

Caching economics: three experiments on the
economic determinants of caching behavior

A thesis
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA
BY

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF SCIENCE

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December 2010

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Acknowledgements

I would like to thank my advising committee: Andrew Simons, Mark Bee, and Dave Stephens for their comments on my manuscript and also for guidance in the previous years. I would also like to thank EEB's behavior group for years of comments about my research and presentations. In addition, the Stephen's lab members have been effective collaborators. My wife, Sarah, has always been supportive and encouraged my work. I would especially like to thank Dave Stephens for his flexibility, loyalty and mentorship. I have learned immense amounts about how to be a better scientist in general and also how to be a great advisor. His faith in me from the beginning has not been matched by many.

Dedication

This thesis is dedicated to all those who have encouraged my studies and passion for science. My parents and family nurtured my joy for science my whole life and my wife has always been a huge supporter. I dedicate this thesis to them.

Abstract

This paper develops a simplified and experimentally tractable version of Andersson and Krebs' (1978) classical model of caching behavior. This study presents three experiments using captive blue jays (*Cyanocitta cristata*) that test the predictions of this model. These experiments explore the effects of three theoretically important variables: availability time (denoted by T_a), handling time (h), and the background foraging rate (γ). Experiment 1 tests the predicted effect of availability time and shows that blue jays cached more food items when availability time was short. Experiment 2 examines the interaction between availability time and handling time. Experiment 2 shows a significant effect of handling time (jays cache more when handling times are short), but no effect of availability time (apparently contradicting experiment 1). Experiment 3 considers the predicted interaction between handling time and habitat richness (as represented by the background foraging rate). This experiment shows significant effects of both handling time and background, but no interaction between the two variables. The implications of these experiments for the further development of our model are discussed.

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Introduction:

Many animals store food for recovery at a later time. Investigators call this behavior hoarding or caching and it can take many forms (see Vanderwall 1990 for an authoritative review). Caching has become an important experimental tool in animal behavior where investigators have exploited caching behavior to study memory (Kamil and Balda 1985, Clayton and Dickinson 1998), learning (Kamil et al. 1998) and other aspects of animal cognition (Pravosudov 1986). Also, investigators have studied the interactions between social behavior and caching (Bednekoff and Balda 1996, Emery et al. 2004, Bugnyar and Heinrich 2005, see Brodin 2010 for review). In addition, some investigators have argued that caching animals may possess neural and cognition specializations that support caching behavior (e.g. specializations in spatial memory and especially an enlarged hippocampus in caching birds—Sherry et al. 1989, Olson et al. 1995). Taken together these studies represent a significant body of work on caching behavior, yet they only address the fitness value of caching behavior indirectly.

Our work considers the benefits of caching behavior theoretically and experimentally. While theoreticians have developed models to predict when caching should occur (Andersson and Krebs 1978, McNamara et al 1990) these models commonly include variables that are difficult to measure or manipulate. For example, in Andersson and Krebs' classical model the variable (G) represents the “fitness gain” associated with caching a single item; a quantity that is difficult to measure or manipulate without additional assumptions. We develop an experimentally tractable version of the Andersson and Krebs model. As in their model, our central premise is that caching exists to exploit temporary food patches. We develop our model in detail below (Table 1) focusing on the effects of three variables: (1) the time a food patch is available (T_a —which we call availability time), (2) the time required to eat a single food item (h —which we call handling time), and (3) the rate of food acquisition available if the forager leaves the food patch and forages elsewhere (γ —which we call the background rate). Following the development of our model, we present a sequence of three experiments that investigate the effects of these three variables.

Our model considers the following situation. A forager encounters a large supply of food (a bonanza). The bonanza is only available for a short period of time that we denote by T_a (the availability time). The forager has a total of T units of time to acquire food, so that when the food pile is no longer available (i.e. after T_a) the forager has $T - T_a$ time units to acquire food at the background rate (γ). The forager must choose between two strategies during T_a : cache or eat. Our model assumes that a forager will cache if caching leads to more food over the total time T . Conversely, we assume that the forager will eat if eating leads to more food over time T . We assume that the food bonanza is large enough that the forager can spend all of T_a caching or all of T_a eating without exhausting the bonanza. Furthermore, the model assumes that the handling time is greater than the caching time.

Table 1

Variable	Definition
<p style="text-align: center;">T</p> <p>T_a =availability time</p> <p>c=caching time</p> <p>h=handling time</p> <p>γ=background rate</p>	<p style="text-align: center;">Total time</p> <p>Time food patch is accessible (subset of T)</p> <p>Time required to cache a food item</p> <p>Time required to handle and consume a food item</p> <p>Average foraging rate outside of patch</p>

Value of caching. If the forager chooses the cache strategy, it caches T_a/c items during the availability time because c is the time required to cache a single item—the caching time. When T_a expires, the caching animal must spend time recovering and consuming each of its cached items. We assume that recovery time is negligible (approximately true in our experimental situation) but that consumption and processing takes h time units per item. So in the simplest case, the caching forager spends hT_a/c time units consuming cached items. If time remains in T , our model assumes that the forager can acquire food at rate γ (which we call the background rate). To formally calculate the value of the caching strategy, we need to distinguish between two cases. In the first case, sufficient time remains after the bonanza’s availability that the forager can consume all of

the items it cached during T_a . This occurs if $hT_a/c < T - T_a$. In this case, a caching strategist obtains:

$$\frac{T_a}{c} + \gamma \left[T - T_a - \frac{hT_a}{c} \right]$$

Where the first component of the sum is the number of items cached during T_a , and the second component is the amount of food acquired elsewhere (at rate γ) after the forager has consumed all the items that it cached. In the second case, the forager does not have enough time to consume everything it cached during T_a . In this situation, the animal spends all the time after T_a eating and the caching strategist obtains:

$$\frac{T - T_a}{h}$$

Taken together, then, the value of caching (V_{cache}) is:

Equation 1

$$V_{cache} = \begin{cases} \frac{T_a}{c} + \gamma \left[T - T_a - \frac{hT_a}{c} \right] & \text{if } \frac{hT_a}{c} < T - T_a \\ \frac{T - T_a}{h} & \text{if } \frac{hT_a}{c} > T - T_a \end{cases}$$

The value of eating (V_{eat}). We can readily calculate the amount of food acquired by an ‘eat’ strategist. The eat strategist eats T_a/h items during T_a , and acquires food at the background rate (γ) in the remaining time ($T - T_a$). Therefore, the value of eating (V_{eat}) is:

Equation 2

$$V_{eat} = \frac{T_a}{h} + \gamma(T - T_a)$$

When is caching best? In the final step of our model, we ask when the value of the caching (V_{cache}) exceeds the value of the eat (V_{eat}); and we—obviously—predict that animals should cache when $V_{cache} > V_{eat}$ and eat otherwise. In the following discussion, we use our expressions for V_{cache} and V_{eat} to make predictions about the effects of three experimentally accessible variables: the availability time, T_a ; the handling time h (which

interacts with T_a), and overall richness of the habitat as measured by our variable background rate.

We review the predictions of our model (equations 1 and 2) focusing on their predictions for the three variables we manipulated experimentally: availability time (T_a); handling time (h) and background rate (γ). This study tests the effects of these variables via three experiments using captive blue jays. Our predictions and experiments flow from the model presented above. Our model assumes that a forager encounters a food bonanza that will only be available for a short time, and it compares the expected value of two strategies: (i) caching the items in the bonanza while they are available and eating them later vs (ii) eating items immediately. Experiment 1 tests the simple prediction that animals should cache more when the bonanza is available for a shorter time. Experiments 2 and 3 explore interactions between our three variables focusing on the handling time. Experiment 2 factorially manipulates handling time and availability time, while experiment 3 factorially manipulates handling time and background rate (a proxy for habitat richness).

General Methods

We collected all birds used in experiments from the wild and hand raised them in our lab. When birds were not in an experiment, we fed them an ad libitum diet of 50% Lafeber's Cockatiel pellets and 50% poultry starter as well as a small egg white cube and a single mealworm daily for a protein supplement. In preparation for an experiment, we reduced each bird's body weight to 90% of its ad libitum body weight. When in an experiment, in addition to sunflower seeds available during trials, I fed the birds enough cockatiel pellets and poultry starter to maintain their weight at a closely-monitored percentage of its ad libitum body weight. We weighed birds each day at the same time to determine whether we needed to adjust their food ration. Each bird was individually housed in a wire cage (measuring 38 X 38 X 61 cm) in a colony of 45 blue jays maintained on a 12 hour light/dark cycle. The sex of the birds was unknown. We did not use any bird in more than one experiment. We exposed all experimental birds to all foods used in the trials previous to the start of each experiment so every bird would have

experience handling the food and to diminish any novelty effects. In all experiments, an item of food was considered cached if it was removed from its original place, replaced in a different location and not eaten within one minute. For all three experiments, we observed individual jays in their standard cages described above. We manipulated standard striped sunflower seeds to create foods with different handling times. We manually removed shells from the whole seed to give a short handling time ($25.8 \text{ s} \pm \text{SE } 16.4 \text{ s}$). We used unmodified seeds with shells as the medium handling time ($93.7 \text{ s} \pm \text{SE } 35.6 \text{ s}$). We covered the shells with a plastic straw belt to make it a long handling time food ($125 \text{ s} \pm \text{SE } 40.5 \text{ s}$).

General Statistical Analysis:

For all experiments, we used ANOVA tests using the Statistica software. We used Microsoft Excel's random number generator to perform all the randomizations required by our designs.

Experiment 1: effect of availability time.

Figure 1 shows the effects of availability time (T_a) on the expected benefits associated with the cache and eat strategies. The 'kinked' curve in the figures shows the value of caching (the kink occurs because the value of caching consists of two linear pieces, see equation 1). The value of caching increases with availability time until there isn't enough time to retrieve all the items the forager caches. After this point 'a', the value of a caching strategy declines with increasing T_a , because a larger T_a means less time to retrieve and eat cached items. In contrast, the value of eating increases linearly with T_a . Typically, then, caching is better than eating at small T_a values (as long as $h > c$), but when the bonanza lasts for a long time (large T_a), eating is better, because an 'eat' and 'cache' strategist can obtain the same amount of food but 'cache' strategists spend $c+h$ time units processing each item, while eat strategists spend only h . Qualitatively, our prediction here is simple. We predict more caching when the availability time is small. This agrees with the intuitive idea that caching exists to capitalize on ephemeral food patches. Our first experiment was a straightforward manipulation of availability time that

tested this prediction. We tested the effect of availability time by comparing a short T_a (5 minutes) to a long T_a (50 minutes).

Experiment 1 Methods

Subjects

We randomly assigned 20 birds (b14, b375, b304, b5, b354, b93, b11, b20, b256, b10, b81, b78, b7, b356, b361, b206, b51, b342, b95 & b208) to either the short availability time (5 minutes; $n=10$) or the long availability time (50 minutes, $n=10$). We tested these birds once a day (hereafter a “trial”) for 30 days. We presented seeds (i.e. the bonanza) in a small dish and removed the dish by hand at the end of the experimentally determined availability time.

Trials

At the start of each trial, we placed 15 intact sunflower seeds (medium handling time) in a small bowl, and placed it in the cage with the bird. From video-recordings, I tabulated each time a bird handled and ate a seed. After 5 minutes elapsed, I removed the bowl and counted the remaining seeds. For birds assigned to the short availability treatment, we discarded the remaining seeds and returned the empty bowl to the cage. For birds in the long availability treatment, we immediately returned the bowl with any remaining seeds to the cage for a further 45 minutes. We performed this ‘sham removal’ to ensure that the interruption caused by the experimenter could not explain any difference we observed between the two groups. We also counted seeds cached around the cage to confirm video counts.

Experiment 1 Results:

Figure 2 summarizes the effect of T_a (availability time) on number of items cached after 5 minutes. The figure shows that, on average, more items were cached in the shorter T_a treatment. Formally, analysis of variance (ANOVA) testing supported our prediction revealing a significant between-subjects effect of availability time ($F_{1,18}= 7.98$, $p=.011$, see Figure 2). This effect is further illustrated in Figure 3 by the individual bird caching results comparing treatments (5 min and 50 min) side by side.

If animals cache or eat at a constant rate we would expect differences in our availability time treatments simply because more time provides more opportunity for action. To account for this possibility, we considered the number of items cached during the first 5 minutes of the availability period for both our short and long availability treatments. In the short availability treatments, jays cached $1.1 \pm \text{SE } .4$ in the first five minutes, while they cached $.3 \pm \text{SE } .4$ in the long availability treatment.

Experiment 2. The interaction between availability time and handling time.

As suggested above, the effect of availability time depends on the magnitude of the handling time. Figure 4 shows the predicted effect of handling time on caching behavior by plotting the difference between the expected value of caching (V_{cache}) and the expected value of eating (V_{eat}) as a function of handling time. The figure shows the interaction between handling time and availability time by plotting the handling time curve for a range of availability times. According to the illustration, our model predicts that animals should cache when handling time falls in an intermediate range, or ‘caching zone’. If handling times are very short the animal does better by simply eating items from the bonanza. On the other hand, if the handling time is very long, it doesn’t pay to cache items because cached items are only valuable if the animal eventually eats them and items with a long handling time carry a high opportunity cost, because time spent eating cached items is time that the forager cannot spend exploiting alternative food sources. In reference to Figure 4, availability time affects the upper limit of the caching zone even though it does not affect the lower limit (assuming, of course, that the other parameters of our model remain fixed). The figure shows that the longest handling time at which the model predicts caching decreases with availability time; that is, we see smaller upper bounds for caching when availability times are long. Our reasoning follows that as handling time increases, an animal can ensure the availability of more food by exploiting the behavior that requires less time (assuming caching time is held constant). This agrees with our idea that small availability times promote caching since, with decreasing T_a , acting quickly becomes increasingly important to ensuring food availability. Therefore, the related idea that long handling times impose an opportunity

cost explains the predicted caching behavior because long handling times and long availability times both reduce the value of food acquired elsewhere. Experiment 2 explores the interaction between handling time and availability time via a factorial manipulation of these two variables.

Experiment 2 Methods:

Experiment 2 tested the interaction between handling time and availability time by factorially manipulating availability time (four treatment levels: 5 minutes, 13 minutes, 21 minutes, and 30 minutes) and handling time (two treatment levels: medium handling time---shells intact---and short handling time---shells removed). We decided to use 5 minutes as a short handling time because it was used in the previous experiment and used 30 minutes because we learned from experiment 1 that the number of seeds eaten did not change after 30 minutes passed. We chose the intermediate availability times because they were equally spaced temporally between the long and short times. For use in experiments 2 and 3, we built a 1-inch deep container that we could open or close remotely (opened by one solenoid, and closed by another).

Subjects

We randomly selected 8 birds that had no previous experience in caching experiments (b222, b21, b93, b91, b12, b5, b7, and b95) from the colony. We used a latin square to determine the treatment order for each subject. Each bird completed 9 trials in each treatment setting up a within-subjects design. Only the data from the last 3 trials were analyzed.

Trials

To begin a trial, the apparatus opened the lid, making 25 seeds available to the subject that it could eat or cache. The apparatus closed the lid at the end of the experimentally determined availability time. Using video recordings of the subject's behavior during the trial, we recorded the occurrence and timing of each of the following events: food removal, handling, consumption, caching, and cache recovery.

Experiment 2 Results:

Figure 5 summarizes the results of experiment 2, illustrating the effect of availability time and handling time. This figure suggests that handling time has a strong effect on caching, while in contrast with experiment 1 availability time seems to have relatively little effect. Formally, repeated measures ANOVA testing incorporating all 8 treatments (2 levels of handling time and 4 levels of availability time) did not show a significant interaction between the two tested variables ($F_{3,21}=0.942$, $p= .431$). The main effect of availability time was also not found to be significant ($F_{3,21}= .217$, $p= .883$). However, the effect of handling time was found to be significant ($F_{1,7}=15.824$, $p=.005$). Figure 6 further illustrates the results by comparing the individual bird performances in reference to each main effect (handling time and availability time).

These results are surprising in two ways. First, although our model can predict increased caching with reduced handling time (see Figure 2), the prediction seems somewhat counterintuitive. Logic leads us to focus on the lower bound of the ‘caching zone’ (Figure 4) where caching becomes valuable because the forager can cache more items than it can eat. In contrast, the logic of the upper bound of the ‘caching zone’ predicting caching is more abstract since consuming recovered items incurs a high opportunity cost. However, the results of experiment 2 focus our attention on the upper bound rather than the lower bound of the ‘caching zone’. Second, we found no effect of availability time here, even though experiment 1 did find an effect. We address this contradiction, and the procedural difference between the two studies in the discussion.

Experiment 3. Handling time and background rate.

Our model suggests that the value of caching depends on the richness of the habitat (represented by the background rate γ in our model). This makes sense intuitively because the value of the bonanza to our hypothetical cacher surely depends on how the bonanza compares to resources elsewhere. In our model, handling time determines the richness of the bonanza (because we measure value in units of one item). For example, the intake rate associated with eating from ‘the bonanza’ is simply $1/h$. It follows that the value of caching should depend in some way on the relative magnitudes of handling

time and background rate. Figure 7 shows the predicted interaction between handling time and background rate. In congruence with Figure 4, we see that our model predicts caching for an intermediate band of handling times, but the size of this ‘caching zone’ depends on background rate. As one might expect, the caching zone is narrow, or nonexistent, in rich habitats (high background rates) and wide in poor habitats. Indeed, the figure shows that the caching zone can disappear completely when the background is sufficiently high; predicting that caching cannot make sense economically when the habitat is very rich. Interestingly, our model predicts that background rate affects the upper and lower bounds of the ‘caching zone’ differently. We predict a relatively modest effect on the lower boundary of the ‘caching zone’, and a much stronger effect on the upper bound as background rate changes. Experiment 3 explores this interaction via a factorial manipulation of handling time (3 levels) and background feeding rate (2 levels).

Experiment 3 Methods:

Experiment 3 tested the interaction between handling time and background rate by manipulating background rate (two treatment levels high and low, see details below) and handling time for food items (three treatment levels: short, medium, and long). Like experiment 2, experiment 3 used a within subjects design in which every subject experienced all 6 treatments.

Subjects

I randomly selected 8 birds that had no previous experience in caching experiments (b14, b86, b81, b375, b383, b11, b361, and b357) from the colony. To manipulate the background rate, a commercial pellet feeder (MED feeder model #ENV-203-20) attached to the top of the cages delivered .02 gram food pellets (made from Lafeber’s cockatiel food and poultry starter) at a fixed rate during the observation period (300 minutes). We chose the delivery rates to create one condition with a poor environment and another with a rich environment. In our low background rate condition we delivered 75% of the food required to maintain the subject at its ad libitum weight; in the rich background condition we delivered 90% of the food required for the subject to maintain its ad libitum weight. We used colony feeding and weight records to determine

these feeding rates. The specific rates varied from one individual to the next because different individuals have different food requirements.

Trials

Trials were organized as described for experiment 2, except that the availability time was always 30 minutes in this study. Each bird finished 5 trials (1 per day) before moving on to the next treatment. Only the last 3 trials were analyzed.

Experiment 3 Results:

Figure 8 shows the mean number of items cached for each of the six treatment conditions in experiment 3. The figure suggests that caching generally decreased with increasing handling time and background rate. Formally, repeated measures ANOVA found no interaction between these two variables ($F_{2,46}=0.327$, $p=0.722$). However the main effect results supported our interpretation, showing significant effects of handling time ($F_{2,46}=15.096$, $p<0.0001$) and background rate ($F_{1,23}=24.684$, $p<0.0001$). Figure 9 illustrates the individual bird performances in reference to each main effect (handling time and background rate).

The effect of background rate was as expected both from our model and intuition. One naturally expects that caching will be more valuable in poor habitats (low background rates). The effect of handling time was more surprising. Our model would lead us to expect low caching rates at small and large handling times while we should see the highest caching at intermediate handling times. Superficially at least, experiment 3 does not support this prediction. The discussion addresses this contradiction.

Discussion:

Review of results.

This study presents a simple model and three corresponding experiments that explore the role of three variables in caching behavior: availability time (T_a), handling time (h) and the background rate (γ). While our experiments suggest that all three variables can affect caching behavior, our data suggests some problems for future analysis. When we decreased availability time (in experiment 1) our subjects cached

more items, yet when we simultaneously manipulated availability time and handling time (in experiment 2) we found that caching decreased with increasing handling time but we found no effect of availability time. Finally, in experiment 3 we manipulated both handling time and background rate, and we found that both variables influence caching decisions. Our jays tended to cache more when handling times were smaller, and the background rate was lower. Although our model predicts that both very short and very long handling times should discourage caching, this study only provides direct support for the claim that long handling times discourage caching.

Significance of results.

Our approach extends and exploits the economic approach to food storage originally advocated by Andersson and Krebs over twenty years ago. While most students of caching acknowledge the fundamental contribution of the Andersson and Krebs paper, most empirical studies of caching have focused on memory and neuroscience (Kamil and Balda 1985, Sherry et al. 1989, Olson et al 1995, Clayton and Dickinson 1998, Pravosudov 2007 book chapter for review, Brodin and Bolhuis 2008) rather than the evolutionary economics of caching (see McNamara et al 1990, Brodin & Clark 1997, Pravosudov and Lucas 2001 for exceptions). Our model modifies the Andersson & Krebs paradigm slightly, by focusing on experimentally manipulated variables that should, in theory, influence the fitness value of caching behavior. We argue that a renewed, experimentally-supported interest in the fitness value of caching could complement the ongoing research program that focuses on the neural and psychological mechanisms of caching. A research program focusing on variables that influence the fitness value of caching might, for example, refine our ideas about the adaptive specializations in memory associated with caching behavior.

Research programs exploring the connections between caching and memory are now a well established part of our field. In contrast, the general subject of decision-making is an emerging topic that generates interest across many disciplines including neuroscience, economics, psychology and behavioral ecology (Glimcher and Rustichini 2004). Non-human caching behavior offers an interesting and under-exploited model of

decision making in at least two senses. First, it offers a non-human example of ‘savings’ decisions—a type of decision that cognitive scientists typically view as advanced or restricted to humans. Second, it offers an intriguing contrast to empirical results of impulsivity in decision-making. Both human and non-human subjects often prefer immediate rewards even if they could achieve greater gains by waiting longer (Stephens 2002, Stevens and Stephens 2008). Yet, in caching behavior we see non-human subjects choosing to defer consumption. While one can imagine several hypotheses to explain this apparent contradiction, it seems likely that exploring these hypotheses empirically could produce a deeper understanding of the origins and mechanisms of impulsivity.

Results in context.

Andersson and Krebs’ foundational paper paved the way for a diverse literature. Some models have explored the role of environmental variability in caching economics (e.g., McNamara et. al., 1990). In these models stored food serves as insurance for an unexpected period of paucity. Although our model can easily be adjusted to be able to test variability in the background rate (γ), our data from experiment 3 may suggest that variability is not essential. We still found a significant main effect of handling time when the rate was held constant throughout the treatment. However, an interesting experiment could test this suggestion. Clearly, one could manipulate variability as well as mean background rate in our experiment preparation; indeed a compelling experiment might manipulate these variables independently in a factorial way.

While several studies have tested the effect of handling time on caching, observed effects seem to vary. American crows (Cristol, 2001) and grey squirrels (Jacobs, 1992) preferred to cache items with long handling times and ate ones with short handling times immediately. Conversely, nuthatches (Woodrey, 1990) preferred to eat items with long handling times first and cache the ones with short handling times. Our model may account for this variation—since it predicts that animals should cache items with intermediate handling time—even if our experiment only supports part of this prediction.

Figure 10 illustrates a hypothetical situation in which relative handling times fit to our model would bring these conflicting results into agreement with each other. Imagine

Species A and species B where both are tested with their own set of short and long handling time foods. Species A's short h food may fall in front of the 'caching zone' and the long h food landing inside the 'caching zone' (A1 and A2). Furthermore, Species B's short h food could land inside the 'caching zone' but the long could fall past the upper bound of the 'caching zone' (B1 and B2) demonstrating how this model can account for the species specific differences of caching economics in reference to handling time.

Our variable of background rate is intuitively simple. While we know of no identical manipulation in the literature, background rate is logically related to the ideas of hunger and motivation—that is, animals will tend to be hungry when the background rate is low. McNamara et al. (1990) consider the effect of hunger theoretically. Clayton and Dickinson (1999) found that less hungry birds cached less. This is consistent with our model if we assume that hunger measures the background rate. Similarly, Pravosudov and Clayton (2001) found that hungry chickadees recovered caches more accurately. Our finding that blue jays with reduced background rates increase caching is in broad agreement with these results about hunger and motivation. As far as we are aware our study is the first to manipulate availability time, even though models have long recognized the theoretical importance of this variable (Andersson and Krebs 1978, McNamara et al. 1990).

Although themes investigated in this study have, to an extent, been previously explored, this study combines several threads in caching theory and tests them in a unique framework. It is well understood that individual factors interact in nature and this set of experiments manipulated these supposed interactions in a controlled setting. We also believe that this setup may generate a new set of ideas to be expanded upon in the study of caching economics. For example, an experiment that allows an animal to obtain food for impulsive decisions and also offers an opportunity to cache this food could raise questions about which is more important; the right now or the later on?

Limitations/further questions.

As with any study there are many possible limitations and extensions. We mention only a handful. First, recall that our model assumes that caching time (c) is

shorter than the handling time (h). We feel that an experiment that somehow manipulated both caching time and handling time would provide important insights into the validity of our approach and more fundamentally into why handling time has the somewhat surprising effect on caching that we report. Second, as suggested above, we feel that our experimental approach could be extended to consider ‘insurance’ hypotheses about caching by factorially manipulating both the magnitude and variability in the background rate. Finally, as with any study, we don’t know whether our results generalize to situations other than our experimental preparation. For example, while some caching animals store and retrieve within a single day, as in our preparation, others cache food for recovery over much longer time scales. While we assume that similar economic variables operate at different time scale, setting up experimental situations to confirm this may be quite difficult.

Final summary.

Behavioral ecologists typically assume that caching exists to exploit ephemeral surpluses. This study has explored this idea via model and experiment. Broadly speaking our results agree qualitatively with this premise, but they also suggest intriguing questions for further analysis. Such as why availability time affects caching in some studies but not others, or whether short handling times generally promote caching (as we observed) or instead if this only happens for ‘longer handling times’ (as our model predicts). Addressing the procedural differences (food holding apparatus differences and between-subjects compared to a within-subjects design) between experiment 1 and 2, as referenced by the results section, may have found agreeing results. Although, superficially the caching rates relative to handling time in experiment 2 and 3 surprised us, we suggest a simple explanation. Where, in reality, the handling times we tested in both experiments fall on the ‘caching zone’ curves is a bit enigmatic. Perhaps all the handling times we used are characterized as intermediate to the jays (as compared to short or long as we characterized them). An experiment testing the extreme upper and lower bounds of the handling time axis may confirm our model’s findings that caching is

not predicted in these cases. In general, we feel that our straightforward experimental preparation offers many possibilities to address these questions and others.

Work cited:

- Andersson, M. & Krebs, J.** 1978. On the evolution of hoarding behavior. *Anim. Behav.*, **26**, 707-711.
- Bednekoff, P. A. & Balda, R. P.** 1996. Social caching and observational spatial memory in Pinyon Jays. *Behaviour*, **133**, 807-826.
- Brodin, A. & J. J. Bolhuis.** 2008. Memory and brain in food-storing birds: space oddities or adaptive specializations. *Ethology*. **114**, **Issue 7**, 633-645.
- Brodin, A.** 2010. The history of scatter hoarding studies. *Phil. Trans. R. Soc. B.* **365**, 869-881.
- Bugnyar, T. & Heinrich, B.** 2005. Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proc. Roy. Soc. B.*, **272**, 1641-1646.
- Clayton, N. & Dickinson, A.** 1998. Episodic-like memory during recovery by scrub jays. *Nature*. **395**, 272-274.
- Clayton, N. & Dickinson, A.** 1999. Motivational control of caching behaviour in the scrub jay, *Aphelocoma coerulescens*. *Anim. Behav.*, **57**, 435-444.
- Cristol, D. A.** 2001. American crows cache less preferred walnuts. *Anim. Behav.*, **62**, 331-336.
- Emery, N.J., Dally, J.M. & Clayton, N.S.** 2004. Western scrub jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics. *Animal Cognition*. **7**, **Number 1**, 37-43.
- Glimcher, P.W. and A. Rustichini.** 2004. Neuroeconomics: the consilience of brain and decision. *Science*. **306 (5695)**, 447-452.
- Jacobs, L. F.** 1992. The effect of handling time on the decision to cache by grey squirrels. *Anim. Behav.*, **43**, 522-524.
- Kamil, A. C. & Balda, R. P.** 1985. Cache recovery and spatial memory in Clark's Nutcracker's (*Nucifraga Columbiana*). *Journal of Experimental Psychology: Animal Behavior Processes*. **11**, **Issue 1**, 95-111.
- McNamara, J. M., Houston, A. I., & Krebs, J. R.** 1990. Why hoard? The economics of food storing in tits, *Parus* spp. *Behav. Ecol.*, **1:1**, 12-23.
- Olson, D. J., Kamil, A. C., Balda, R. P., & Nims, P. J.** 1995. Performance of four seed-caching corvid species in operant tests of nonspatial and spatial memory. *Journal of Comparative Psychology*. **109**, **2**, 173-181.
- Pravodusov, V. V.** 1986. Individual differences in the behavior of the Siberian tit (*Parus cinctus*) and the willow tit (*Parus montanus*) in foraging and storing food. *Soviet Journal of Ecology*. **17**, 237-241.
- Pravosudov, V. V.** 2007. The relationship between environment, food caching, spatial memory, and the hippocampus in chickadees. In: K. Otter, ed., *Ecology and Behavior of Chickadees and Titmice: an Integrated Approach*. Oxford University Press, pp. 25-41.
- Pravosudov, V.V., & Clayton, N. S.** 2001. Effects of demanding foraging conditions on cache retrieval accuracy in food-caching mountain chickadees (*Poecile gambeli*). *Proc. R. Soc. London B.* **268**, 363-368.

- Pravosudov, V. V., & Lucas, J. R.** 2001. A dynamic model of short-term energy management in small food-caching and non-caching birds. *Behavioural Ecology*, **12**, No. 2, 207-218.
- Sherry, D. S., Vaccarino, A. L., Buckenham, K., & Herz, R. S.** 1989. The hippocampal complex of food-storing birds. *Brain Behav. Evol.*, **34**, No. 5, 308-317.
- Shettleworth, S.J. & Krebs, J. R.** 1982. How marsh tits find their hoards: the roles of site preference and spatial memory. *Journal of Experimental Psychology: Animal Behavior Processes*, **8**, Issue 4, 354-375.
- Stephens, D. W.** 2002. Discrimination, discounting and impulsivity: a role for an informational constraint. *Phil. Trans. R. Soc. Lond. B.* **357**, No. 1427, 1527-1537.
- Stevens, J. R. & Stephens, D. W.** 2008. Patience. *Current Biology*, **18**(1), R11-R12.
- Vanderwall, S. B.** 1990. *Food Hoarding in Animals*. Chicago: University of Chicago Press.
- Woodrey, M. S.** 1990. Economics of caching versus immediate consumption by white-breasted nuthatches: the effect of handling time. *Condor*, **92**, 621-624.

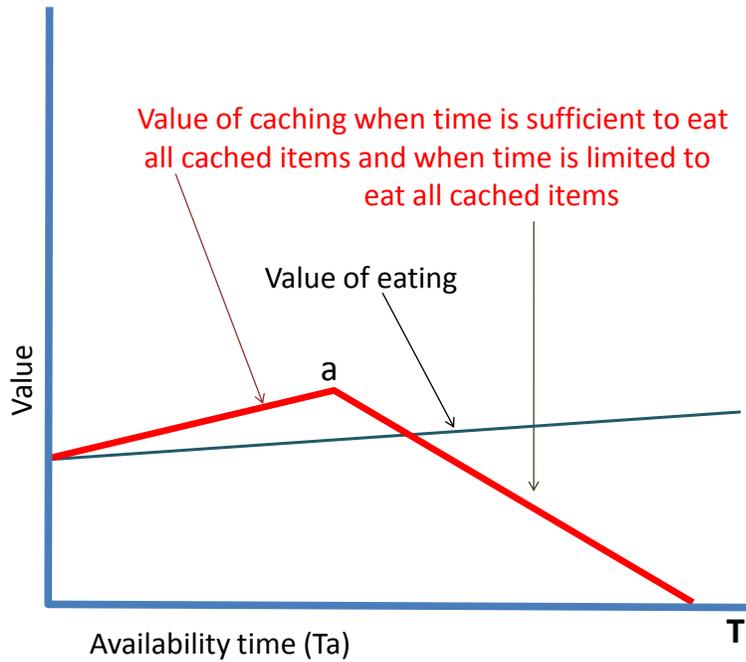


Figure 1 Value of caching items during the availability time (T_a) increases until the animal experiences an availability time (T_a), in this case 'a', that does not allow sufficient time left in T (total time) to recover and consume all cached items. The value of caching thereafter continues to decrease since the number of items the animal can eat decreases with increasing T_a . At some point, 'eating' becomes the better strategy (has a greater value) than 'caching'.

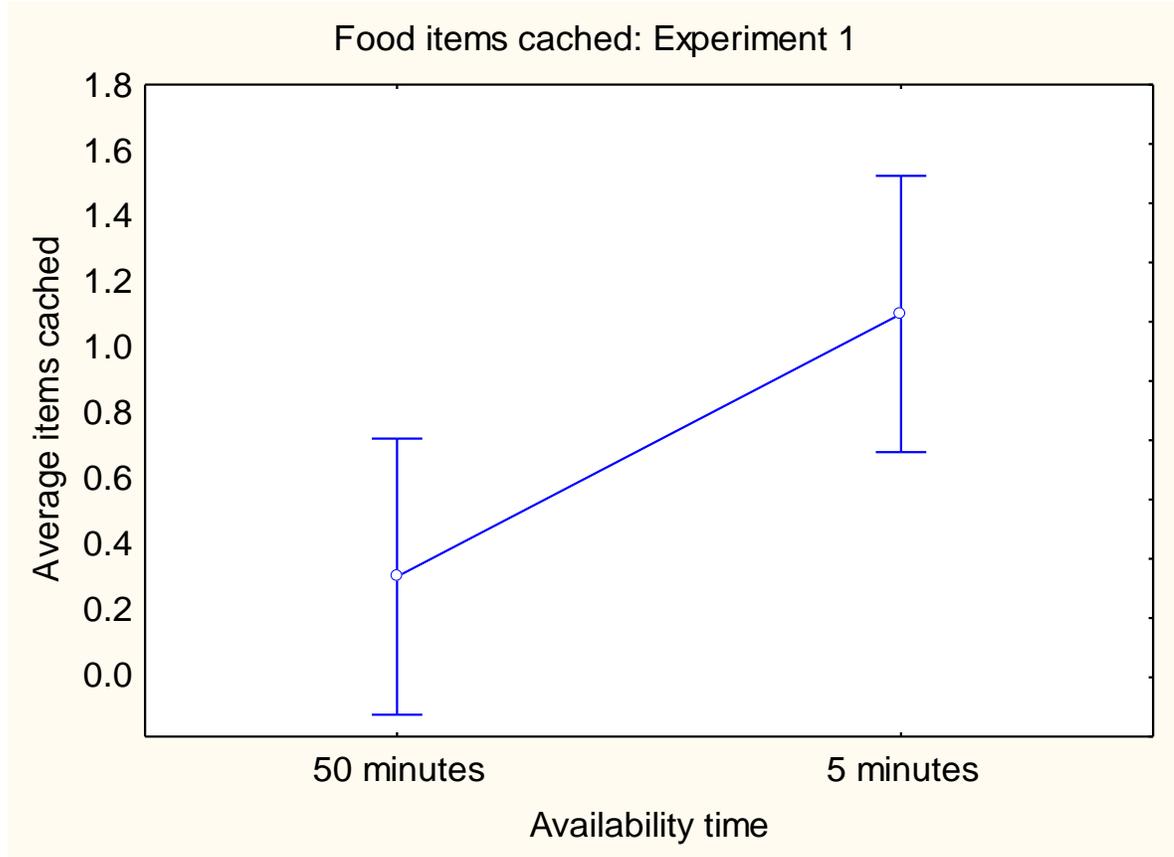


Figure 2 Main effect of availability time on average number of items cached for all birds $F(1,18) = 7.98$ $p = .011$. Bars indicate .95 confidence intervals.

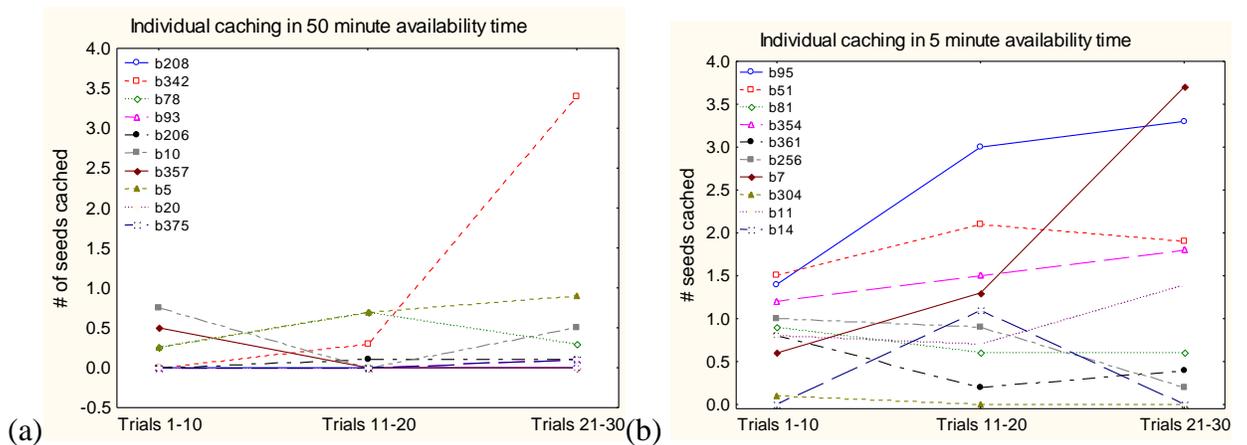


Figure 3 (a and b) shows the mean number of seeds cached by each individual for successive blocks of 10 trials. We assume that subjects must learn a new availability time parameter so that later trials give the clearest indication of their response to the availability time treatment. While figure 5 shows considerable individual variation, a comparison of panels a and b supports our basic prediction that jays cache more when time is short.

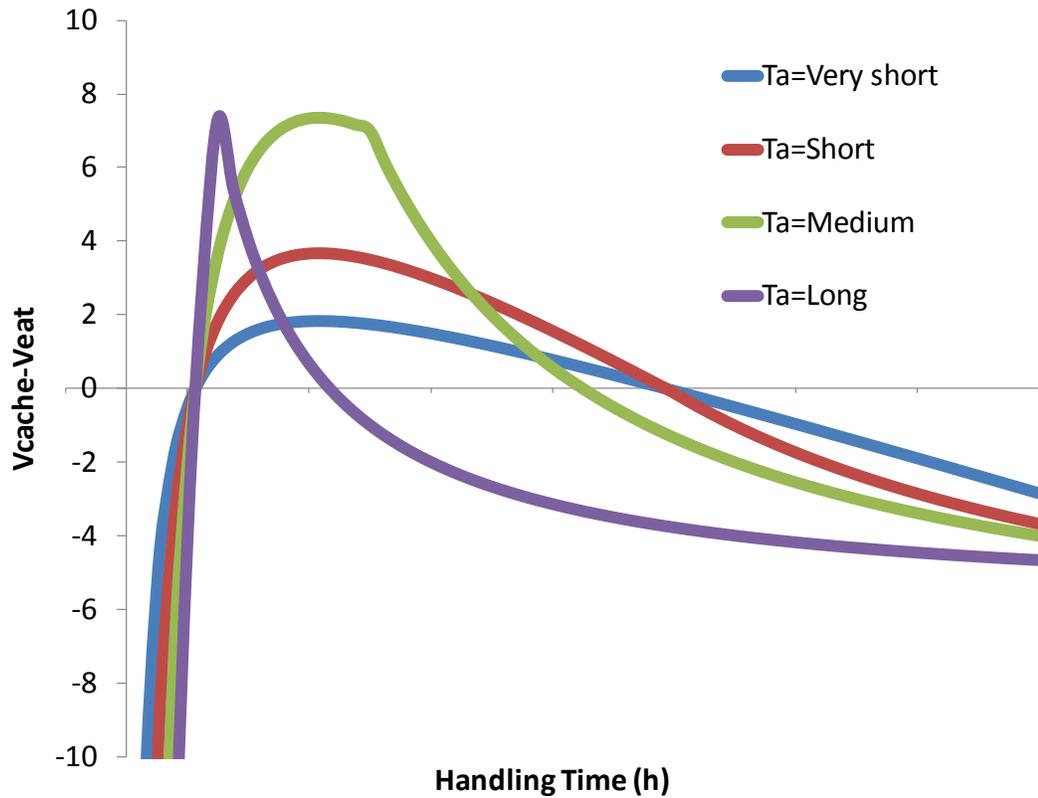


Figure 4 The four lines represent different lengths of availability time (T_a) on a handling time (h) horizontal axis. The y scale represents the difference between V_{cache} and V_{eat} . When the line is above the handling time axis, caching is better than eating. Notice that shorter availability times cover a wider range of handling times (h) when caching is better than eating.

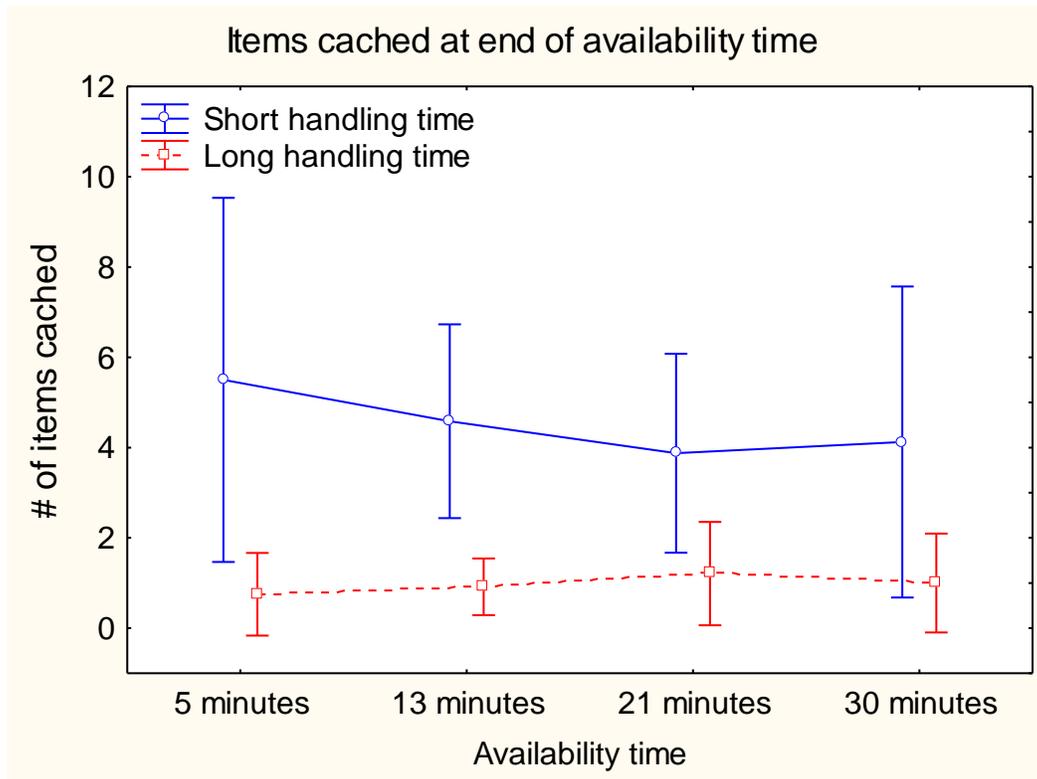


Figure 5 This figure summarizes the results of experiment 2. The interaction between availability time and handling time was not found significant ($F_{3,21}=0.94$, $p= .431$). Bars indicate .95 confidence intervals. This figure suggests that handling time has a strong effect on caching ($F_{1,7}=15.824$, $p=.005$), while in contrast with experiment 1 availability time seems to have relatively little effect ($F_{3,21}=.217$, $p=.883$).

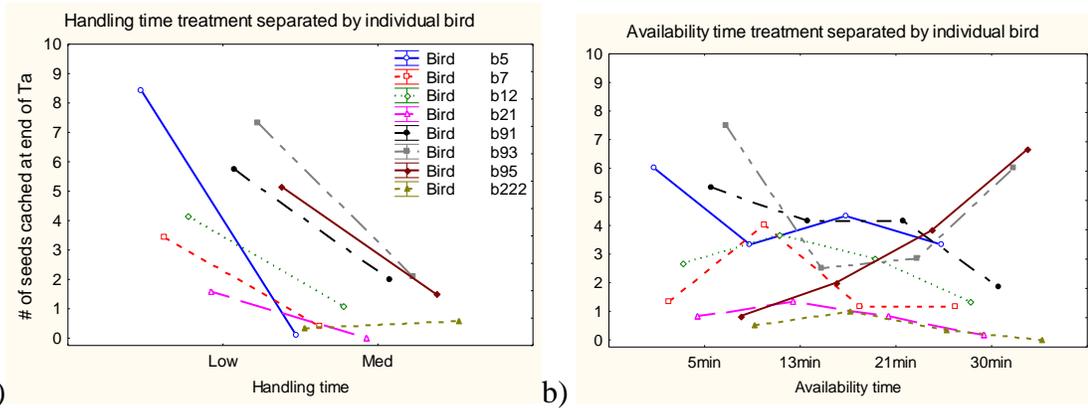


Figure 6 Each line represents a single bird's performance in each level of treatment for experiment 2. Both a and b share the legends and y axis titles. Notice the trend with respect to handling time (a) is to cache more items in the low handling time treatment (7 out of 8 birds). With respect to availability time (b), there is no consistent trend between birds.

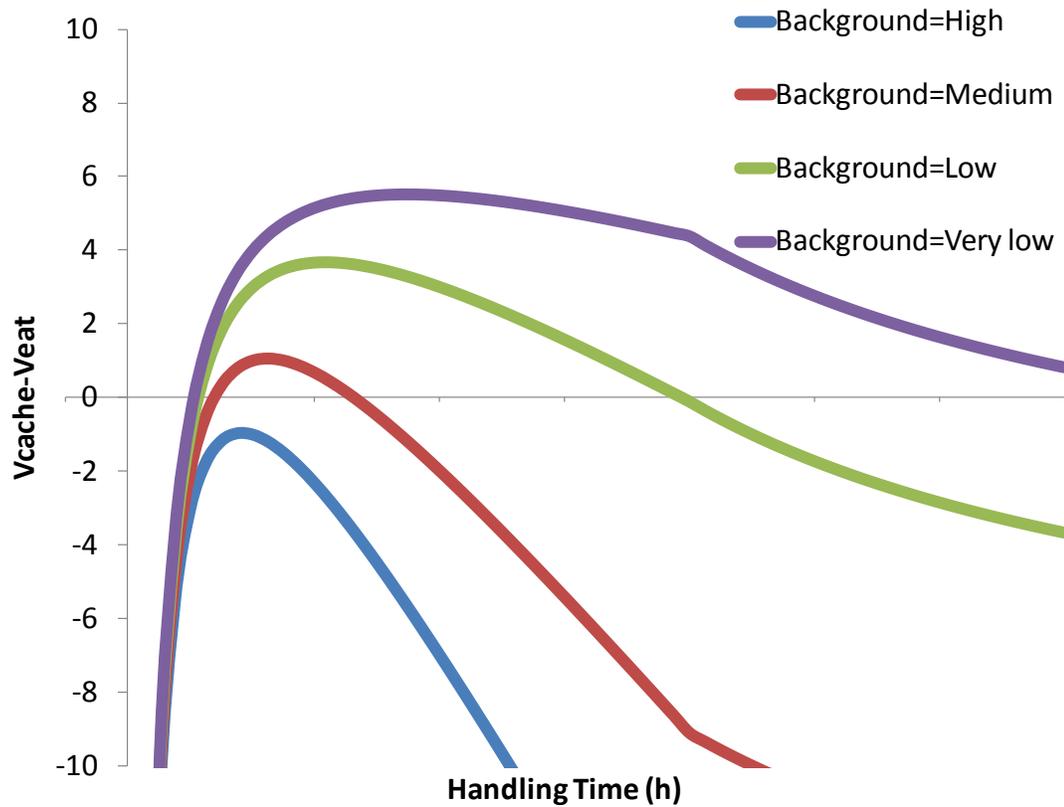


Figure 7 The four lines represent different background rates (γ) along the handling time (h) axis. The y axis represents the difference between V_{cache} and V_{eat} . When V_{cache} is greater than V_{eat} the line lies above the handling time axis indicating caching is better than eating. Notice that the highest background rate (γ) makes eating always better than caching.

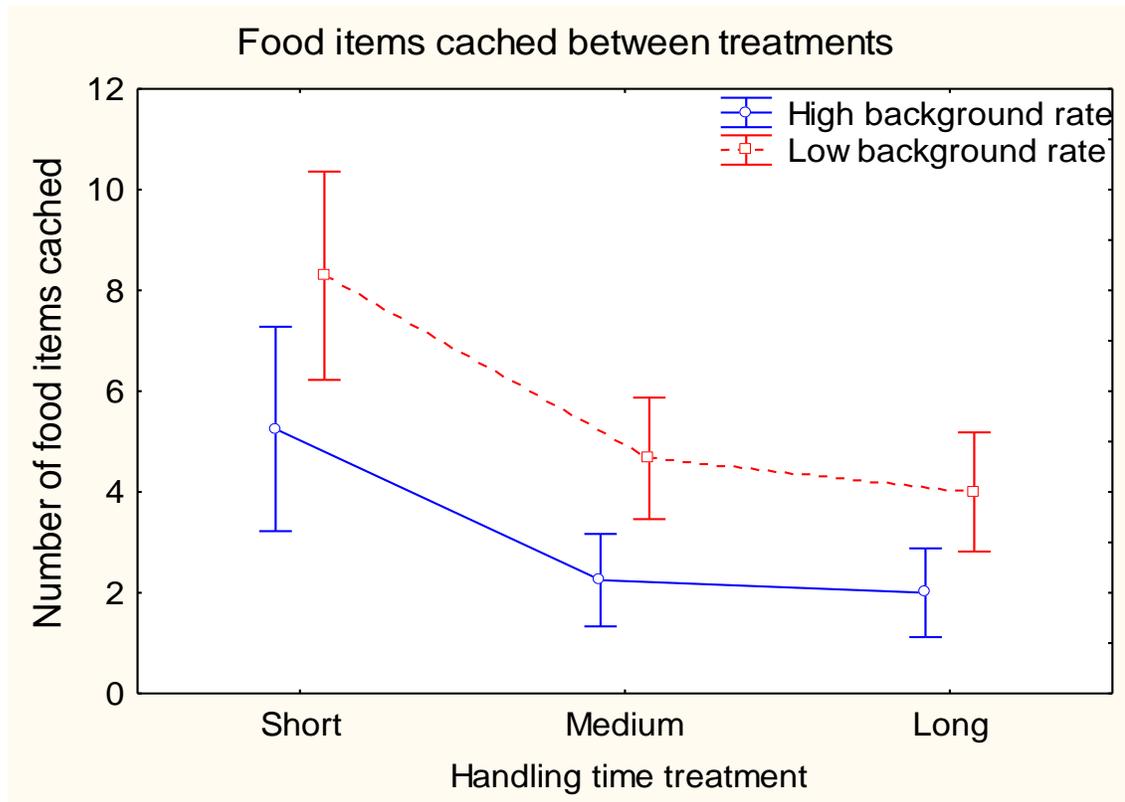
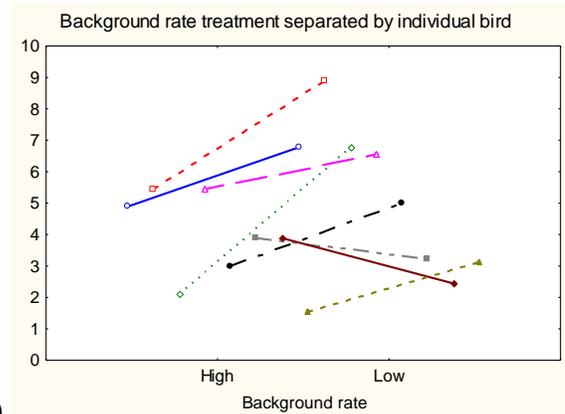
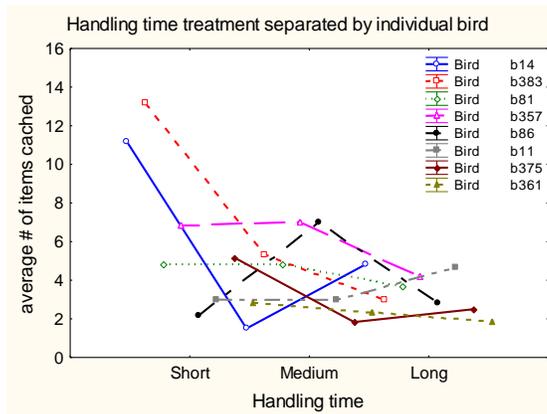


Figure 8 This figure shows the mean number of items cached for each of the six treatment conditions in experiment 3. The figure suggests that caching generally decreases with increasing handling time and background rate. A repeated measures ANOVA supports this interpretation, showing significant effects of handling time ($F_{2,46}=15.096$, $p<.0001$) and background rate ($F_{1,23}=24.684$, $p<.0001$), but no interaction between these two variables ($F_{2,46}=.327$, $p=.722$). Bars indicate .95 confidence intervals.



a) b)

Figure 9 Each line represents an individual bird's average performance broken down by level of treatment. Both a and b share legends and y axis titles. With respect to handling time (a), the trend shows short handling time foods being cached most (6 of 8 birds). Medium foods were cached more than long in the high background rate treatment (5 out of 8 birds). With respect to (b), the data show a strong trend for caching less in the high background rate treatment (6 out of 8 birds).

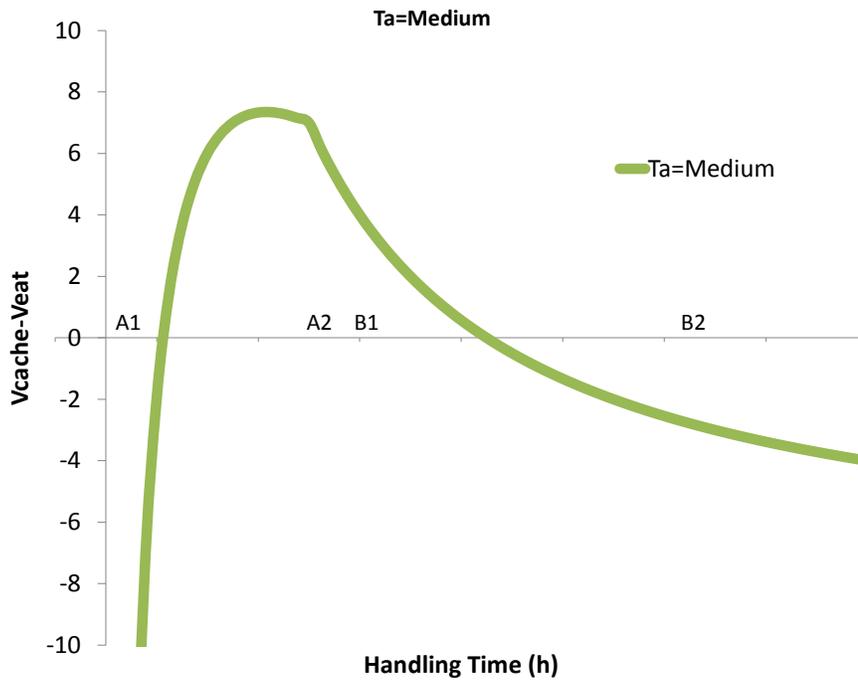


Figure 10 A and B refer to 2 hypothetical species tested with 2 different handling times. Our model predicts that in one situation, it is realistic to say that one species would eat short handling time foods and another would cache them (A1 and B1). Further, it may also be valid to suggest one species would cache long handling time foods and another would eat them (A2 and B2).