Food Caching by Western Scrub-Jays (*Aphelocoma californica*) is Sensitive to the Conditions at Recovery

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Abstract

Western Scrub-Jays cached perishable and non-perishable food items, which they could recover after both short and long retention intervals. When perishable items were always degraded at recovery, jays decreased the number of perishable items cached and increased their caching of non-perishable items, relative to a control group whose caches were always fresh at recovery. Jays reduced the number of non-perishable items cached, however, when highly preferred food items were degraded only after the long retention intervals. The findings are discussed in terms of the role of retrospective and prospective processes in the control of caching.

The last two decades have seen an increasing interest in the cognitive processes involved in cache recovery by food-hoarding animals. Many species scatterhoard food throughout their winter territories when food is abundant only to recover it at some later time (Vander Wall, 1990). It is now well established that successful recovery is based, at least in part, on memory for the location of the caches (Shettleworth, 1995). Moreover, recent research from our laboratory has demonstrated that western scrub-jays (*Aphelocoma californica*) remember what they cached and where (Clayton & Dickinson, 1999a) as well as how long ago these caches were created (Clayton & Dickinson, 1998, 1999c), and that the birds form integrated and flexible 'what-where-and-when' memories of specific caching events (Clayton, Yu, & Dickinson, 2001, 2003).

By comparison, the processes controlling the act of caching itself have received relatively little empirical investigation. Most of this research has been directed at the proximal control of caching by seasonal, nutritional and motivational factors. For example, the seasonal variation in the intensity of food caching (e.g. Odum, 1942; Shettleworth et al, 1995) appears to be regulated by photoperiod (e.g. Krebs et al, 1995; Clayton & Cristol, 1996; Macdougall-Shackleton et al, 2003) even in the absence of seasonal differences in food consumption (e.g., Clayton, Mellor, & Jackson, 1996). However, food-caching intensity is also potentiated by food deprivation at the time of caching (e.g., Lucas & Walter, 1991). Indeed, the motivational control can be very specific in that Clayton and Dickinson (1999a) found that pre-feeding a particular food type selectively depressed caching of that food by scrub-jays. There is also evidence for an interaction between motivational and nutritional state because thin chickadees were found to cache irrespective of whether they were hungry or sated, whereas fat chickadees only cached when food deprived (Lucas, Peterson, & Boudinier, 1993). In addition to motivational control by hunger and

general nutritional state, Clayton and Dickinson (1999b) have argued that caching is autonomously motivated because jays cache inedible items, such as stones, when suitable food items are not available (Clayton, Griffiths & Bennett, 1994; Clayton & Dickinson, 1999a).

There is also evidence that caching decisions depend upon the nutritional value of the food items. American crows *(Corvus brachyrhynchos)*, for example, preferred to eat English walnuts rather than black walnuts, yet they were more likely to cache the black walnuts. When they did cache the more preferred English walnuts then they spent more time in the act of hiding each cache (Cristol, 2001). Food-storing squirrels also cached items of greater nutritional value at lower density than items of lower value (Hurly & Robertson, 1987; Stapanian & Smith, 1984).

By contrast to the effects of proximate factors on caching, there is relatively little research on whether the state of caches at the time of recovery affects subsequent caching. Both chickadees (Hampton & Sherry, 1992) and Clark's nutcrackers (Kamil et al, 1993) learn to avoid caching in sites that are consistently pilfered, probably because, at the time of recovery, non-pilfered cache sites are more strongly associated with food reward than pilfered sites. In the present studies, we investigated whether western scrub-jays can learn to change their preference for caching different types of food, depending upon the state of the caches at recovery.

The studies used the procedure developed by Clayton and Dickinson (1999b) to study the role of memory in cache recovery. When the jays cached non-perishable peanuts in one caching tray and perishable wax worms in another tray, they rapidly learned to refrain from searching for the wax worms after retention intervals that led to the degradation of this food. In the first

experiment we investigated whether experience of recovering perished wax worms would also affect the propensity of these birds to cache wax worms on subsequent caching opportunities. By contrast, the wax worm cache sites were always replenished with fresh, palatable worms before recovery for jays in the control, replenish group, so we expected these birds to cache wax worms in preference to peanuts throughout training. At issue, however, was whether the consistent degrade group would learn to refrain from caching wax worms when these food items were always degraded at recovery.

A third, partial degrade group was also included because of an incidental observation by Clayton and Dickinson (1999b) concerning the caching behaviour of birds which recovered fresh wax worms after a short, 4-h retention interval (RI) but perished wax worms after a long, 5-day RI. Somewhat paradoxically, these jays progressively cached more wax worms and fewer peanuts across a series of caching-and-recovery trials until, by the end of this training, these birds were caching significantly more wax worms than peanuts. A comparable difference was not observed in a replenish group for which the wax worms were always fresh at recovery. At the time of caching, the birds did not know whether their caches would be returned to them after a short or a long RI. So Clayton and Dickinson (1999b) speculated that this increase in the number of wax worms cached by birds in the partial degrade group might be due to an attempt to compensate for the fact that their wax worm caches were sometimes degraded at the time of recovery. Thus these jays might cache more worms on every trial in the hope that there would be more fresh wax worms available at recovery on those trials in which the worms had not perished.

In summary, each jay was allowed to cache peanuts and wax worms in a single caching tray, and then given the opportunity to recover these caches after a short (4-hr) or long (100-hr) retention interval. The wax worms were always fresh at recovery for the replenish group, but always degraded at recovery for the consistent degrade group. Finally, the partial degrade group replicated the degrade group of Clayton and Dickinson (1999b) in that the wax worms were fresh at recovery after the short RI but degraded at recovery after the long RI. The aim of experiment 1 was to test whether the state of the wax worm caches at recovery affected both the absolute and relative amounts of caching of each food type.

Experiment 1

Method

Subjects and Apparatus

Six female and six male sexually mature western scrub-jays (*Aphelocoma californica*) were housed individually in cages measuring 91 cm wide by 91 cm high by 76 cm deep. The birds had most recently participated in a series of experiments on cache recovery reported by Clayton et al. (2001, 2003) that did not involve the caching of wax worms. The jays were maintained under artificial light on a 10:14 hr light:dark cycle and fed a diet of shelled peanuts, sunflower seeds, grains, and dog biscuits, which we gave them in a finally powdered form to ensure that the birds cached only during the experimental trials. During caching periods, whole peanuts and wax moth larvae (wax worms) were presented in 15-cm-diameter bowls. Birds cached in plastic ice-cube trays (6 cm wide by 25 cm long), which consisted of a 2 by 7 array of 2.5-cm cube moulds filled with dry sand, each of which was a potential cache site. Each tray was attached to a wooden board

(15 cm wide by 32 cm long) and rendered visuo-spatially distinct by a structure made of Lego bricks (Nefield, CT) that was placed next to one of the long sides of the tray (see Clayton & Dickinson, 1998, 1999).

Procedure

At the start of the experiment in November 2000, four jays were assigned to each of three groups: replenish, consistent degrade, and partial degrade. All the birds had prior experience with caching and recovering peanuts and wax worms in the studies reported by Clayton and Dickinson (1999c) and each of the present groups was composed of one bird from the replenish group, one from the degrade group and two from the pilfer group of the Clayton and Dickinson (1999c) experiments. So one bird in each group had prior experience with recovering degraded wax worms 2.5 yr previously.

The birds received 6 trials, one per week, such that each bird received three trials with the short (4-hr) RI between caching and recovery, and three with the long (100-hr) RI. Half of the birds in each group received a $4 - 100 - 100 - 4 - 4 - 100$ trial order, whereas the remaining birds received the inverse $100 - 4 - 4 - 100 - 100 - 4$ order. Each trial consisted of a 15-min caching period followed after the RI by a 10-min recovery period. The maintenance diet was removed from the home-cage just prior to the onset of the dark period on the evening prior to the day of a trial so that the birds were mildly hungry at the time of caching during the next morning. At the start of the caching period we placed a trial-unique caching tray along with a bowl containing 50 peanuts and 50 wax worms into the bird's home cage. These items were then removed after 15 min along with any detectable caches the bird had made outside the trays. We recorded the

location and types of caches in the trays by inspection before they were returned to the home cages for the recovery period after the appropriate RI.

Prior to the recovery period, trays were refilled with new sand and the peanut and wax worm caches replaced in the locations in which the bird had stored them. The wax worms were always fresh for the replenish group and always degraded for the consistent degrade group. For the partial degrade group the trays were restocked with fresh wax worms after the 4-hr RI but with degraded wax worms after the 100-hr RI. The degraded wax worms were made unpalatable by soaking them in a solution of dark green food colouring and unscented washing-up liquid, and leaving them to dry until they turned black. The behaviour of the jays was not recorded during recovery.

Finally, in order to determine whether prior experience with recovering degraded wax worms had affected the preference for fresh wax worms, all birds received a feeding test after the last trial. In this test, a bowl containing 50 peanuts and 50 wax worms was placed in the home cage without a caching tray for 15 min, and the number of items eaten was recorded, as well as the order in which they were taken.

(insert Figure 1 here)

Results and Discussion

Figure 1 illustrates the mean number of peanuts and wax worms cached by the three groups on each trial. The reliability of differences in caching was assessed against a Type I error rate of

.05 by mixed analyses of variance with groups as the between-subjects variable and food type and trials as within-subjects variables. Post-hoc pair-wise contrasts were evaluated by the Newman-Keuls procedure. There was no evidence that the caching levels were initially biased by the group allocation of the jays in that neither the group effect, $\underline{F}(2, 9) = 1.79$, nor the Group X Food Type interaction, $\underline{F} < 1$, was significant for the number of food items cached on the first trial. However, the birds did cache reliably more wax worms that peanuts on this first trial, $F(1, 9) = 13.79$, $MSE = 39.28$. A subsequent overall analysis of caching across all of the trials yielded a Group X Food Type X Trial interaction, $F(2, 45) = 3.18$, $MSE = 13.98$, which prompted separate analyses of relative caching of the two food types within each group and of caching of each food type across groups.

Both the replenish and partial degrade groups cached more wax worms than peanuts, $F(1, 3) = 10.96$, $MSE = 50.52$ and $F(1, 3) = 85.15$, $MSE = 13.74$, respectively. Although the graph (Figure 1 – top panel) suggests that the magnitude of this difference decreased across trials in the replenish group, the Food Type X Trial interaction was not significant, $F(5, 15) = 1.34$. By contrast, the consistent degrade group did show a reliable change in the number of both types of food cached across trials, $F(5, 15) = 12.24$, $MSE = 10.77$, in that the number of wax worms cached decreased across trials, $F(5, 15) = 3.29$, $MSE = 8.63$, whereas the number of peanuts cached increased, $F(5, 15) = 10.31$, $MSE = 14.06$ (Figure 1 – middle panel). The consistent degrade group cached more worms than peanuts on the initial trial, but this pattern reversed across training trials, such that for the last four trials these birds cached more peanuts than wax worms, $Fs(1, 3) > 18.10$.

Overall, the groups differed in the number of wax worms cached, $F(2, 9) = 12.81$, $MSE = 63.20$, with the consistent degrade group caching significantly fewer wax worms than the replenish and partial degrade groups, which in turn did not differ. A significant Group X Trial interaction, $F(10, 45) = 3.99$, $MSE = 9.83$, demonstrated that the groups also differed in the number of peanuts cached on some trials and analyses of the simple main effects and pair-wise comparisons revealed that the partial degrade group cached fewer peanuts than the replenish and consistent degrade groups on the last four trials, $Fs(2, 19) > 3.68$. These differences arose from the fact the replenish and consistent degrade groups, $Fs(5, 45) > 3.29$, $MSE = 9.83$, unlike the partial degrade group, $F < 1$, increased the number of peanuts cached with training.

The primary finding in this experiment was that birds in the consistent degrade group were highly sensitive to the state of the wax worms at recovery. These birds cached fewer wax worms than the replenish group and showed a complementary increase peanut caching. The low level of wax worm caching did not reflect a general loss of the attractiveness of wax worms because the consistent degrade group showed just as strong a preference as the replenish group for the wax worms in the final feeding test. In this test the first item eaten by all birds was a wax worm and, except for one bird in each group, none of the remaining jays ate any peanuts. Moreover, these three birds ate only a single peanut. The groups did not differ in that the mean number of wax worms eaten, $F < 1$, which was 8.0 for the replenish and consistent degrade groups and 6.3 for the partial degrade group. As the relative preference for caching the two foods at the end of training was exactly the opposite of that for eating them in the consistent degrade group, it difficult to argue for a generalised loss of attractiveness of the wax worms.

Finally, caching by the partial degrade group confirmed the paradoxical effect of this schedule observed by Clayton and Dickinson (1999b). Although experience with partially degrading wax worms had no reliable impact on the caching of this food type relative to the replenish group, the level of peanut caching by the partial degrade group was very low.

Experiment 2

The aims of the second experiment were twofold. The first was to replicate the two main effects of Experiment 1, specifically the reduced caching of consistently perishable wax worms and the minimal level of caching of the non-perishable peanuts apparently induced by experience with partially perishable wax worms. To this end, the three groups (replenish, consistent degrade and partial degrade) were run under similar contingencies to those in Experiment 1. The second aim was to compare the effects of pilfering and perishability on caching. As we noted in the introduction, it is already known that food-caching birds avoid caching in sites that are consistently pilfered (Hampton & Sherry, 1992; Kamil et al., 1993). At issue in the present experiment is whether the jays reduce their caching of a food type that is consistently pilfered. Therefore, for the birds in the consistent pilfered group, the wax worms (but not the peanuts) were removed from the caching trays before recovery on all trials.

Finally, we also included a partial pilfer condition to investigate whether partial pilfering has an effect on caching comparable to that observed for the partial degrade group in the first experiment. Clayton and Dickinson (1999b) examined caching under a partial pilfer contingency in which the wax worm caches were removed from the caching tray prior to recovery after the long RI but not after the short RI. The peanut caches always remained intact. In contrast to the

partial degrade contingency, in their experiment there was no difference in the relative caching of peanuts and wax worms by the partial degrade and replenish groups. However, in the Clayton and Dickinson (1999b) study, the birds cached the peanuts and wax worms in separate trays at different times and, therefore, it is possible that the caching procedure employed in Experiment 1, in which the birds had a choice between caching the two foods at the same time in the same tray, might be more sensitive and reveal an effect of partial pilfering.

In summary, the five groups tested in Experiment 2 examined two sets of contrasts, one between the replenish group and the consistent and partial degrade groups, thereby replicating the contrasts of Experiment 1, and a second two-variable contrast in which one variable distinguished between pilfering and perishability, and the other differentiated between the consistent and partial application of these treatments.

(insert Table 1 here)

Method

Subjects and Apparatus

Eight female and fourteen male sexually mature western scrub-jays were housed and maintained under the same conditions as in Experiment 1. The food items and caching trays were also the same as those used in Experiment 1 except that the caching substrate in the trays was corn kibble rather than sand.

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Procedure

At the start of the experiment in September 2001, birds were assigned to the five groups. All but one of these birds had participated in the experiments reported by Clayton and Dickinson (1999b) and/or Experiment 1 and the history of the birds in each group is given in Table 1. An important feature to note is that none of the birds in the consistent degrade group had previous experience of recovering wax worms that were always degraded.

All birds received a series of eight trials consisting of a 15-min caching period followed by a 10-min recovery period after a short or long RI. The procedure was the same as that employed in Experiment 1 unless otherwise stated. Although the wax worms were fresh when recovered after the short RI by the replenish, partial degrade and partial pilfer groups, after the long RI they were perished for the partial degrade group but fresh for the replenish group. The wax worm caches were not replaced in the trays after the long RI for the partial pilfer group. The wax worm caches were either degraded or not replaced in the trays after both RIs for the consistent degrade and consistent pilfer groups, respectively. While the short RI interval remained at 4 hr, the long retention interval was shortened to 28 hr to increase the rate at which trials could be administered.

(insert Figure 2 here)

Results and Discussion

Replication of Experiment 1

In order to assess whether caching was biased by the group allocation, we conducted an initial analysis of caching on the first trial. Neither the main effect of group not the Group X Food

Type interaction was significant, Fs < 1, although the birds did cache more wax worms than peanuts on this first trial, $F(1, 14) = 21.91$, $MSE = 23.43$. As Figure 2 shows, subsequent caching replicated the pattern observed in Experiment 1 in that the consistent degrade group reversed their initial preference so that by the end of training they were caching more peanuts than wax worms. By contrast, the preference for caching wax worms was sustained by both the replenish and the partial degrade groups across trials, with the partial degrade group caching very few peanuts by the end of training.

This description was supported by statistical analysis. An overall analysis of variance of caching by the replenish, consistent degrade and partial degrade groups yielded a significant Group X Food Type X Trial interaction, $F(14, 63) = 5.08$, $MSE = 10.44$. A borderline Group X Trial interaction for the number of worms cached, $F(14, 63) = 1.70$, $MSE = 23.1$, $p < .08$, prompted analyses of simple main effects, which in turn revealed a significant decrease in caching by the consistent degrade group, $F(7, 63) = 4.39$, $MSE = 23.1$, but not by the replenish and partial degrade groups, Fs(7, 63) < 1.06. The effect of group was significant on Trials 3, 4, 7 and 8, Fs(2, 9) > 4.19, which prompted pre-planned comparisons of caching on Trials 3-8 based upon the results observed in Experiment 1. During these trials, there was no reliable difference between the caching of wax worms by the replenish and partial degrade groups, $F(1, 9) = 2.04$, whereas the consistent degrade group cached significantly fewer wax worms than the other two groups combined, $F(1, 9) = 9.79$, $MSE = 132.4$

A comparable analysis of peanut caching also yielded a Group X Trial interaction, $F(14, 63) = 3.82$, $MSE = 5.20$, which was due to an increase in caching by the consistent degrade group,

$F(7, 63) = 6.48$, $MSE = 5.20$, but there was no change in the amount of peanut caching by the replenish and partial degrade groups, $Fs(7, 63) < 1.58$. There was a significant effect of Group on Trials 4-8, $Fs(2, 9) > 7.80$, and pre-planned comparisons revealed than not only did the partial degrade group cache fewer peanuts than the replenish group on these trials, $F(1, 9) = 4.88$, $MSE = 25.12$, but that the consistent degrade group also cached more peanuts than the replenish group, $F(1, 9) = 13.86$, $MSE = 25.12$. As this latter difference was not predicted by the results of Experiment 1, we confirmed the reliability of the effect using the Newman-Keuls procedure.

In summary, the results confirmed the findings of Experiment 1. Whereas the replenish and partial degrade groups showed a sustained preference for caching wax worms rather than peanuts, the consistent degrade group reversed this initial preference by both decreasing the number of wax worms cached and increasing the number of peanuts cached. In addition, the finding that the partial degrade group cached peanuts at a very low level was also replicated.

Effect of Pilfering

The effect of pilfering was contrasted with the effect of cache degradation by comparing caching by the consistent and partial pilfer groups with that by the consistent and partial degrade groups. Figure 2 illustrates that pilfering the wax worm caches had a similar effect on the relative caching of the two food types as degrading the wax worms. On the very first trial these groups did not differ reliably in their relative caching of the two foods, $Fs(3,14) < 1.09$, and they all showed the initial preference for caching wax worms over peanuts, $F(3, 14) = 21.91$, $MSE = 23.43$. Like the consistent degrade group, the consistent pilfer group reversed this preference with training, although the rate of reversal was slower under the pilfer condition than under the degrade

condition. By contrast, the partial pilfer group, like the partial degrade group, showed a sustained preference for caching wax worms.

The reliability of these effects was evaluated by a mixed analysis of variance with two between-subjects variables that distinguished between the degrade and pilfer treatments and whether these treatments were consistent or partial. The consistency of the degrade and pilfer treatments interacted with the food type and trials, $F(7, 98) = 9.17$, $MSE = 11.11$, which prompted separate analyses of caching in the consistent and partial conditions. In the partial condition, there was just a main effect of food type, $F(1, 7) = 21.60$, $MSE = 118.9$, which did not interact with whether the wax worms were degrade or pilfered. By contrast, in the consistent condition the effect of whether the wax worms were degraded or pilfered entered into a 3-way interaction with food type and trials, $F(7, 49) = 3.72$, $MSE = 7.40$, which we investigated by separate simple main effects analyses. Whereas the consistent degrade group reliably cached more peanuts than wax worms from Trial 4 onwards, $Fs(1, 3) > 30.38$, this difference was significant for the consistent pilfer group on only the last two trials, $Fs(1, 4) > 11.50$.

In summary, caching was sensitive to the consistent pilfering of the caches in a manner that parallels the degrading of caches. However, the jays appear less sensitive to pilfering than to the degradation of caches in that the preference for caching the non-pilfered food type emerged more slowly than the preference for caching the non-degrading food.

Experiment 3

Although the first two experiments demonstrated reliable effects of both degradation and pilfering on subsequent caching behaviour, these treatments were confounded with food type. In both experiments, the degrading food was wax worms, the preferred food of these scrub-jays, both in terms of eating and caching. So the next experiment examined whether the effects of the degradation treatment were independent of the food type to which it was applied. To this end, the jays cached two new food types, pieces of salami and dried pineapple chunks, both of which could be artificially degraded. The pineapple was degraded at recovery after both the short and long RI for half the birds in the consistent degrade group, but only after the long RI for half of the jays in the partial degrade group. For these birds, salami was always fresh and palatable at recovery. The remaining birds in each group always received fresh pineapple at recovery, but the salami was degraded, either after both RIs (consistent degrade group) or only after the long RI (partial degrade group). If the differential caching observed in the previous experiments reflected the degradation treatment applied to the food, then we expected that the consistent degrade group should progressively cache less of the degrading food type and more of the non-degrading type. By contrast, based on the results of the previous experiments, we predicted that the partial degrade group might prefer to cache the partial degrading food rather than non-degrading food.

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Method

Subjects and Apparatus

Three female and eleven male sexually mature western scrub-jays were housed and maintained under the same conditions as in Experiment 2. The caching trays and substrate were also the same as those used in Experiment 2.

Procedure

At the start of the experiment in November 2001, six birds were assigned to the consistent degrade group and eight birds to the partial degrade group. These birds had participated in Experiments 1 and/or 2, but none of them had any prior experience with the novel foods used in the present experiment. All birds received a series of ten trials consisting of a 15-min caching period followed by a 10-min recovery period. The RI between caching and recovery was 4 hr on half of the trials and 28 hr on the remaining trials. The main procedural difference from Experiment 2 was that the two foods types were small (approx 0.5 cm^3) pieces of dried pineapple and salami (Pepperoni). The dried pineapple chunks were degraded in the same way as wax worms, by soaking them in a solution of dark green food colouring and unscented washing-up liquid, and leaving them to dry until they turned black. Salami could not be degraded in this way because the washing up liquid would not easily penetrate the dense meat, so salami pieces were boiled in the dark green coloured washing up liquid solution for at least one hour to ensure that the cooked, soaked salami became unpalatable to the birds.

Half of the birds in each group recovered fresh and palatable pineapple after both RIs, whereas for the remaining birds it was the salami that was always fresh at recovery. The other

food was degraded at recovery for the consistent degrade group after both RIs but only after the

long RI for the partial degrade group.

(insert Figure 3 here)

Results and Discussion

The number of food items cached was analysed by a mixed analysis of variance with two

between-subjects factors: group and food type, which distinguished between whether the

pineapple or salami degraded. The two within-subject factors were trial and degrade, which

distinguished between caching the degrading food type and the non-degrading food.

Unfortunately, as Figure 3 shows, the consistent degrade group cached relatively few of the to-be-

degraded food items on the first trial. However, this bias was not statistically reliable in that

neither the main effect of whether the food would be degraded at recovery, $\underline{F}$ <1, nor the Group X

Degrade interaction, was significant, $F(1, 10) = 1.44$, for caching on the first trial. Moreover, the

caching of the degraded food by the consistent degrade group recovered the levels of the

replenished food on Trials 2 and 3 and, consequently, we do not believe that subsequent caching

levels were compromised by an initial bias.

This overall analysis yielded a significant 3-way interaction between the group, degrade and

trial variables, $F(9, 90) = 1.99$, $MSE = 15.28$. Figure 3 illustrates the source of this interaction.

Whereas the partial degrade group cached a similar number of degraded and replenished food

items, jays in the consistent degrade group diverged in their caching of the two foods so that by

the end of training they were caching more of the replenished food than of the degraded food.

This interaction was evaluated by separate statistical analyses for each group.

For the consistent degrade group, this analysis yielded a significant Degrade X Trial interaction, $F(9, 36) = 2.75$, $MSE = 15.78$, and simple main effects analyses demonstrated that these birds cached more of the replenished food on Trial 4 and Trials 6-8. This pattern confirms the different caching of consistently degraded and replenished foods observed in the previous two experiments and shows that this effect is not restricted to the degradation of a highly preferred food, such as wax worms. There was no significant effect of whether it was pineapple or salami that degraded, $Fs < 1$ and $F(9, 36) < 1.22$.

A similar analysis for the partial degrade revealed no reliable effects or interactions involving the degrade variable, $Fs < 1$. There was, however, a significant Food Type X Degrade interaction, $F(1, 6) = 7.07$, $MSE = 98.58$, which on analysis turns out to be due to the fact that these birds on average cached 10.5 pieces of salami but only 6.4 pieces of pineapple, irrespective of which food type was partially degraded. The failure to replicate the greater level of caching of partially degraded food observed by Clayton and Dickinson (1999b) and in our previous experiments suggests that this difference may only emerge when the partially degraded food is highly preferred over the replenished food, as was the case when the caching of partially degrading wax worms was contrasted with the caching of peanuts.

In summary, the third experiment demonstrates that the sensitivity of caching to the state of the food items at recovery is not restricted to highly preferred food items, such wax worms, in that the jays stopped caching arbitrarily selected food types when they were consistently unpalatable at recovery. Moreover, this sensitivity did not depend upon extensive prior

experience with the food types in different states. Prior to Experiment 3, the jays had no experience with salami and pineapple in the degraded state and yet learned within a few trials to reduce caching the food type that was consistently degraded at recovery.

Experiment 4

Delayed reinforcement and punishment provide possible mechanisms by which caching is sensitive to the state of the caches at recovery. This account assumes that the behaviour of caching of a particular food is maintained by the delayed positive reinforcement engendered by the recovery of that food in a palatable form. Consistently pilfering the caches removes this source of reinforcement so that caching extinguishes. Moreover, encountering a degraded food at recovery may well be aversive and therefore act as a delayed punisher, which should be more effective in suppressing caching than the simple non-reinforcement resulting from pilfering. This explanation accords with the more rapid decline in the number of wax worms cached by the consistent degrade group than by the consistent pilfer group of Experiment 2.

The delayed reinforcement account requires that the positive reinforcement and punishment operated across a delay of at least 4 hr between caching and recovery, the shortest RI. The traditional assumption is that, with the exception of food aversion conditioning, reinforcement becomes ineffective when delayed for more than a few seconds in the absence of conditioned reinforcement (e.g., Grice, 1948). However, there are claims that positive reinforcement can operate across a relatively long delay under the appropriate conditions. For example, Lett (1974) trained rats to enter one arm of a T-maze by removing them immediately after a choice and then

returning them to the choice box after a delay spent in their cage. There they received a reward if the immediately preceding choice was correct. Using this procedure, she demonstrated that rats learn a visual discrimination with a delay of reward of 1 min (Lett, 1974, but see Roberts, 1976 for a failure of replication) and a spatial discrimination with delays up to 60 min (Lett, 1975).

There are, however, a number reasons for doubting that the differential caching observed in the consistent degrade and pilfer groups represents a direct effect of positive reinforcement on caching by recovery of palatable food items and/or punishment of caching by recovering degrade food across a delay. First, the 4-hr delay over which the reinforcement and punishment would have to operate is four times as long as the maximum employed by Lett (1975). Second, the speed of learning by the consistent degrade group is orders of magnitude faster than that observed by Lett (1975), who found little evidence of any learning with a 1-hr delay for 30 training trials. It might be argued that the jays had extensive prior experience with degrading wax worms and that this experience established some form of learning set that enhanced the rate of subsequent learning when the birds again encountered perished wax worms. It should be noted, however, that none of the birds in the consistent degrade groups of Experiments 1 and 2 had previously experienced consistently degraded wax worms and that prior to the respective experiment they had always cached wax worms at high levels. Similarly, none of the birds had received any prior experience with degrading pineapple and salami before Experiment 3.

Even so, it is important to determine whether the state of caches at recovery can affect caching over a retention interval of sufficient length to remove any possibility of direct reinforcement and/or punishment. Consequently, in the final experiment we allowed the birds to

cache peanuts and fresh meal worms before recovering the caches at least two days later with the meal worms in a degraded state. On the first trial, we expected that the birds would cache at least as many meal worms as peanuts. At issue was whether they would learn to stop caching the meal worms, while continuing to cache the peanuts, even though the retention interval was sufficiently long as to render any direct reinforcement or punishment highly implausible.

Method

Subjects and Apparatus

Three female and three male sexually mature western scrub-jays were housed in pairs in cages measuring 2 m wide by 1 m high by 1 m deep. During the testing period, each bird was confined by itself to one half of the home cage. The caching trays were the same as those used in the other three experiments, and the caching substrate was corn kibble, as used in Experiments 2 and 3.

Procedure

This experiment was conducted during September 2004, using birds had participated in the previous experiments. More importantly, however, their only prior experience with caching and recovering meals worms was nearly five years previously in the experiments reported by Clayton *et al*. (2001). In these experiments the birds had cached peanuts and meal worms before recovering them 4 hr later on some trials and either 1 day or 4 days later on the other trials. For three of the birds that had come from the replenish group, the meal worms had always been fresh at recovery, whereas for the remaining three birds that had come from the degrade group, the meal worms had been fresh after 4 hr but degraded after 1 and 4 days.

In Experiment 4, all six birds received the same experience. There were four trials, each starting with a 15-min caching period during which the birds were presented with a bowl containing 50 peanuts and 50 live meal worms. There was a long RI between caching and recovery of 76 hr in Trials 1 and 3, and 52 hr on Trial 2 and 4. Following the RI, the caching trays were replaced in the home cages for a 10-min recovery period on Trials 1-3. At recovery all the fresh meal worm caches were replaced with meals worms that had been artificially degraded using the same procedure as for wax worms in Experiments 1 and 2. On Trial 4, however, the recovery period was replaced by a test in which each bird was given a bowl containing 50 peanuts and 50 live meal worms and the first 10 items removed from the bowl were recorded. The caching trays were not present during this test. In all other respects, the procedure was the same as that used in Experiment 1.

(insert Figure 4 about here)

Results and Discussion

Caching was evaluated by an analysis that distinguished between the jays drawn from the degrade and replenished groups of the experiments reported by Clayton *et al*. (2001). As there was no significant main effect or interactions arising from this history, Fs < 1, Fs(3, 12) < 2.97, the mean number of items cached was averaged across these groups for presentation in Figure 4.

The birds rapidly learned to stop caching the meal worms even though the minimum delay of any punishment induced by recovery of degrade worms was over 2 days. On average the birds cached more meal worms than peanuts on the first trial but by the fourth trial the birds had almost

completely stopped caching meal worms. By contrast, they continued to cache peanuts on each of the four trials. There was a significant interaction between food type and trials, $F(3, 12) = 12.83$, $MSE = 26.65$, and on the last trial the birds cached more peanuts than meal worms, $F(1, 4) = 18.42$, $MSE = 31.92$. Moreover, there was a significant decline in the caching of meal worms, $F(3, 12) = 16.93$, $MSE = 30.44$, and an increase in the caching of peanuts, $F(3, 12) = 4.14$, $MSE = 8.76$.

Give the consistently long retention intervals in this experiment, we think that it is very implausible that the control of caching particular food items by their state at recovery was mediated by direct delayed reinforcement and/or punishment. Moreover, the observation of the first items selected from the bowl on Trial 4 confirmed the conclusion from the feeding test of Experiment 1, namely that the decline in the caching of degrading food does not reflect a general loss in the general incentive value of a food type. The first 10 choices by four of the jays were exclusively meal worms. Of the remaining two birds, one selected three peanuts having taken four meal worms, whereas the other choose one peanuts after first selecting six meal worms. It was also notable that all of the birds cached some of these meal worms in various places within their home cage, exclusively in sites that the experimenters could not access easily and were thus unlikely to be pilfered by humans.

General Discussion

These results establish that food caching by western scrub-jays is sensitive to the state of the caches at recovery. The birds reduced their caching of a particular food in the caching trays when

that food was consistently degraded at recovery. Two findings suggest that this effect was not due to a loss in the intrinsic value of the food type that degraded. In Experiment 1 the consistent degrade group showed as strong a preference for eating wax worms as the replenish group at the end of training, whereas the birds in Experiment 4 consistently selected meal worms in preference to peanuts, even though the latter were more profusely cached in the trays. Second, the consistent pilfer group of Experiment 2 also cached fewer wax worms when these food items were consistently pilfered at recovery. These birds only encountered fresh wax worms, so there is no reason why pilfering should have reduced their intrinsic value. Therefore, it is unlikely that the reduced caching by the consistent degrade groups was due to the conditioning of a food aversion reinforced by recovery of the degraded food. Furthermore, the fact that the birds rapidly stopped caching degraded meal worms in their caching trays in the final experiment, despite a minimum retention interval of over two days, argues strongly against any role for the direct reinforcement and/or punishment of caching by the state of the caches at recovery.

Alternative accounts appeal to the role of mnemonic processes in controlling caching. In their experimental analysis of Lett's (1974, 1975) delayed reinforcement procedure, Lieberman, McIntosh, and Thomas (1979) suggested that the learning observed under delayed reward was due to the retrieval of a memory of the choice response at the time of reward, and an analogous explanation could be given for the present results. It is already well-established that searching for caches at recovery by scrub-jays is controlled by a detailed memory of the caching episode (Clayton & Dickinson, 1998; Clayton & Dickinson, 1999a; Clayton & Dickinson, 1999c; Clayton et al., 2001; Clayton et al, 2003; Emery & Clayton, 2001). A retrieval account of caching assumes that the recovery of a particular food retrieves a memory of the caching of that food type, which

then results in an association of the caching of that food with rewarding or punishing effects induced by the food at recovery. This process would therefore result in an association between the caching of the degrading food with either punishment in the consistent degrade groups or non-reinforcement in the consistent pilfer group, which would result in a decline in the subsequent caching of this food type.

There is good evidence that animals can associate retrieved representations with a current event. Perhaps the most pertinent are demonstrations of mediated learning (see Holland, 1990, for review). For example, Holland (1981 – see also Dwyer, 1999) established a tone or light as a signal for a particular food before pairing the signal with toxicosis. This treatment established an aversion to the food, which Holland attributed to a pairing of a representation of the food retrieved by the signal with toxicosis. This process is analogous to the retrieval account of the decrement in the caching of foods that degrade at recovery. Subsequently, Holland and Forbes (1982) demonstrated mediated extinction by a treatment that retrieved a food representation in the absence of the reinforcer, which is analogous to the reduction in the caching of consistently pilfered food.

Whatever the merits of the retrieval account of caching by the consistent degrade and pilfer groups, it does not offer a ready explanation of the impact of the partial degrade schedule on the caching of wax worms and peanuts. When the jays cached wax worms and peanuts in separate caching episodes, Clayton and Dickinson (1999b) found that they cached more wax worms than peanuts under the partial degrade schedule, a difference that was not observed in the replenish condition. They suggested that this difference may have reflected enhanced caching of wax

worms in compensation for their partial degradation at recovery. The present results cast doubt on this interpretation, however. When the jays had the opportunity to cache the two food types concurrently, all birds showed an initial preference for caching the wax worms and the impact of the partial degrade schedule was manifest as a reduction in the level at which the peanuts were cached relative to the replenish condition in both Experiments 1 and 2 rather than an enhancement of the caching of wax worms. Although the underlying process remains obscure, the present data suggest that the effect depends upon two conditions being met.

First, the fact that the partial pilfer schedule did not reduce peanut caching in Experiment 2 suggests that the effect depends upon encounters with degraded food items at recovery. This conclusion is reinforced by the fact that the partial pilfer schedule, unlike the partial degrade schedule, had no impact on the relative caching of wax worms and peanuts in the Clayton and Dickinson (1999b) study. Second, the absence of a detectable partial degrade effect in Experiment 3 suggests that the effect also depends upon the caching of foods of different value, such as the wax worms and peanuts.

In conclusion, the present studies demonstrate that caching is not just controlled by proximal factors acting at the time of caching but that this behaviour is also sensitive to its consequences at recovery. Clayton and Dickinson and colleagues (e.g., Clayton, Bussey, & Dickinson, 2003; Clayton et. al., 2003) have argued for a role of episodic-like memory in the control of cache recovery by scrub-jays. When taken together with Emery and Clayton's (2001) demonstration that re-caching is sensitive to the social context of caching, the present findings suggest that mnemonic process also play a major role in the control of caching.

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Table 1 – Distribution of western scrub-jays in Experiment 2

Group	N	C & D (1999c)			Experiment 1		
		R	D	P	R	CD	PD
R	4	1	2	1		1	1
CD	4	1	1	2	1		1
PD	4		2	2	1	1	1
CP	5		2	2	1	1	1
PP	5	3		1	1	1	1

The number of birds in each group tested in Experiment 2, and the number of these birds and the groups to which they had been allocated when previously been tested in (a) the experiment reported by Clayton & Dickinson (1999c) and (b) Experiment 1. These groups are Replenish (R); Degrade (D); Pilfer (P); Consistent Degrade (CD); and Partial Degrade (PD).

Figure Captions

Figure 1. Experiment 1: Mean number of wax worms (worms) and peanuts (nuts) cached by the replenish, consistent degrade and partial degrade groups.

Figure 2. Experiment 2: Mean number of wax worms (worms) and peanuts (nuts) cached by the replenish, consistent degrade and partial degrade groups (left panels) and by the consistent pilfer and partial pilfer groups (right panels).

Figure 3. Experiment 3: Mean number of partially- or consistently-degraded and replenished food items cached by the consistent degrade and partial degrade groups.
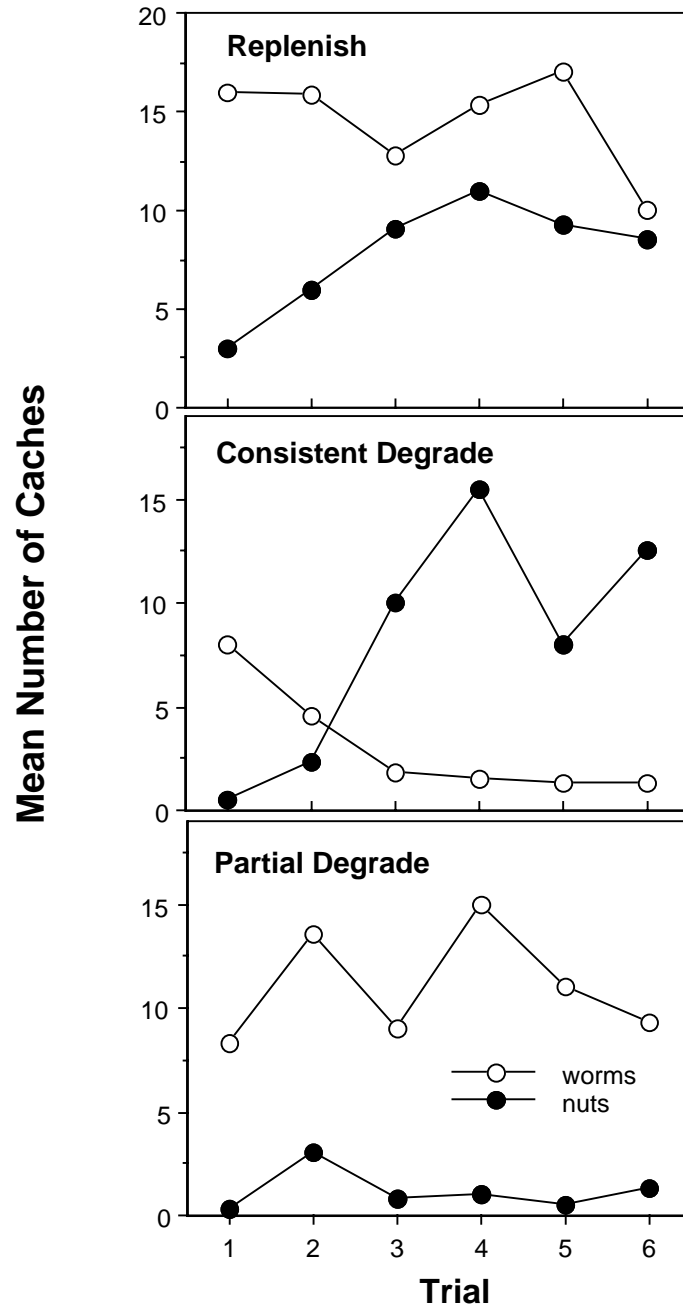
Figure 4: Experiment 4: Mean number of meal worms (worms) and peanuts (nuts) cached.
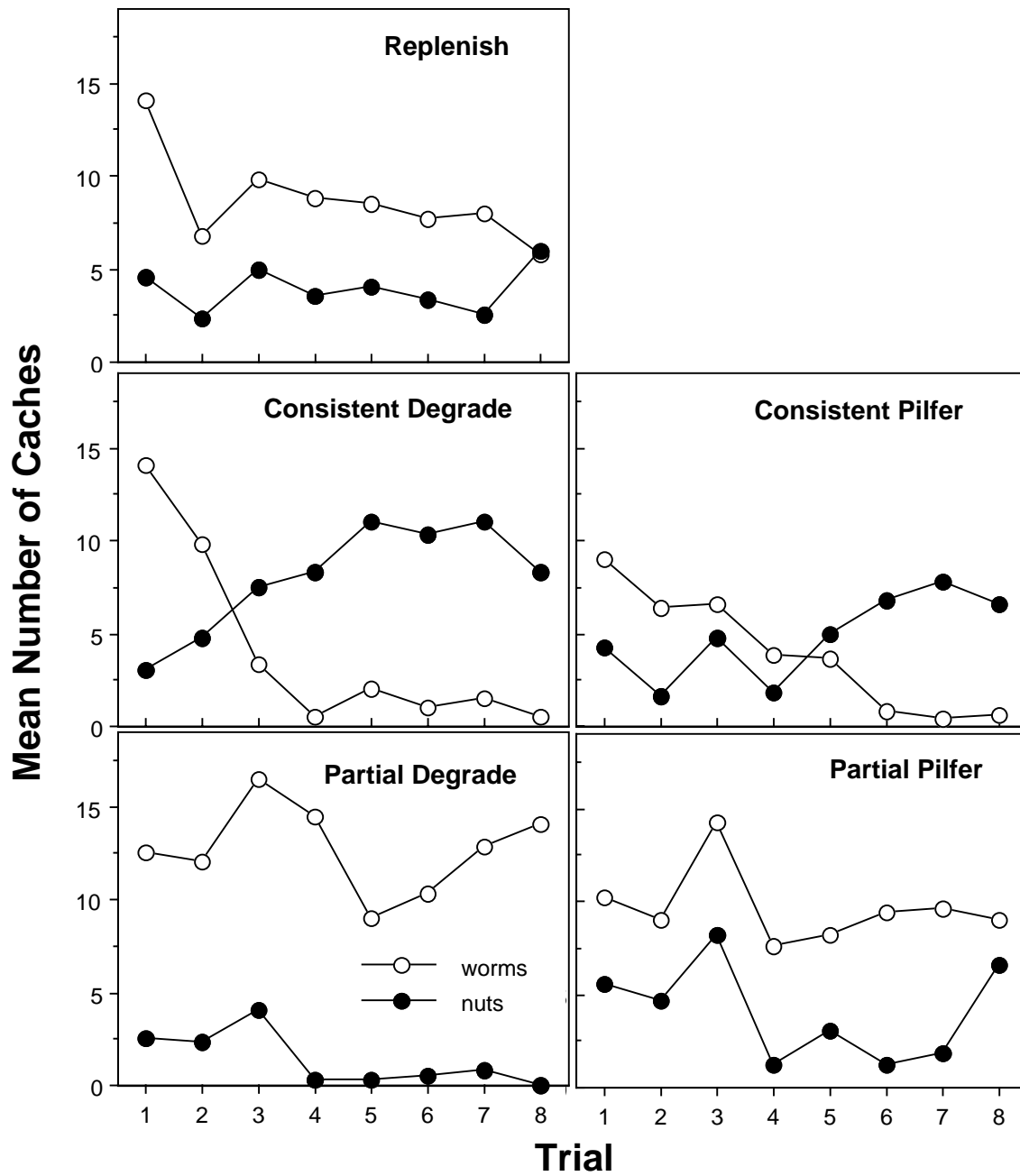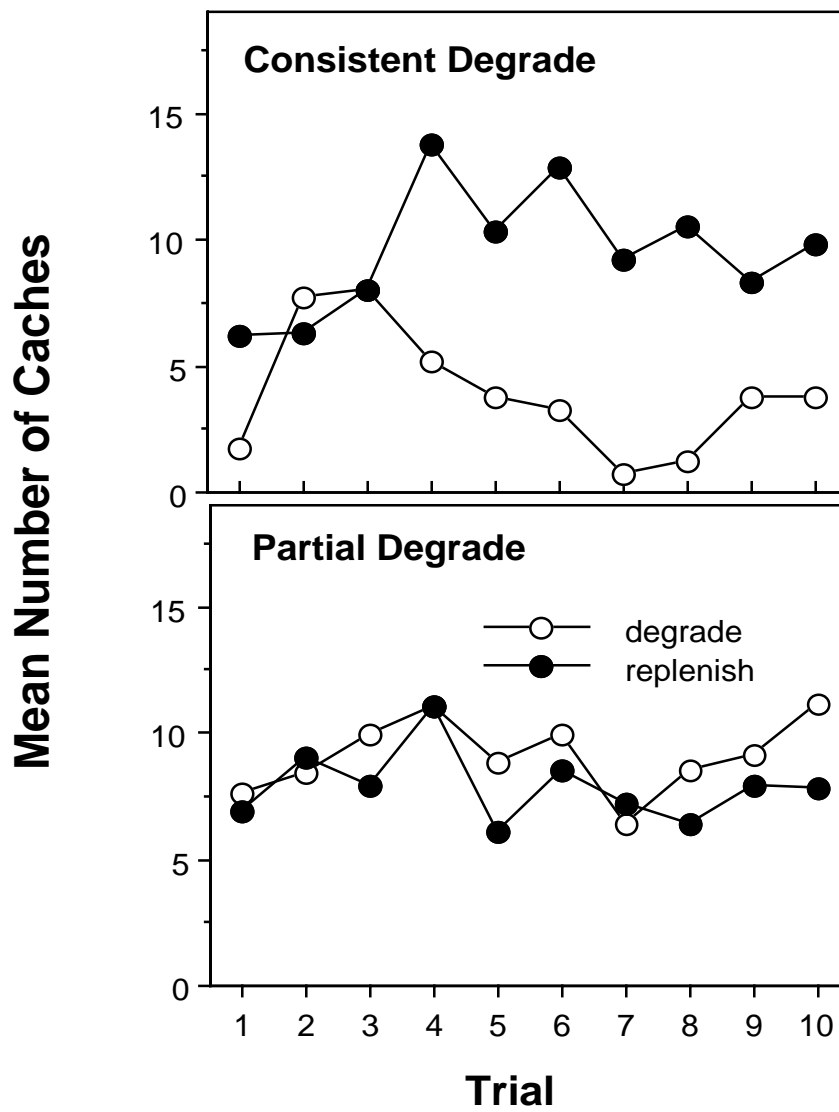
Figure 1.

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Figure 2.

Figure 3.

Figure 4.