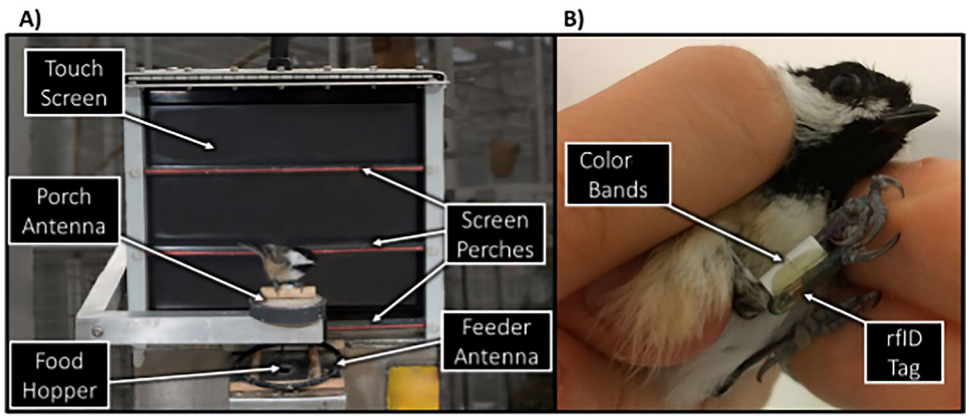

Fig. 1 The touchscreen apparatus. (**A**) A black-capped chickadee working on the touchscreen apparatus. Birds initiated trials by landing on the porch antenna. Stimuli appeared on the touchscreen. Birds could land on screen perches to peck onscreen stimuli. Correct responses were rewarded with access to the food hopper. (**B**) Birds were individually identified by color bands to which an rfID tag was affixed. Birds could be visually identified by their color bands or identified by the touchscreen apparatus by their rfID tag

General task properties. A stimulus consisting of a red textured circle with a white border (50-pixel diameter) was displayed on the touchscreen in one of twelve 256 × 256 pixel squares arranged in three rows of four such that the array filled the screen. The boundaries of the 12 squares were not indicated on the screen. Pecking within the invisible boundaries of the square that contained the stimulus was scored as a response and raised the food hopper to provide a food reward. Stimuli were presented on wallpaper-like scenes that filled the screen. Scenes were color photographs of buildings and landscapes (see details, below). Birds completed different tasks intermixed within the same sessions. We did not provide explicit cues to tell the birds which task they were completing. However, in learning the tasks, birds may have been cued by the presence or absence of a sample, or by the context provided by the distinct background scene and the distinct test location configurations. The ambiguity between the appearance of the different tasks during the test phase allowed us to conduct probe trials on which birds' responses could be controlled by more than one type of memory.

Discrimination. Discriminations assessed habit memory. Birds initiated a trial by landing on the porch. Three red dots appeared on one of 12 background scenes. Each red dot appeared in a different one of the 12 screen squares. The placement and configuration of the three red dots were unique to each of the 12 background scenes, creating 12 distinct Discrimination problems, specific to these trial types. For the three locations linked to each background scene, one red dot location was always the correct target and the other two locations were always incorrect distractors. Birds learned by trial and error which stimulus was associated with food reward in each of the 12 Discriminations.

Match-to-Sample. This task tested one-trial memory. Birds initiated a trial by landing on the porch. A sample stimulus appeared on a background scene in one of the 12 square response locations (Fig. 2). Pecking the stimulus produced a food reward and made the sample stimulus and background disappear, responses made to locations other than the sample did not produce any outcome. The first return to the porch after at least 1 s had elapsed following the end of sample presentation caused three red dots to appear on the same background scene, one dot in the original location and two distractor dots in other squares. Pecking the stimulus in the original location produced a food reward. Pecking a distractor location resulted in the stimuli and background disappearing and a 3-s timeout during which they could not initiate new trials. The complete stimulus set consisted of 12 different three-stimulus arrays, each with its unique associated background scene. The background scenes and stimulus arrays used on Match-to-Sample trials differed from those used on Discrimination trials. Each member of a given three-stimulus array served as the sample equally often in pseudo-random sequence, for a total of 36 different Match-to-Sample tests.

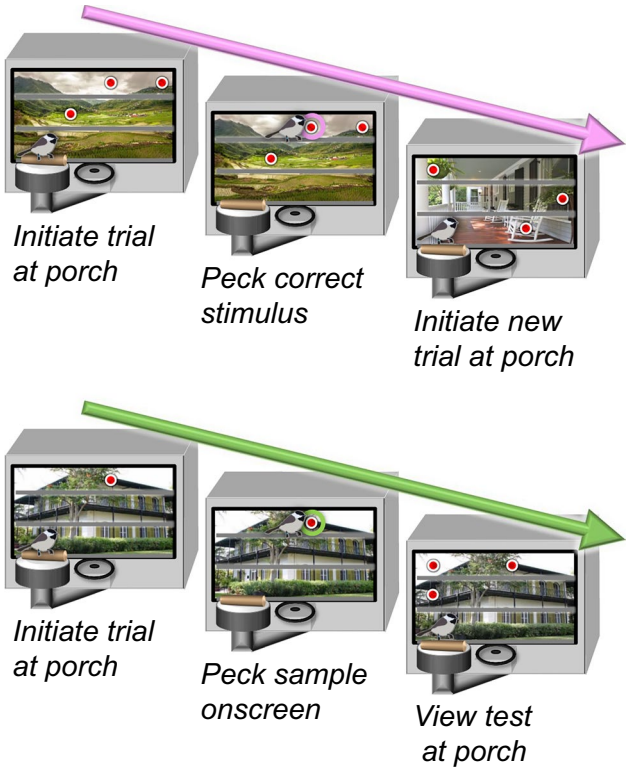

Fig. 2 **Upper:** Discrimination task. Birds landed on the porch to initiate trials. Birds were presented with three locations marked with red dots. Selection of the correct stimulus resulted in a food reward (*not shown)*. Upon returning to the porch, birds were presented with a new trial. **Lower:** Match-to-Sample task. Birds landed on the porch to initiate trials. Birds pecked the red dot sample location to advance the trial. Birds returned to the porch to view a test that consisted of a red dot sample and two red dots in distractor locations. Following a correct response at test, birds could briefly access reinforcement at the food hopper (*not shown*)

Biased Matching. These trials were the same as Match-to-Sample trials except that for each background scene, a particular response location was overrepresented as sample, to allow for formation of a habit. On Biased-Matching trials, the same location on a given background was always the sample and the correct matching choice. The complete stimulus set consisted of 12 different three-stimulus arrays, each with its unique associated background scene for a total of 12 different Biased-Matching tests. Stimulus sets and background scenes differed from those used in Match-to-Sample and Discrimination trials.

Biased-Matching probe trials. Birds met a training criterion of at least 85% correct on Discrimination, Match-to-Sample, and Biased Matching for two consecutive sessions. Then, birds completed Biased-Matching probe trials intermixed with Discrimination and Match-to-Sample trials. Match-to-Sample trials proceeded as they had in training.

Probe trials used the same three-stimulus arrays and background scenes as in training. On Biased-Matching probe trials, the sample phase was omitted. Biased-Matching probe trials and Discrimination trials were reinforced as though they were correct, regardless of the item selected at test. If birds developed habits during training with the Biased-Matching stimulus sets, then they should continue to select the same high-frequency target on probe trials, even in the absence of a sample. Incorrect trials of the Match-to-Sample task were repeated until correct.

Results and discussion

In Experiment 1, we intended to train habits in Biased-Matching trials that could then be used to investigate the degree to which chickadees and juncos relied on one-trial memory and habit. We found no evidence of habits on Biased-Matching probes and no species differences in task performance.

There was no main effect of species, meaning chickadees and juncos did not differ significantly in their overall accuracy on Match-to-Sample, Discrimination, or Biased-Matching probes ($F_{1,8}=0.36$, $p=0.57$) nor was there a significant interaction of species and trial type (Fig. 3; $F_{1.13,9.07}=0.01$, $p=0.95$). Chickadees showed similar highly accurate performance on Match-to-Sample and Discrimination control tasks that they had learned to do in training, as did juncos (paired t-test chickadees: $t_4=1.96$, $p=0.12$; juncos $t_4=0.46$, $p=0.67$), and performance by both species was significantly greater than chance on Match-to-Sample (paired t-test chickadees: $t_4=22.5$, $p<0.001$; juncos $t_4=22.81$, $p<0.001$) and Discrimination (paired t-test chickadees: $t_4=18.06$, $p<0.001$; juncos $t_4=7.16$, $p<0.01$). Accuracy on Biased-Matching probe trials, in which we expected the formation of habits, was significantly lower than accuracy on Discrimination trials, in which birds did form habits (paired t-test chickadees: $t_4=11.98$, $p<0.001$; juncos: $t_4=4.86$, $p<0.01$). Accuracy on Biased-Matching probe trials did not differ from chance (paired t-test chickadees: $t_4=0.72$, $p=0.51$; juncos $t_4=0.94$, $p=0.40$).

In Experiment 1, birds maintained high levels of accuracy on Match-to-Sample and Discrimination tasks that they had learned in training; however, on Biased-Matching probe trials, in the absence of a sample stimulus, birds performed at chance, suggesting that neither chickadees nor juncos had established habits in the Biased-Matching condition. We found no evidence that chickadees and juncos differed in their reliance on one-trial memory and habit memory.

Experiment 2

In Experiment 1, both chickadees and juncos performed at chance accuracy on Biased-Matching probe trials, which assessed the degree to which birds had formed habits as a result of Biased-Matching training. The birds' performance suggested that they had not formed habits that controlled behavior in Biased Matching. Discrimination trials required birds to build a habit to respond to the target on the basis of trial-and-error learning. Because Biased-Matching trials were presented as often as Discrimination trials in training, we expected that there was sufficient time and reinforcement history to build a habit of selecting the high-frequency target stimulus in this task as well.

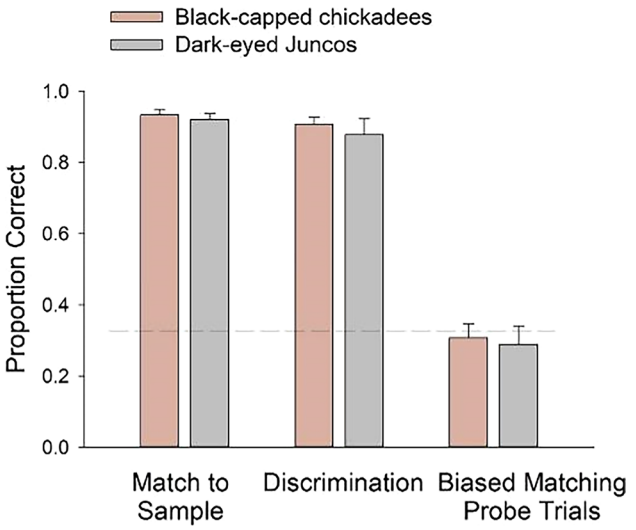

Fig. 3 Accuracy on Experiment 1 probes. Chickadees and juncos performed significantly above chance (dashed line) on Match-to-Sample and Discrimination trials, but showed no evidence of habits in the Biased-Matching probe trials. Error bars are ± 1 SEM

An alternative to the interpretation that birds simply failed to form habits on the Biased-Matching trials is that habits were suppressed on probe trials because the birds learned to associate the red dot arrays and background images presented on Biased-Matching trials with one-trial memory during training. We could not distinguish between failure to learn habits and failure to express them under the training conditions in Experiment 1. In Experiment 2, chickadees and juncos built habits only in the context of Discrimination, and Biased-Matching trials were omitted. After training, they completed probe trials that mixed Discrimination and Matching trials and allowed us to measure the relative contributions of habit and one-trial memory to their performance.

Method

Birds performed Match-to-Sample and Discrimination trials as in Experiment 1 to establish a baseline level of performance of at least 90% correct for each of these tasks in two sessions. Following training, birds were given

two sessions of 108 trials each consisting of probe trials, Match-to-Sample trials, and Discrimination trials. On probe trials, a sample preceded the three-stimulus Discrimination array on its usual background scene. Probe trials were of two kinds (Fig. 4). In Congruent probe trials, the sample stimulus and the rewarded matching choice was the stimulus rewarded for Discrimination trials with that background image and array of test locations. In Incongruent probe trials, the sample stimulus and the rewarded matching choice was one of the two stimuli not previously rewarded for Discrimination trials with that background image and array of test locations. Incongruent probes created a conflict to choose between the stimulus indicated by the sample and the stimulus normally rewarded in that Discrimination array. On probe trials, birds were reinforced for selecting the item that they saw during the sample phase. Each session consisted of four trial types: Congruent probes (with an 8-s delay between sample and choice stimuli), Incongruent probes (with an 8-s delay between sample and choice stimuli), Discrimination trials (as in training) and Match-to-Sample trials (as in training, with a 1-s delay between sample and choice stimuli on two-thirds of trials and an 8-s delay on the remaining one-third of trials). The 8-s delay in probe trials and one-third of the Match-to-Sample trials was longer than the 1-s delay that they experienced during training. We imposed this longer delay to challenge the birds' memory for the sample stimulus and hence their reliance on one-trial memory. These delays were selected on the basis of previous research (unpublished personal observation) to be long enough to induce some forgetting, but short enough to give birds sufficient motivation to continue to complete trials. The four trial types were presented in random order within a session but the number of trials of each type differed: 12 Congruent probes, 12 Incongruent probes, 12 Discrimination trials, and 72 Match-to-Sample trials. Non-probe Match-to-Sample trials were intended to encourage birds to continue to attend to sample presentations. Incorrect trials of the Discrimination task only were repeated until correct to maintain habits.

Results and discussion

Chickadees and juncos did not differ significantly in accuracy on Discrimination probe trials (Fig. 5; $t_8 = 1.25$, $p = 0.25$). On Match-to-Sample probe trials, there was a main effect of delay, such that accuracy at the 8-s delay was significantly lower than after a 1-s delay ($F_{1,8} = 57.38$, $p < 0.001$). Chickadees were more accurate than juncos on Match-to-Sample trials as demonstrated by a main effect of species ($F_{1,8} = 8.13$, $p = 0.021$) but the interaction between species and delay was not significant ($F_{1,8} = 1.13$, $p = 0.32$).

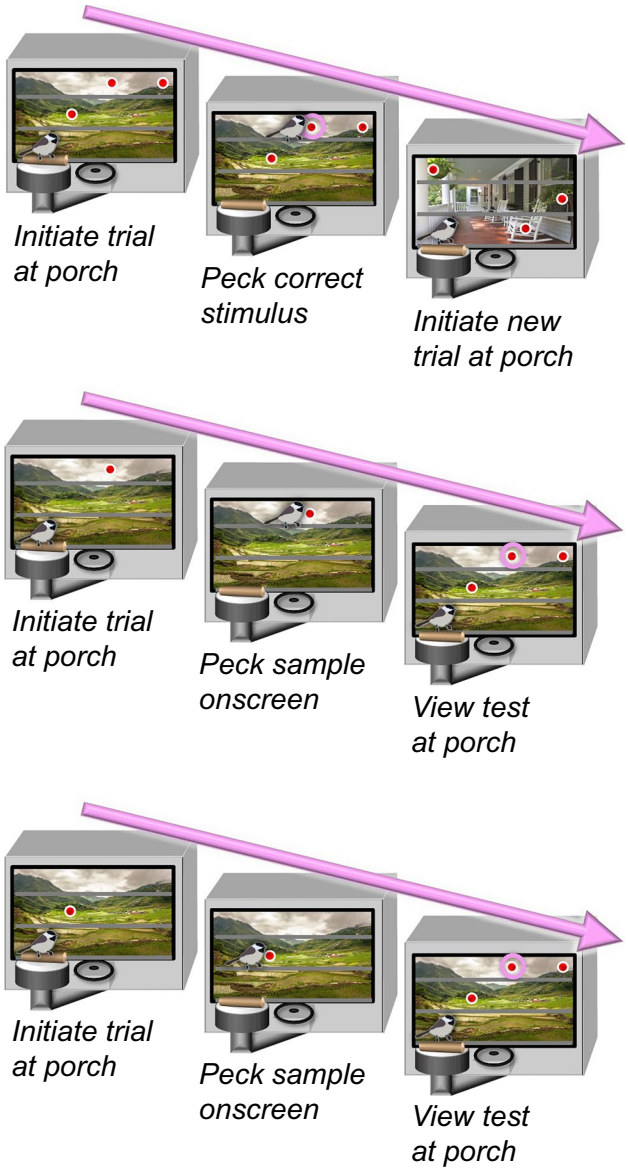

Fig. 4 Probe trial types in Experiment 2 consisted of Match-to-Sample and Discrimination trials as shown in Fig. 2, along with Congruent and Incongruent probes. In a Discrimination trial (**Upper**), the same member of the stimulus array (shown by the purple circle) was always correct. Congruent probes (**Middle**) presented a sample stimulus that was the same as the correct Discrimination choice for that background scene. Incongruent probes (**Lower**) presented a sample stimulus different from the correct Discrimination choice for that background scene

On Congruent probe trials, birds chose the correct Match-to-Sample stimulus, which was also the rewarded choice in Discrimination trials on that background scene, at accuracies greater than 0.90. On Incongruent trials, birds were significantly less likely to choose the stimulus rewarded in Discrimination trials on that background scene, as shown by a main effect of trial type ($F_{1,8} = 20.84$, $p = 0.002$). That is, the Incongruent sample presentation

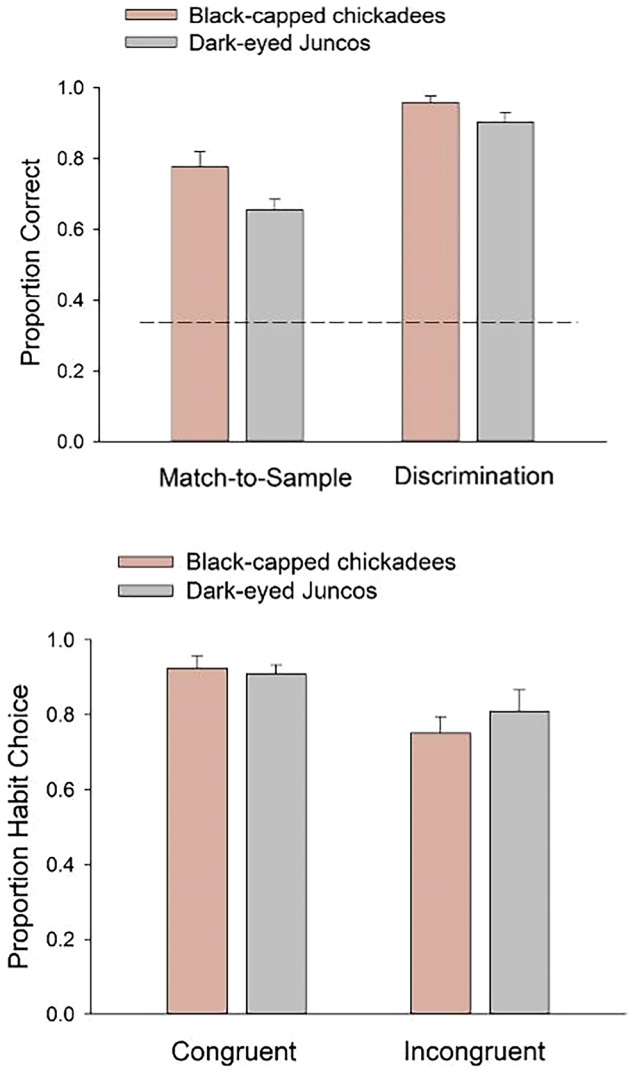

Fig. 5 Accuracy on Experiment 2 probes. **Upper panel:** Chickadees performed significantly better than juncos on Match-to-Sample but not Discrimination probe trials. **Lower panel:** On Congruent probe trials, both species were significantly more likely to choose the stimulus that had been rewarded on Discrimination trials – the habit memory choice – than they were on Incongruent probe trials. Chickadees and juncos did not differ significantly. Dashed line indicates chance performance. Error bars are ± 1 SEM

drew choice away from the stimulus specified by habit memory, indicating that one-trial memory did indeed compete with habit for control of choice. The proportion of choice of the stimulus specified by habit memory, however, remained high, from 0.75 to 0.80. There was no main effect of species ($F_{1,8} = 0.002$, $p = 0.97$) nor was there an interaction between species and the type of probe trial ($F_{1,8} = 2.58$, $p = 0.15$).

We calculated PDP scores for Experiment 2, using the proportion of Congruent and Incongruent trials on which birds selected the stimulus that had been rewarded on Discrimination trials to calculate the relative contributions of habit memory and one-trial memory to performance on probe trials. Habit memory scores significantly exceeded one-trial memory scores (see Table 1). We found no main effect of species on PDP scores. The full statistical analysis of PDP scores for Experiment 2 can be found in the OSM.

In contrast to Experiment 1, we found that habit strongly controlled performance on probe trials in Experiment 2. We found no evidence that chickadees and juncos differed in their reliance on one-trial memory and habit memory.

Experiment 3

In Experiments 1 and 2, we reversed the context in which habits were trained. In Experiment 1, habits were trained in the context of Biased Matching, where certain Match-to-Sample trials consistently reinforced the same high-frequency target, then tested on probe trials in which no sample was presented; in Experiment 2, habits were trained in the context of Discrimination trials, then tested on probe trials that presented a sample before the test. In Experiment 1, when we attempted to train habits in the context of a Match-to-Sample task, no habits were evident.

In Experiment 2, when habits were trained in the context of a Discrimination task, birds' performance on probe trials indicated that habit strongly controlled choice. It is possible that in Experiments 1 and 2, the background scenes served as a context that conditioned the use of one-trial memory or habit (Roberts et al., 2016a). In Experiment 3, habits were trained in two contexts before they were tested in probe trials. Habits were trained through Discrimination trials in which birds had to learn by trial-and-error which item was the target for a given background. The same habits were also trained through Biased-Matching trials, in which the same high-frequency sample was always the target for a given background. Because a given habit was trained in both Discrimination and Match-to-Sample trials, the scene background alone did not predict the type of test that would follow. Therefore the background could not determine the type of memory used on probe trials.

Subjects

Subjects were the same as in previous experiments except that one chickadee was replaced by a different chickadee.

Method

Birds performed Match-to-Sample, Discrimination, and Biased-Matching trials as in Experiment 1 to establish a baseline level of performance. Discrimination and Biased-Matching

trials, however, used the same background scenes so that the presentation of a given background scene did not predict the type of test that would follow. Thus, on a Discrimination trial, three stimuli appeared in three different screen squares and birds determined by trial and error which stimulus could be pecked for food reward. On Biased-Matching trials, the same three stimuli appeared in the same screen squares on the same background scene but were preceded by presentation of a sample stimulus. The sample stimulus and the correct matching choice were the same stimulus that was correct on the Discrimination task for that background scene. There were 12 different three-stimulus arrays, each with its unique associated background scene, and these were the same stimulus arrays and scenes for both Discrimination and Biased-Matching trials. These differed from the 12 different three-stimulus arrays and associated background scenes used for Match-to-Sample trials. Birds had to perform at 90% correct on each of the tasks in two sessions to advance to the next phase of testing.

Following training, birds were given two sessions of 108 trials each. Each session consisted of four trial types presented in random order: Congruent probes as in Experiment 2 (with an equal number of 4-s and 16-s delays between sample and choice stimuli), Incongruent probes as in Experiment 2 (with an equal number of 4-s and 16-s delays between sample and choice stimuli), Discrimination trials (as in training) and Match-to-Sample trials (as in training, with an equal number of 1-s, 4-s, and 16-s delays between sample and choice stimuli). The numbers of trials of each type in a session differed: 12 Congruent probes, 12 Incongruent probes, 12 Discrimination trials, and 72 Match-to-Sample trials. On Congruent probes, as in Experiment 2, the sample stimulus was the stimulus rewarded in the Biased-Matching task on that background scene, which was also the correct choice in the Discrimination task for that background scene. On Incongruent probes, as in Experiment 2, the sample stimulus and the rewarded matching choice was one of the two stimuli not rewarded in the Discrimination task and the Biased-Matching task for that array and background scene. As in Experiment 2, birds were reinforced on probe trials for selecting the item that they saw during the sample phase.

Delays of 4 s and 16 s between presentation of the sample stimulus and the choice array were used on Congruent and Incongruent probes to manipulate the degree to which birds were expected to remember the sample stimulus and thus rely on one-trial memory in probe trials. The 4-s and 16-s delays were longer than the 1-s delays used in training, so we expected them to challenge birds' memory for the sample stimulus. In the probe sessions (exclusively) delays of 1 s, 4 s and 16 s were also used in Match-to-Sample trials. These delays were selected on the basis of previous research (unpublished personal observation) to be long enough to induce some forgetting, but short enough to give birds sufficient motivation to continue to complete trials. Incorrect trials of the Discrimination task only were repeated until correct to maintain habits.

Results and discussion

On Match-to-Sample trials, accuracy at the 16-s delay was significantly lower than after the 1-s delay (Fig. 6; $F_{2,16} = 26.87$, $p < 0.001$). Chickadees and juncos forgot at similar rates with increasing delay and there was no main effect of species on Match-to-Sample trials ($F_{1,8} = 2.10$, $p = 0.19$) nor was there an interaction between species and delay ($F_{2,16} = 1.25$, $p = 0.31$). Chickadees and juncos did not differ significantly in accuracy on Discrimination trials (Fig. 6; $F_{1,8} = 0.94$, $p = 0.36$).

On Congruent probe trials, birds chose the correct Match-to-Sample stimulus, which was also the rewarded choice in Discrimination trials on that background scene, with high accuracy at both 4-s and 16-s delays. There was no main effect of species ($F_{1,8} = 3.23$, $p = 0.11$) and no main effect of delay ($F_{1,8} = 1.01$, $p = 0.34$) on Congruent trial performance (Fig. 7). On Incongruent trials, birds were significantly less likely to choose the stimulus rewarded in Discrimination trials on that background scene than on Congruent trials as shown by a main effect of trial type ($F_{1,8} = 30.46$, $p < 0.001$). Chickadees and juncos showed similar selection of the habit choice – the stimulus that was correct on Discrimination trials – and the species did not differ ($F_{1,8} = 0.18$, $p = 0.69$) nor was there an interaction between species and whether the trial was Congruent or Incongruent ($F_{1,8} = 2.20$, $p = 0.18$).

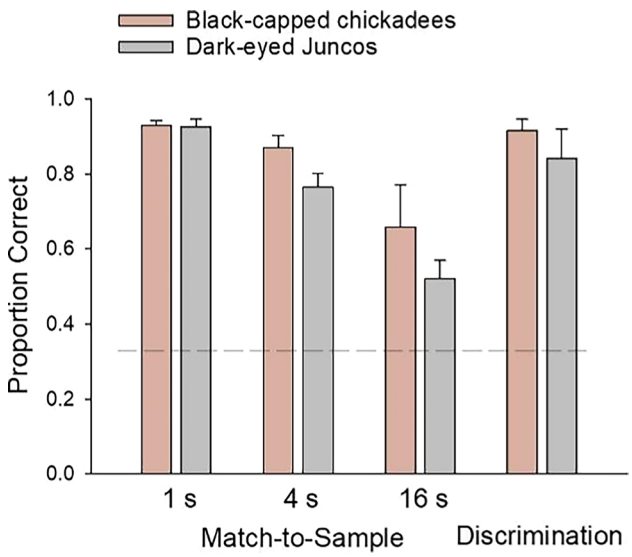

Fig. 6 Accuracy on Experiment 3 probe trials. Chickadees and juncos performed well on short delay Match-to-Sample trials and Discrimination trials. As the delay increased on Match-to-Sample trials performance declined for both species. Dashed line shows chance performance. Error bars are ± 1 SEM

Delay affected selection of the high-frequency image on probe trials differentially on Congruent and Incongruent probes as shown by the significant interaction between delay and type of probe trial ($F_{1,8} = 9.46$, $p = 0.02$).

Habit controlled memory more strongly than one-trial memory ($F_{1,8} = 96.29$, $p < 0.001$). Delay, however, did affect reliance on one-trial memory versus habit; longer delays increased reliance on habit, as shown by a significant interaction between delay and one-trial memory versus habit scores ($F_{1,8} = 6.99$, $p = 0.03$).

We calculated PDP scores for Experiment 3 using the proportion of Congruent and Incongruent trials on which birds selected the stimulus that had been rewarded on Discrimination trials to calculate the relative contributions of habit memory and one-trial memory to performance on probe trials. Delay affected reliance on one-trial memory versus habit (see Table 1). We found no evidence that chickadees and juncos differed in their reliance on one-trial memory and habit memory. The full statistical analysis of PDP scores for Experiment 3 can be found in the OSM.

General discussion

We conducted a series of three experiments that used a process dissociation paradigm to evaluate the ways in which one-trial memory and habit control memory performance in black-capped chickadees and dark-eyed juncos. We found no reliable species differences in the relative use of one-trial memory and habit. Nonetheless we were able to measure both kinds of memory and found that relative use of one-trial memory decreased with delay. Thus, our measures appear appropriate for detecting species differences. We also found that the context in which tasks were learned controlled expression of these two memory systems, as reported previously (Roberts et al., 2016b).

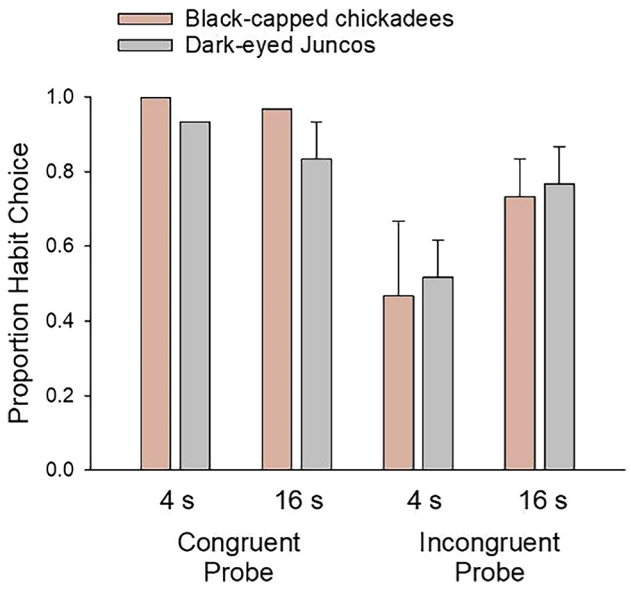

Fig. 7 Performance on Experiment 3 probes. Habit choice on Congruent and Incongruent probe trials is choice of the stimulus that was correct on Discrimination trials for each background scene. Birds were significantly less likely to make a habit choice on Incongruent probe trials. Delay significantly affected choice on Incongruent but not Congruent probe trials. Error bars are ± 1 SEM. Absence of error bars indicates SEM ≈ 0

In Experiment 1 we did not find a species difference in memory system use, and unexpectedly neither species expressed habits during probe trials. The birds' performance on probe trials suggested that they had not formed habits to respond to the high frequency targets, despite performance on Discrimination trials that indicated that they had adequate time and reinforcement experience to build such habits. In Experiment 2, when habits were learned as discriminations, both species showed significant habit expression in probe trials. In Experiment 3, ambiguous contextual cues resulted in memory systems competition on probe trials in both species; performance on the probe trials was controlled strongly by habit, but also by one-trial memory.

The comparison of chickadees and juncos was motivated by differences in their foraging ecology that might cause differences in memory. The hypothesis that the ability to return to the locations of cached food might be supported by specialized memory is well-supported. Within species of chickadees, harsher environments are associated with higher propensity to engage in food caching and with enhanced spatial memory (Croston et al., 2016; Freas et al., 2012; Roth et al., 2012a). Caching birds outperform birds with lower or no propensity to cache on a variety of spatial memory measures (Hampton & Shettleworth, 1996b; McGregor & Healy, 1999; Olson, 1991; Olson et al., 1995). There are also exceptions, and in some studies, robust differences in memory have not been found to correlate with the propensity to cache food (Hampton & Shettleworth, 1996a; Healy, 1995; Healy & Suhonen, 1996). Gould-Beierle (2000) found that in four species of corvids completing a spatial foraging task that relied on working and reference memory, species performance did not correlate simply with dependence on cached food.

We found no reliable differences between species in dependence on one-trial and habit memory. Although we hypothesized that we might see species differences due to the demands that food-caching may have placed on one-trial memory in black-capped chickadees, no species differences were observed. Instead, birds' performance across the three experiments seemed to indicate that birds responded to memory tests according to the type of test predicted by the training context.

The touchscreen memory tasks that we used in our experiments may not readily detect species differences in memory

between chickadees and juncos because we presented all stimuli in the egocentric visual field. Chickadee memory for the location of caches is hippocampus-dependent, and the hippocampus may be more important for allocentric spatial memory than for egocentric spatial memory. Different performance on allocentric navigation-based tasks versus egocentric spatial memory tasks have been obtained in other species in laboratory settings. For instance, in the brown-headed cowbird, an obligate brood parasite, females may have a hippocampus adaptively specialized for spatial memory to find and track appropriate host nests (Guigueno et al., 2016). Guigueno et al. (2014) found that female cowbirds outperform males in the laboratory on a spatial open field foraging task. However, female cowbirds did not outperform males on a spatial Match-to-Sample task when it was presented on a touchscreen (Guigueno et al., 2015). Similarly, there is evidence that non-navigational, but not navigational, spatial memory is spared following hippocampal lesions in rhesus monkeys (Basile & Hampton, 2019). Nevertheless, there are laboratory studies which suggest that chickadees, compared to juncos, preferentially rely on spatial information in operant tasks that utilize a constrained visual space (e.g., Brodbeck & Shettleworth, 1995), which suggests that touchscreen operant tasks are capable of simulating the same spatial memory demands as non-touchscreen tasks.

Our finding that context influenced memory system use in our birds is consistent with previous work by Roberts et al. (2016a, b) showing that context had powerful control over performance on a comparable task in pigeons. While there is considerable overlap in experimental design, our work differed in the context cue type and presentation. Roberts et al. (2016a, b) intentionally used context as an experimental cue by pairing ambient light in an operant chamber with one-trial memory and habit training, whereas our background scenes were incidentally encoded as a cue for memory system use. In another intentional manipulation of context, brightness, and texture of the surface on a radial arm maze was used to cue use of one-trial memory or habit in rats (Roberts et al., 2016a). While effects in rats were not as large as those shown in pigeons, testing in a context previously paired with one-trial memory did reduce competition from habit memory. Taken together, these findings and our own suggest that situational factors can influence memory competition across a variety of cue types, training procedures, and species, making it clear that context affects the interaction between memory systems. Caching itself could act as a contextual cue that controls the expression one-trial memory for chickadees foraging in the wild.

Uncertainty remains about the specific nature of some memory processes addressed in the experiments described here. Here, one-trial memory is an operational term for a system that has not been well enough characterized to place reliably in standard memory system taxonomies. Working memory is a strong candidate, though other candidate processes could also include episodic memory, recollection, or familiarity. It is likely that Match-to-Sample performance relied heavily on working memory in this study because we drew from a small, repeating set of 12 screen locations (e.g., Brown & Hampton, 2020). With a small, repeating set of stimuli, every location has been seen recently and is highly familiar, which diminishes the utility of familiarity for identifying the most recently seen target location. We also do not know if the contextual cues that controlled reliance on one-trial memory versus habit memory in our experiments are explicitly or incidentally encoded. It will be informative in future research to further specify these processes.

Chickadees and juncos likely use both one-trial memory and habit in their daily lives. Both chickadees and juncos must find food patches, which requires repeatedly locating the same food patches, or food patches with the same properties across time. Thus, we would expect habits to be useful in foraging for both species. We hypothesized that the natural foraging behavior of chickadees might predispose them to rely more on one-trial memory because successfully retrieving caches and avoiding emptied cache sites relies on frequently and flexibly updated memory. However, we would also expect that one-trial memory is useful in foraging for juncos. For instance, one-trial memory would allow a junco to return to a fruitful foraging patch after just one visit. Indeed, juncos perform well on a variety of one-trial memory tasks in the lab: juncos and chickadees have shown comparable accuracy on spatial matching tests that we might expect to rely on one-trial memory (Hampton & Shettleworth, 1996a; Shettleworth & Westwood, 2002).

We evaluated hypotheses about the degree to which chickadees and juncos rely on habit and one-trial memory as a consequence of evolutionary pressures imposed by each species' behavior and ecology, and by the immediate pressures of situational context. We did not find reliable differences in performance between chickadees and juncos in the experiments presented here. However, we did find evidence that both species responded on probe tests on the basis of training context. At least in these experiments, memory was likely controlled by the context in which the stimuli were learned.

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Availability of data and materials (data transparency) The datasets from the current study are available from the corresponding author on reasonable request.

Code availability (software application or custom code) The codes from the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval All procedures were carried out under Western University Animal Care protocol 2015–019 and conformed to Canadian Council on Animal Care guidelines.

Consent to participate N/A

Consent for publication All authors consent to the publication of this article.

Conflicts of interest/Competing interests The authors declare no conflicts of interest.

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