

Interacting Cache Memories: Evidence for Flexible Memory Use by Western Scrub-Jays (*Aphelocoma californica*)

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When Western Scrub-Jays (*Aphelocoma californica*) cached and recovered perishable crickets, N. S. Clayton, K. S. Yu, and A. Dickinson (2001) reported that the jays rapidly learned to search for fresh crickets after a 1-day retention interval (RI) between caching and recovery but to avoid searching for perished crickets after a 4-day RI. In the present experiments, the jays generalized their search preference for crickets to intermediate RIs and used novel information about the rate of decay of crickets presented during the RI to reverse these search preferences at recovery. The authors interpret this reversal as evidence that the birds can integrate information about the caching episode with new information presented during the RI.

Western Scrub-Jays (*Aphelocoma californica*, formerly a subspecies of *A. coerulescens*¹), like other food-storing species, cache numerous food items throughout their territories and recover a large proportion of them over the course of the ensuing winter and spring. For example, in the Florida Scrub-Jay (*A. coerulescens*), a species closely related to the Western Scrub-Jay, 29% of the food items that breeding females receive from their mates during the egg-laying and incubation period consists of stored acorns (DeGange, Fitzpatrick, Layne, & Woolfenden, 1989). Although it is now well established that many food-storing species use memory to relocate their caches (see Shettleworth, 1995), a series of studies of cache recovery by captive, hand-raised birds suggest that Western Scrub-Jays remember not only where they stored their caches but also what type of food was cached and, possibly, how long ago a particular type of food was stored (Clayton & Dickinson, 1998, 1999a, 1999b; Clayton, Yu, & Dickinson, 2001).

In one series of studies, the jays were allowed to cache different food items in the two sides of trial-unique visuospatially distinct

caching trays (Clayton, Yu, et al., 2001). On all trials, the birds cached peanuts in one side of the tray and either mealworms or crickets in the other side of the tray. The peanuts were always fresh at recovery, whereas the mealworms and the crickets decayed at different rates across the retention intervals (RIs) between caching and recovery. Of relevance to the present study is the fact that the crickets were fresh after a 28-hr or 1-day RI but they had decayed after a 100-hr or 4-day RI. To give the birds the opportunity to learn about the rates at which crickets (and mealworms) decayed, each bird first received four training trials at each RI in which they were allowed to recover and eat the cached food items. Following this training, the birds received test trials to assess whether the pattern of searching at recovery was based on memory for the caching episode (see Clayton, Yu, et al., 2001). These test trials differed from the training trials in that the cached food items were not present in the tray at the time of recovery so that differential searching in the two sides of the tray must have been based on memory for the caching episode.

The results of this experiment provided evidence that the birds learned about the rate at which crickets decayed and remembered the caching episode. Whereas the majority of birds directed their searches to the cricket side of the tray after the 1-day RI, their preference switched after the 4-day interval, with the majority of birds searching predominately in the peanut side. This recovery profile suggests that the birds in this degrade group learned about the rate at which the crickets decayed during training, a conclusion

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¹ In previous publications (Clayton & Dickinson, 1998, 1999a, 1999b; Clayton, Yu, et al., 2001, Emery & Clayton, 2001), we have referred to our Scrub-Jays as *Aphelocoma coerulescens*. However, the American Ornithologists' Union (1995) now uses *A. coerulescens* to refer exclusively to the Florida Scrub-Jay, and the Western Scrub-Jay is classified as a separate species, *A. californica* (see Emery & Clayton, 2002).

reinforced by the fact that the same preference reversal was not observed in a control, the replenish group. For this group, the crickets were always fresh at recovery, and the birds searched the cricket side preferentially after both the 1- and 4-day RIs.

On the basis of these recovery profiles, we suggested that Western Scrub-Jays form episodic-like memories of individual caching episodes. In other words, the birds encode information about the location and content of the caches as well as the time at which caching occurred in the form of an integrated, “what–where–when” representation of the caching episode (Clayton, Griffiths, & Dickinson, 2000; Clayton, Griffiths, Emery, & Dickinson, 2001; Griffiths, Dickinson, & Clayton, 1999).

Although our studies (Clayton & Dickinson, 1998, 1999a, 1999b; Clayton, Yu, et al., 2001) have established that searching at recovery is controlled by the retrieval of information about the location and content of their caches, what may be more contentious is whether the birds remembered when the caching occurred (Roberts, 2002). For example, the reversal in searching at recovery from a preference for cricket sites after a 1-day RI to a preference for peanut sites after a 4-day RI may have reflected differential forgetting of the peanut and cricket caches rather than memory for the time of caching. The fact that the replenish group did not show a comparable reversal with RI established that the intrinsic properties of the peanut and cricket caches did not induce different rates of forgetting. However, the varying states of the caches at recovery experienced by the degrade group may have done so. Although peanuts were always palatable at recovery, the state of the cricket caches at recovery was uncertain at the time of caching. Past experience with the fact that the crickets were sometimes unpalatable at recovery may have led the birds to devote less time and/or attention to encoding the location of the crickets than those of the peanuts at the time of caching, with the consequence that the cricket caches might have been forgotten more rapidly.²

In the present studies, we examined this encoding-induced forgetting account of the temporal control of recovery. Following the training and testing reported by Clayton, Yu, et al. (2001), we tested the recovery preference of the same birds at RIs intermediate to the trained intervals of 1- and 4-days to determine whether progressive forgetting occurred. Then, in a second experiment, we provided these birds with information about the state of the caches at recovery during the RI to determine whether this new information that had been acquired after caching altered the temporal control of search at recovery. As this information was supplied after caching, it should have had no impact on the temporal control of recovery if this control reflected variations in forgetting induced by differential encoding at caching.

Experiment 1

There is a general consensus that forgetting occurs progressively with lengthening of the RI (see Baddeley, 1997, for a review). To determine whether the temporal control of searching for crickets established by Clayton, Yu, et al. (2001) showed this characteristic of forgetting, we gave the birds test trials after untrained RIs of 2, 3, and 5 days. On each of these trials, both the degrade and replenish groups cached peanuts in one side of the caching tray and crickets in the other before being allowed to search in the tray after the requisite RI. If the low levels of searching in cricket sites by the degrade group after the trained 4-day retention reflected forgetting

of the cricket caches, we expected the number of searches by the degrade group to have declined across the 2- and 3-day RI and to have remained at a low level after the 5-day interval.

Method

Subjects and Apparatus

Sixteen, sexually mature, hand-raised Western Scrub-Jays (*Aphelocoma californica*) of unknown sex were housed individually in cages measuring 91 cm wide × 91 cm high × 76 cm deep. The birds had most recently participated in a series of experiments reported by Clayton, Yu, et al. (2001), and they remained in the degrade ($N = 8$) and replenish ($N = 8$) groups established in those studies. The birds were maintained in natural daylight and fed a diet of shelled peanuts and Iams minichunk dog food kibbles, which we gave in a finely powdered form to ensure that the birds only cached during the experimental trials. During caching periods, whole peanuts and crickets were provided in 15-cm diameter bowls. Birds cached in plastic ice-cube trays (6 × 25 cm), which consisted of a 2 × 8-array of 2.5-cm cube moulds filled with sand, each of which was a potential cache site. Each tray was attached to a wooden board (15 × 32 cm) and made visuospatially distinct by a Lego Duplo structure that was placed next to one of the long sides of the tray (see Clayton & Dickinson, 1998, 1999a).

Procedure

General procedure. The general procedure was the same as that used by Clayton, Yu, et al. (2001). Each trial consisted of two caching periods followed after a RI by a recovery period. The maintenance diet was removed from the home cage 4 hr before the first caching period, during which a caching tray and a bowl of 50 food items was placed in the cage. We restricted access to one half of the tray by placing a transparent Perspex cover over the left- or right-hand side of the tray, and bulldog clips were attached to each side to keep it firmly in place. Each bird was allowed to eat and cache freely in the open side of the tray. After 15 min, the tray and bowl were removed. The Perspex cover was moved to the other half of the tray (thereby covering the sites just cached in) and replaced in the same location in the cage, together with a bowl containing the other food items for a further 15 min. The Lego structure surrounding the caching tray not only differed on every trial for each bird but also from all of the structures previously presented to that bird. On each trial, the birds cached peanuts in one side of the tray and crickets in the other side, with the order of caching counterbalanced across the birds within each group. Furthermore, the order of caching alternated across trials and the side of the trays on which the two foods were cached also varied across trials in a double alternation schedule so that no particular side was selectively associated with one type of food.

At the end of the second caching period, the experimenter removed the tray from the home cage before recovering the food items from the tray and recording the location of each cache. The maintenance food was then returned to the bird's home cage at the start of the RI and removed 4 hr prior to the recovery period except when the shortest RI (4 hr) was used.

² As the training procedure in Clayton, Yu, et al. (2001) included a 4-hr retention after which the crickets were fresh, as well as the 1-day (28-hr) and 4-day (100-hr) intervals, the jays encountered degraded crickets during a third of the recovery periods. This study also included trials in which peanuts and a third food type, mealworms, were cached and recovered after the same three RIs. As the mealworms degraded after 1 day, the jays encountered degraded mealworms on two thirds of recovery. Consequently, the encoding-induced forgetting account can explain why these birds failed to search in mealworm sites after 1 day if it is assumed that encoding of caching is determined by the likelihood of encountering a fresh food type at recovery.

On these trials, the birds remained without the maintenance diet during the RI, which was then returned after the recovery period. Prior to each recovery period, the sand substrate was replaced and smoothed over to remove any local visual and olfactory cues about the location of cache. On training trials, the trays were restocked with the number and types of food items that the bird had cached on that trial in the same locations. When appropriate, the crickets were rendered unpalatable by soaking them in unscented washing-up liquid and leaving them to dry until they turned black. By contrast, the food items were not returned to the trays on test trials, and the trays were filled with fresh sand to test for memory in the absence of cues emanating from the food. During the 5-min recovery periods, the tray was returned to its original location in the home cage, and the birds were allowed to search their caches from both sides of the tray. At the end of the recovery period, the experimenter removed the tray and returned the maintenance diet to the cage. The caching periods occurred in the morning, and the recovery periods occurred 4 hr later, in the afternoon. Consequently, as the caching and recovery occurred at the same time of day on all trials, the birds could not use diurnal cues to control their recovery preferences. At least 1 day intervened between successive trials.

Summary of prior training and testing in Clayton, Yu, et al. (2001). Using this general procedure, the birds had received four of each of six types of training trials in Experiment 1 of Clayton, Yu, et al. (2001). On all training trials, they cached peanuts in one side of the tray and either mealworms or crickets in the other side before recovering these food items after RIs of 4, 28, and 100 hr. For the degrade group, the mealworms were decayed at recovery after RIs of 28 and 100 hr, whereas the crickets were decayed after only the 100-hr RI. All caches were palatable at recovery for the replenish group. Following this training, each of these six types of trials was repeated as test trials, with all of the caches removed prior to recovery. Experiments 2 and 3 each consisted of two test trials in which the birds cached mealworms in one side of the tray and crickets in the other side before being allowed to search for these caches after 4 and 28 hr. Experiment 4 also assessed searching for caches on two, interleaved test trials with a 4-hr and 28-hr RI, but on these trials the birds cached peanuts in one side of the tray and mealworms in the other side.

Forgetting tests. Following the last test trial of Experiment 4 of Clayton, Yu, et al. (2001), the jays received two forgetting test trials in December 1999. In these and all subsequent training and test trials, they cached peanuts in one side of the tray and crickets in the other. On one trial, the RI was 2 days (52 hr), and on the other trial it was 3 days (76 hr). A month later in January 2000, the birds received retraining trials with 4-hr and 4-day (100-hr) RIs followed by a second pair of test trials; on one trial the RI was again 3 days, and on the other it was 5 days (124 hr). Within each pair of trials, the 3-day trial was presented first for half of the birds in each group and second for the remaining birds, and the test trials of each pair were separated by a 4-hr retraining trial.

Behavioral measures and analysis. The number and location of the food caches were recorded by determining which cube moulds contained caches at the end of each caching period. During recovery, birds searched for food by probing the sand substrate and by repetitively swiping at the sand with their bills in an apparent attempt to clear the sand from the cube mould. The total number and location of bill probes and bill swipes was recorded by direct observation, and specific cube-mould sites inspected by the birds during recovery were then verified by noting the disturbances in the sand substrate in each cube mould. To minimize observer bias, different experimenters recorded the behavior during the caching and recovery periods. Therefore, during recovery the experimenter was unaware of the type of food that had been cached in each side of the tray.

We recorded three measures during the recovery periods: the total number of bill probes and swipes directed to each side of the tray, the number of searches on each side of the tray, and the side of the first search. The first probe or swipe to a cube-mould site counted as a search, and a further search was recorded whenever a bird returned to that site having searched in another cube mould. The total number of bill probes and swipes

and the total number of searches yielded the same pattern of recovery. We therefore report only analyses based on the total number of searches, which is the same measure as reported in our previous studies of cache recovery (Clayton & Dickinson, 1998, 1999a, 1999b; Clayton, Yu, et al., 2001). These analyses used a mixed analysis of variance, with group or condition as the between-subjects variable and RI and food type (peanuts vs. crickets) as the within-subjects variables. Group differences in the side of first search were evaluated by the Fisher exact probability test. In all cases, we evaluated significance against a Type I error rate of .05.

Results

We assessed recovery preference by two measures: the proportion of birds in each group that directed their first search to the cricket side of the tray (top panel of Figure 1) and the number of searches in the cricket side of the tray as a proportion of the total number of searches for each bird (bottom panel of Figure 1). To derive a measure for the 3-day interval, the proportions from the two tests with this RI were averaged, except for 1 bird in the degrade group that failed to cache any crickets on the second 3-day trial. Consequently, the 3-day proportion for this bird was based solely on the first trial. In addition, 2 birds were dropped from the replenish group for failing to cache either crickets or peanuts on the 2-day or 5-day trial. The proportions for the 1-day (28-hr) and 4-day (100-hr) RIs were taken from the test trials of Experiment 1

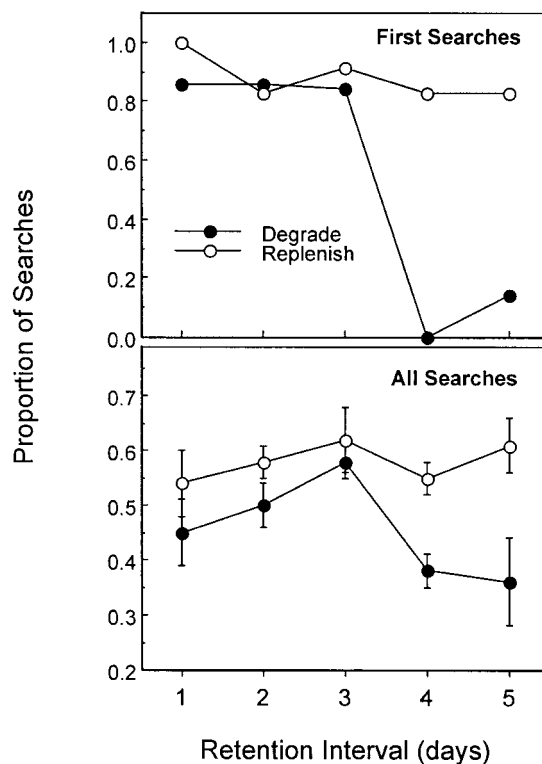


Figure 1. Proportion of birds that directed their first search to the cricket side of the tray at recovery (top panel) and the mean proportion ($\pm SEM$) of searches directed to this side (bottom panel) at the different RIs by birds in the degrade and replenish groups. The proportions for the 1-day and 4-day retention intervals are taken from Experiment 1 of Clayton, Yu, et al. (2001), and the proportion for the 3-day retention intervals is averaged across the two tests with this interval.

of the Clayton, Yu, et al. (2001) report (see previous description). The inclusion of these data required the omission of a further bird from the degrade group that failed to cache both food items on these test trials. In summary, the proportions illustrated in Figure 1 are based on 7 birds in the degrade group and 6 in the replenish group.

As the top panel of Figure 1 illustrates, the replenish group showed stable proportions of first searches in the cricket cache sites across variations in the RI, with no more than 1 bird in this group directing its first search to the peanut side at each RI. By contrast, the proportion of first searches varied with RI for the degrade group. As in the replenish group, only a single bird in the degrade group searched the peanut side first after the 1-, 2-, and 3-day RIs. However, this preference switched completely after longer RIs, with all of the degrade group directing their first search to the peanut side after the 4-day RI, and 6 of the 7 birds doing so after the 5-day RI. Consequently, the degrade group showed a reliably lower proportion of first searches in the cricket side on the 4-day ($p = .01$), and 5-day ($p = .02$) test, although there were no differences between the groups for the 1-, 2-, and 3-day retention tests ($ps > .50$).

The bottom panel of Figure 1 shows that this profile was recapitulated in the proportion of all searches directed to the cricket side of the tray. Although the proportions for the degrade group were slightly, but not significantly, lower than those for the replenish group for the 1-, 2-, and 3-day RIs, the 4- and 5-day RIs produced a marked divergence between the groups, with the degrade group searching preferentially in the peanut sites after the longer RIs. An analysis of the proportion of searches directed to the cricket sites yielded only a significant main effect of group, $F(1, 44) = 4.40$, $MSE = 0.03$, but no significant Group \times Retention Interval interaction $F(4, 44) = 1.63$. However, simple main effects analyses revealed a significant difference between the degrade and replenish groups at the 4- and 5-day intervals, smallest $F(1, 11) = 7.01$, $MSE = 0.03$, but not at the 1-, 2-, and 3-day RIs, largest $F(1, 11) = 2.13$. The effect of RI was significant for the degrade group, $F(4, 44) = 3.86$, $MSE = 0.01$, but not for the replenish group ($F < 1$). We analyzed the source of the RI effect for the degrade group by a series of orthogonal contrasts. There was no significant difference between the proportions for the 2- and 3-day intervals or between these proportions combined and that for the 1-day interval ($Fs < 1$). Similarly, the proportions for the 4- and 5-day intervals did not differ ($F < 1$). Importantly, however, the combined proportions for 4- and 5-day intervals were significantly lower than the combined proportions for the 1-, 2-, and 3-day intervals, $F(1, 24) = 15.33$, $MSE < .01$.

Finally, it should be noted that these recovery profiles were not confounded with differences in the number of caches. There was no significant difference in the overall number of peanuts (9.3 ± 1.5) and crickets (7.7 ± 1.6) cached, $F(1, 11) = 1.71$, and no significant effects of group on caching ($Fs < 1$).

The profile of recovery provided little evidence that the cricket caches were progressively forgotten, with an increasing RI in the degrade group. Neither the direction of the first search nor the proportion of all searches at recovery detected forgetting of the cricket caches across a tripling of the RI from 1 to 3 days. It is true that the degrade birds failed to search in the cricket side after the longer and untrained 5-day RI, but this preference was appropriate given that the birds had received information that the crickets had

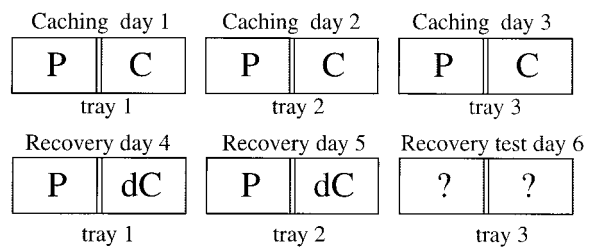
perished 4 days after caching. Rather than progressively forgetting the cricket caches as the RI increased, the degrade group appeared to make a categorical-like decision about whether to search for the crickets at recovery depending on the RI. Thus the birds searched predominantly for crickets with RIs of 3 days or less but primarily for peanuts at longer RIs.

Experiment 2

The profile of temporal control over searching at recovery observed in Experiment 1 provided us with the opportunity to undertake a more stringent test of forgetting induced by a failure of encoding. The central idea behind this test was to provide the birds with new information about the state of the cricket caches at recovery after an untrained RI to see whether information impacted searching at recovery. The critical feature of this test is that the information was provided during the RI, that is, after caching had taken place, so that any effect at recovery could not be mediated by variation in encoding at the time of caching.

The design of this test is illustrated in Figure 2 for the degrade group. The degrade group cached peanuts and crickets in three trial-unique trays, Trays 1 to 3, across 3 successive days. The birds were then allowed to recover their caches from Trays 1 and 2 on Days 4 and 5 after a 3-day RI. As the caches had been removed prior to the recovery test after a 3-day RI in Experiment 1, these recoveries provided the birds for the first time with information about the state of the cricket caches after a 3-day RI. The impact of this information was then assessed by recording the search preferences shown during recovery from Tray 3 on Day 6. As in the standard recovery test, all of the cached food items were removed prior to recovery from Tray 3, and the trays were filled with fresh sand to test for memory in the absence of cues emanating from the food.

Reversed



Consistent

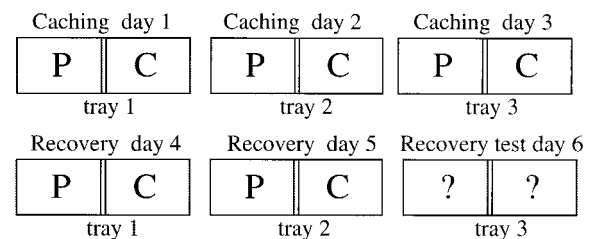


Figure 2. Design of the reversed and consistent conditions. P = peanuts; C = fresh crickets; dC = decayed crickets; ? = empty tray.

Both the degrade and replenish groups were divided into two subgroups, a consistent group and a reversed group, that differed in the information supplied during recovery about the state of the cricket caches after a 3-day RI. The birds in the consistent condition recovered fresh crickets from Trays 1 and 2, which was consistent with their preference for searching in the cricket sites that was observed in Experiment 1 after a 3-day RI. Therefore, we expected these birds to continue to search for crickets in Tray 3 during the recovery test trial. By contrast, the reversed subgroup found degraded crickets in Trays 1 and 2, thereby providing them with evidence that the crickets did in fact degrade after a 3-day RI. At issue is whether this information caused the birds in the reversed condition to reverse their searching preference during recovery from Tray 3, given that they now had information that crickets perished in 3 days.

The critical prediction from the encoding-induced forgetting account is that the information supplied during the RI should have no impact on searching in Tray 3 at recovery. According to this account, whether a bird searches for crickets will depend on whether it has remembered those caches, which in turn will be determined by the processing devoted to encoding the location and content of the caches during the caching period. Once the encoding has taken place, any subsequent information should have no impact on the rate of forgetting. As a consequence, the forgetting account predicts that both the reversed and consistent subgroups should continue to show a preference for searching for crickets in Tray 3, given that Experiment 1 established that the birds remembered the location of the cricket caches after a 3-day RI.

This prediction is predicated on the assumption that the recovery of degraded crickets in the reversed condition does not lead to a general devaluation of this type of food. Clayton and Dickinson (1999a) demonstrated that devaluation of a food type by prefeeding just prior to recovery reduced subsequent searching for that food type. To determine whether experience with the degraded crickets in the reversed condition produced a general devaluation of the crickets, all birds were also given a recovery test after a 1-day RI. A general devaluation of the crickets should have produced a reduction in searching for this food type at all RIs.

Finally, the replenish group also received the reversed and consistent treatments with tests after 1-day and 3-day RIs, but in this case we were concerned that the information supplied in the reversed condition conflicted with the training experience of the replenish group. Recall that these birds had previously received numerous trials in which they recovered fresh crickets after a 4-day RI in Experiment 1 of Clayton, Yu, et al. (2001). Therefore, by the time the birds from the reversed condition of the replenish group came to recover from Tray 3, they had been exposed to apparently conflicting evidence that the crickets had perished by 3 days after caching and yet were fresh after a 4-day RI. To assess the effect of the reversal treatment in the absence of conflicting information, we subsequently gave the replenish group a replication of the reversal and consistent treatments after a 5-day RI.

In summary, if the reversal treatment produces a general devaluation of the crickets, the birds should avoid searching for cricket caches at all RIs. In the absence of a general devaluation effect, however, the encoding-induced forgetting hypothesis predicts that the reversal treatment should not have a selective impact on searching in Tray 3 after the 3-day RI for the degrade group, and after the 3-day and 5-day RIs for the replenish group.

Method

Subjects and Apparatus

The birds, their group allocation, housing conditions, and apparatus were the same as those used in Experiment 1.

Procedure

Following the last test trial of Experiment 1, the birds in both groups received a 4-hr and a 100-hr retraining trial. They were then divided into two subgroups ($N = 4$), which were subsequently trained and tested in either the consistent or reversed condition. The general procedures were the same as those used in Experiment 1. Training and testing occurred during February and March 2000.

3-day reversal test. The birds cached peanuts in one side of a caching tray and crickets in the other side in different trays on 3 successive days (Days 1–3; see Figure 2). The order of caching the two food types was counterbalanced within the consistent and reversed conditions. Trial-unique trays were used for each caching episode (Trays 1–3), and the double alternation schedule that determined that side in which the peanuts and crickets were cached was continued (see *General procedure* of Experiment 1). As a consequence, a particular food type was cached in the same side of the trays during two of these caching periods but in the other side during the other period. On the next day (Day 4), the birds were allowed to recover the food items from Tray 1, and on the subsequent day (Day 5), the birds were allowed to recover the food items from Tray 2. These trays were restocked prior to recovery with fresh crickets in the consistent condition but with unpalatable, degraded crickets in the reversed condition. During the test trial on Day 6, the birds were allowed to search in Tray 3 in the absence of any food caches.

5-day reversal test. Following the test trial with the 3-day interval, the procedure was repeated for the replenish group alone but now with a 5-day RI. The replenish group cached peanuts and crickets in trial-unique Trays 1, 2, and 3 on Days 1, 2, and 3, respectively, before recovering these items from Trays 1 and 2 on Days 6 and 7. The crickets were again fresh for birds in the consistent condition but decayed for those in the reversed condition. Finally, the birds searched in Tray 3 on Day 8 in the recovery period of a test trial, during which there were no food items in the tray.

1-day reversal test. Following the 3-day interval test trial for the degrade group and the 5-day interval test trial for the replenish group, all birds received a test trial with a 1-day RI. Again, the birds cached peanuts in one side of a trial-unique tray and crickets in the other before searching for these items in a recovery test on the next day when the caches had been removed.

Results and Discussion

Degrade Group

The right panel of Figure 3 illustrates that the birds in the consistent and reversed conditions of the degrade group showed the opposite search preferences on the recovery test with Tray 3 after a 3-day RI. Recall that the birds in the reversed condition, unlike those in the consistent condition, had previously experienced that the crickets perished after 3 days during recovery from Trays 1 and 2. In accord with this experience, the birds in the reversed condition directed more searches to the peanut side of Tray 3, whereas those in the consistent condition continued to search the cricket side of the tray preferentially. Moreover, the avoidance of the cricket side of the tray by the birds in the reversed condition was selective to the 3-day RI. When given a recovery test after 1 day, birds in both conditions preferentially searched in the cricket side. A comparison of the mean number of searches

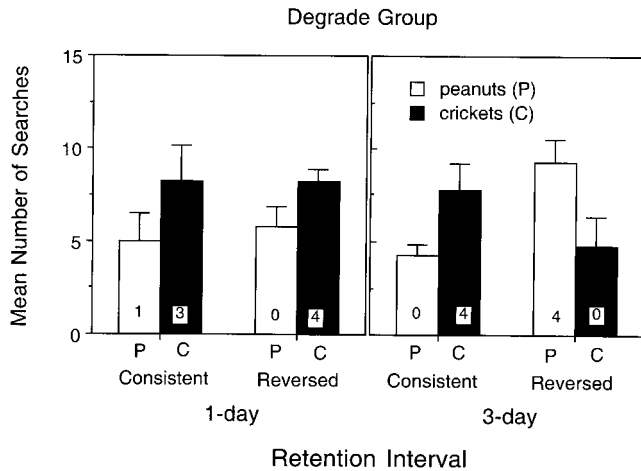


Figure 3. Mean number of searches (+SEM) to the peanut (P) and cricket (C) sides of the tray during the recovery probe tests (when no food was present) in the consistent and reversed conditions for the degrade group. The data are shown separately for the 1-day (left panel) and 3-day (right panel) retention intervals. The numerical inserts are the numbers of birds in each condition that directed their first search to the P and C sides of the caching tray.

after the two RIs yielded a significant Condition \times Retention Interval \times Food Type interaction, $F(1, 6) = 7.44$, $MSE = 3.53$, and an analysis after the 1-day interval alone produced just a significant main effect of food type, $F(1, 6) = 11.10$, $MSE = 2.98$, but no interaction with condition ($F < 1$). By contrast, the Condition \times Food Type interaction was significant for searching after the 3-day RI, $F(1, 6) = 21.33$, $MSE = 3.00$, and simple main effects analyses showed that the jays in the reversed condition searched more in the peanut side than in the cricket side, $F(1, 6) = 13.50$, $MSE = 3.00$, whereas the opposite pattern was seen in the consistent condition, $F(1, 6) = 8.17$, $MSE = 3.00$. In addition, the jays in the reversed condition searched more in the peanut side than those in the consistent condition, $F(1, 6) = 12.77$, $MSE = 3.92$, although there was no reliable difference between conditions for the number of searches in the cricket side, $F(1, 6) = 1.88$.

Figure 3 also shows that the number of jays that directed their first search to either the peanut or cricket side of the tray matched the preference pattern for the total number of searches. We analyzed the side of the first search using the chi-square statistic. Although the expected frequencies in these analysis were low, the uncorrected chi-square test is robust against the inflation of the Type I error rate with respect to small expected frequencies (Bradley, Bradley, McGrath, & Cutcomb, 1979). This analysis divided the jays into four categories depending on whether their first search was to the peanut (P) or cricket (C) side: PP, PC, CP, and CC, where the first and second letters designate the side of the first search after the 1- and 3-day RIs, respectively. There was a reliable difference between the categories of first searches in the reversed and consistent conditions, $\chi^2(2, N = 8) = 8.00$, with the CC category predominant in the consistent condition and the CP category predominant in the reversed condition.

There was no significant difference in the overall number of peanuts (9.9 ± 2.8) and crickets (7.0 ± 1.0) cached, $F(1,$

6) = 1.77, and no significant effects of condition on caching, largest $F(1, 6) = 1.46$.

In summary, experience with recovering degraded crickets from Trays 1 and 2 during the RI for Tray 3 reversed the search preference during recovery from Tray 3 in the reversed condition. Whereas the consistent group continued to search preferentially in the cricket side of Tray 3, the reversed group preferred to search in the peanut side. This switch in preference did not reflect a general devaluation of crickets in the reversed condition because when these birds were tested with a 1-day RI, they revert to their prior preference for crickets.

Replenish Group

Figure 4 shows the mean number of searches directed to the peanut and cricket sides of Tray 3 at recovery after the three RIs by the replenish group. One jay was omitted from the reversed condition because it failed to cache any crickets on the test trial with the 1-day RI. Experience of recovering decayed crickets from Trays 1 and 2 in the reversed condition produced a reliable shift in the search preference for the replenish group after both the 3-day (middle panel) and 5-day (right panel) RIs relative to the consistent condition, although the magnitude of the effect appeared to be somewhat larger after the longer interval. Whereas the jays in the reversed condition searched the two sides of the tray equally frequently after the 3-day RI, the 5-day interval produced a complete reversal of the relative preference for crickets exhibited by birds in the consistent condition. In contrast to the degrade group, however, this change in search preference from crickets to peanuts was not specific to particular RIs but generalized from the 3- and 5-day intervals to the 1-day (left panel) RI.

The contrasting search patterns for the consistent and reversed conditions was supported by a significant Condition \times Food Type interaction, $F(1, 5) = 80.99$, $MSE = 2.09$, and the absence of any significant interactions involving the RI, largest $F(2, 10) = 3.46$, $MSE = 2.66$, substantiated that the search pattern did not vary reliably with the interval. Separate analyses confirmed that the Condition \times Food Type interaction was significant at each RI, smallest $F(1, 5) = 9.66$, $MSE = 1.67$. Simple main effects analyses of the overall interaction supported the claim that jays in the reversed condition searched the peanut side more than the cricket side, $F(1, 5) = 10.25$, $MSE = 2.09$, whereas those in the consistent condition showed the opposite preference, $F(1, 5) = 17.98$, $MSE = 2.09$. In addition, birds in the reversed condition searched more in the peanut side, $F(1, 5) = 11.52$, $MSE = 5.64$, but less in the cricket side, $F(1, 5) = 39.37$, $MSE = 2.71$, than those in the consistent condition.

Figure 4 also shows that the number of birds directing their first search to each side of the test tray yielded the same pattern as the total number of searches. However, when the birds in each condition were divided into the eight categories reflecting the different patterns of first searches across the three RIs, there was no significant difference between the two conditions, $\chi^2(5, N = 7) = 6.00$.

There was no significant difference in the number of peanuts (11.1 ± 3.1) and crickets (6.5 ± 1.4) cached, $F(1, 5) = 2.44$, and no significant effects of condition on caching ($F_s < 1$).

The effect of the reversal treatment in the replenish group differed from that observed in the degrade group. Whereas the reversed condition in the degrade group produced a change in

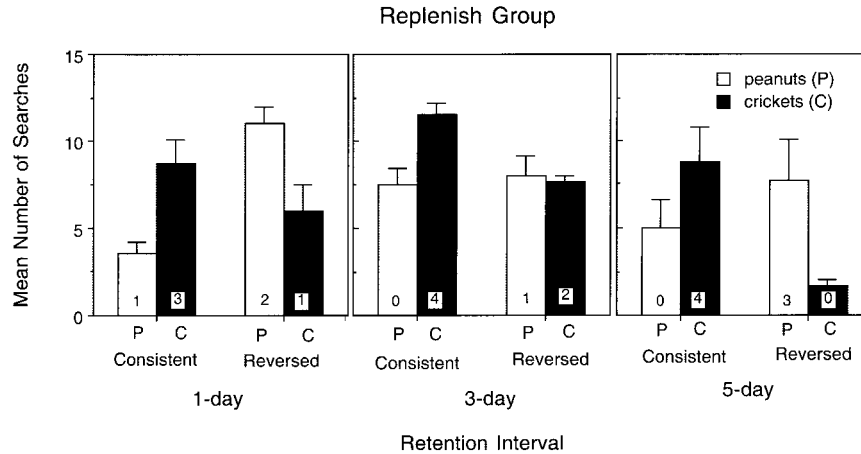


Figure 4. Mean number of searches (+SEM) directed by the replenish group to the peanut (P) and cricket (C) sides of the tray during recovery probe tests in the consistent and reversed conditions. The data are shown separately for the 1-day (left panel), 3-day (middle panel), and 5-day (right panel) retention intervals. The numerical inserts are the numbers of birds in each condition that directed their first search to the P and C sides of the caching trays.

search preference away from the cricket side that was selective to the 3-day RI, the reversal of the search preferences in the replenish group was general being observed at all three RIs. Clearly, this general reversal suggests that experience with recovery of the degraded crickets from Trays 1 and 2 produced a general devaluation of the crickets. Unfortunately, we cannot determine the source of the difference between the two groups because the different training regimes received by the two groups were confounded with the fact that the replenish group, but not the degrade group, received additional experience with degraded crickets during testing with the 5-day RI before the selectivity of the search preference was tested at the 1-day RI.

Whatever the source of this difference, the critical finding in this study is that the reversal condition of the degrade group produced a selective reversal of the search preference at the 3-day RI. This finding challenges an account of the temporal control of searching at recovery in the degrade group in terms of encoding-induced forgetting of the cricket caches. Such an account does not allow for the presentation of new information during a RI to alter searching at recovery, and yet this is exactly the effect observed in the reversed condition for the degrade group.

General Discussion

Our experiments examined the processes mediating the temporal control of searching for caches at recovery by Western Scrub-Jays that were established by Clayton, Yu, et al. (2001). Specifically, we were concerned with whether the reason why the birds in the degrade group refrained from searching for cricket caches after a 4-day RI was because they had forgotten these caches. Moreover, we suggested a possible mechanism that could have enhanced forgetting of the cricket caches. The birds in the degrade group might have devoted less resources to encoding the location and content of the crickets at the time of caching simply because these food items were partially associated with the perished and unpalatable state and, therefore, may have had an ambivalent value as

cachable food items at the time of caching. The results presented here provide no support for this encoding-induced forgetting account.

When searching at recovery was probed at untrained RIs in Experiment 1, there was no evidence for progressive forgetting of the cricket caches by the degraded group. Rather these birds appear to make a categorical-like decision by searching preferentially in the cricket sites following RIs of 3 days or less but in peanut sites at longer intervals. Experiment 2 tested the encoding-induced forgetting hypothesis directly by providing birds in the reversed condition with information that the cricket did in fact degrade after 3 days. According to the encoding-induced forgetting account, this information should have had no impact on the search preferences at recovery because it was supplied during the RI, long after the birds had finished caching and in fact 3 days after the birds had encoded information about the content and location of caches in that particular tray. But in contrast to this prediction, degrade group birds in the reversed condition did search preferentially in the peanut side of the caching tray at recovery after the 3-day RI.

An alternative forgetting-based account can be derived from the so-called directed forgetting paradigm (Roper & Zentall, 1993) that, it is claimed, demonstrates that information presented during a RI can induce forgetting of previously encoded information. According to such an account, the experience of recovering perished crickets from Trays 1 and 2 caused the birds to forget the caching episode in which they stored crickets in Tray 3. In a directed-forgetting study that has some similarity to our caching paradigm, Colwill (1984) trained pigeons on two conditional simultaneous discriminations: a color discrimination and a line-orientation discrimination. On trials preceded by a noncontingent presentation of food, responses to one stimulus from each discrimination were reinforced, whereas on the remaining no-food trials, birds were rewarded for choosing the other stimulus. As a short interval intervened between the food presentation and the presen-

tation of the choice stimuli, successful performance on this task required the birds to remember the food presentation across this RI. In this respect, therefore, the presentation of the food is analogous to the caching of the crickets, whereas the choice of the correct visual stimulus is analogous to searching in cricket sites at recovery.

Having established these discriminations, Colwill (1984) introduced an auditory cue in the RI between the presentations of the food and the color choice stimuli. This auditory stimulus signaled that the reinforcement contingencies for the choice between the color stimuli were reversed so that the choice that was normally correct on nonfood trials was rewarded. However, the critical finding occurred when the auditory stimulus was unexpectedly presented during the RI on probe test trials with line orientation choice stimuli. Colwill (1984) found that some of her birds reversed their choice by responding to the line orientation that was previously correct following a nonfood sample even though they had never been trained with this contingency between the food sample, the auditory stimulus, and line orientation choice stimuli.

One interpretation of this result is that the auditory stimulus functioned as a “forget” cue, causing the pigeons to forget the occurrence of the food sample; the consequence was that at the time of choice, the birds chose the stimulus that was trained as correct for a nonfood sample. As noted previously, to apply an analogous directed-forgetting account to Experiment 2, we should have to argue that the experience of recovering the perished crickets from Trays 1 and 2 during the RI caused the birds to forget the cricket caches in Tray 3. In evaluating this account, however, two points should be noted. Whereas our birds required only two recovery experiences in the RI to readjust the temporal control, over 50% of Colwill’s (1984) pigeons never learned to use the forget cue even after more than 350 training trials with the cue, suggesting that different processes were operating in the two cases. Moreover, a directed-forgetting explanation offers no mechanism or process by which the recovery of degraded crickets from Trays 1 and 2 could have induced forgetting of the cricket caches in Tray 3.

As we noted at the beginning of this article, we have argued for an interpretation of the temporal control over cache recovery in terms of episodic-like memory processes involved in the recollection of specific past experiences (Clayton et al., 2000; Clayton, Griffiths, et al., 2001; Griffiths et al., 1999). Recent characterizations of human episodic memory have emphasized the phenomenological characteristics of recollection, such as “autonoetic awareness” (Tulving & Markowitsch, 1998), which cannot be assessed in nonlinguistic animals. It is for this reason that we have referred to the memories mediating cache recovery by Western Scrub-Jays as episodic-like (Clayton et al., 2000; Clayton, Griffiths, et al., 2001; Griffiths et al., 1999) by reference to Tulving’s (1972) original characterization of episodic memory as a form of memory that “receives and stores information about temporally dated episodes or events, and temporal-spatial relations among those events” (p. 385). By this what–where–when criterion, the bird’s memory of the caching episodes is episodic-like because it involves recall of the content (what) and location (where) of their cache, and we have argued that it also involves a temporal component (when).

If it is accepted that the temporal control of searching in the degrade group does not reflect enhanced forgetting, then at the

time of recovery these birds must have access to information that in one way or another encodes the time that has elapsed since caching. We think that it is unlikely that the birds learned to conditionalize their search preference on the strength of a decaying memory trace of the caching episode for a number of reasons. First, we have been unable to detect any independent evidence that the memory traces decay over the RIs tested in our studies. In Experiment 1, the birds in the replenish group showed perfect retention of the location of the cricket caches for up to 5 days, and Clayton and Dickinson (1999a) found no loss of information about cache content and location with a RI of up to 7 days. An alternative is that the birds start some form of internal timer or counter of, for example, diurnal cycles and learn to conditionalize their recovery search on the output of the timer or counter (e.g., McCormack, 2001). It should be noted, however, that the ability of the degrade group birds in the reversal condition to use the information gained during recovery from Trays 1 and 2 to alter recovery from Tray 3 selectively after a 3-day RI means that caching in each of the trays must have initiated separate timers or counters that then function simultaneously, but independently, during the overlapping RIs. There is good evidence that animals are capable of such independent, asynchronous timing at least for much shorter intervals (e.g., Meck & Church, 1984).

The integration of information about the states of the crickets in the different cache sites has further implications for the nature of these cache memories. Tulving and Markowitsch (1998) viewed human episodic memory as being embedded within a more general declarative framework so that specific episodic information can be integrated with more general declarative knowledge of factual (semantic) information (Tulving, 1972, 1983). Clayton, Yu, et al. (2001) suggested that learning about the perishability of the different types of food could be viewed as the acquisition of nonepisodic (semantic) declarative information that was accumulated across a number of caching–recovery experiences and was generally applicable to different caching and recovery episodes. According to this account, therefore, searching at recovery was controlled by the interaction of episodic-like recall of the what–where–when information for the specific caching episode and general declarative knowledge about the perishability of the cached foods.

Ever since the initial discussions of the distinction between declarative and procedural representations (e.g., Anderson, 1976; Winograd, 1975), it has been recognized that the cardinal feature of declarative memory is its flexibility. The issue of mnemonic flexibility was raised explicitly by Tulving (2001) in reference to the role of declarative memory in cache recovery when he asked “could Clayton and her colleagues (or someone else) get their scrub jays, who remember what kind of food is where, to do something other with that information than act on it ‘inflexibly’?” (p. 1513). It can be argued that the reversal of the search preference shown by the degrade group birds in the reversal condition provides evidence for just such mnemonic flexibility. In terms of a declarative account, these birds encoded an episodic-like what–where–when memory for the cricket caches in Tray 3 at a time when their nonepisodic declarative knowledge represented crickets as fresh and palatable after a 3-day RI. However, the subsequent recovery of perished crickets from Trays 1 and 2 after 3 days would have revised the general representation of the perishability of crickets so that when presented with Tray 3 at recovery, the episodic-like memory of the caching episode would have been

integrated with this changed generic representation of cricket perishability, thereby producing a reversal of the search preference. Whether this form of mnemonic flexibility meets Tulving's challenge is unclear in the absence of a specific conception of flexibility, but it does suggest the birds are capable of integrating episodic-like information with diverging nonepisodic knowledge to generate different behavioral outcomes.

Whatever psychological processes mediating the mnemonic flexibility demonstrated in the present experiments, there are obvious functional benefits of learning flexible rules about the circumstances in which foods perish and the length of time it takes for an item to degrade. The rate at which a perishable item degrades depends on a number of ecological factors, including the temperature and humidity of the ambient environment, the type of substrate in which the food is cached, and even the depth and location within a particular substrate. Of course, perishability may be irrelevant for species that live in extremely harsh environments where the climate is so cold that items will rarely perish, for example, Siberian tits and Alaskan chickadees, or for species that do not cache the perishable foods at all, for example, gray squirrels (Hadj-Chikh, Steele, & Smallwood, 1996) and eastern woodrats (Gendron & Reichman, 1995; Reichman, 1988). But this is not the case for Western Scrub-Jays living in the Central Valley in California, which do cache perishable foods and where the temperatures rarely fall below 10 °C but may rise to over 40 °C in the months of July to September. At such temperatures, caches that consist of various invertebrates, for example, will degrade rapidly in the heat and more slowly in cold. The problem for the food cacher, then, is not only to learn how quickly a particular food type degrades but also to be able to update this information in a flexible manner, on the basis of the ecological conditions that occur in the interim between caching the item and recovering it. Perhaps, therefore, the most important conclusion from our studies is that in Western Scrub-Jays, cognition meets this ecological demand.

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