Recovery of Cached Food by Captive Blue Jays (*Cyanocitta cristata*)

by

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RECOVERY OFCached FOOD BY CAPTIVE BLUE JAYS (CYANOCITTA CRISTATA)

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Corvids are important seed and nut dispersers in North America. To date, the caching and recovery behaviors of four North American Corvids have been documented, most notably Clark’s Nutcracker (Nucifraga columbiana). Blue Jays (Cyanocitta cristata) are important dispersers of Quercus, Fagus, and Castanea nuts in eastern North America and their caching behavior in the wild has been well documented. Recovery of caches by the same individual Blue Jay that created the caches has not been demonstrated. In order to do this, I conducted a laboratory study in which I examined caching and recovery behaviors. I compared the performance of caching birds with non-caching birds and with a random foraging model. Blue Jays do return to their own caches with success rates higher than predicted by random searching and they also probe fewer sites than predicted by random. They also recover caches at success rates higher than non-caching birds searching for the same caches as well as probe fewer sites than the non-caching birds. There is a difference in probing patterns for recovered caches between caching birds and non-caching birds that suggests the use of spatial memory by caching birds and a difference in
foraging strategies between the two groups. Cache recovery order does not exhibit either a primacy or recency effect and cache recovery order does not appear to correlate to nearest neighbor distance models.
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Introduction: The Blue Jay

The Blue Jay is a year round resident throughout most of eastern North America. Its range extends westward to the Rocky mountains and northward to the middle latitudes of Canada (Bent 1946). The Blue Jay dwells in mixed and deciduous forests, open woodlands and developed areas such as parks and neighborhoods (Ehrlich et al. 1988). Bent (1946) provides much natural history for the Blue Jay, but his accounts are largely anecdotal. The Blue Jay consumes an abundance of nuts when available, particularly acorns (Quercus) and beech nuts (Fagus). Jays are prolific hoarders of nuts, and this behavior has been well documented. Blue Jays were observed caching Quercus palustris acorns in developed areas that would be comparable to disturbed environments in nature (Darley-Hill & Johnson 1981). Johnson & Adkisson (1985) documented the movement of at least 100,000 beech nuts (Fagus grandifolia) from a single woodlot in southeastern Wisconsin to cache sites in the birds' breeding territories up to 4 km away. Blue Jays have also been observed caching in woody habitats and forest edges (Johnson & Webb 1989). A careful examination of the Blue Jay diet reveals that the amount of mast (nuts) eaten peaks in November and again in February (Beal 1896). This pattern indicates that Jays are eating large amount of nuts when they are unavailable from source trees. Thus the jays are utilizing their caches to supplement food resources when food items, such as insects, are in low abundance.
Through the caching of *Castanea*, *Fagus* and *Quercus* nuts, it is believed that Blue Jays were an important dispersal agent for Chesnut, Beech and Oak trees during the most recent post glacial period and are still important today. Bennett (1985) examined the pollen evidence for the dispersal of *Fagus grandifolia* over the last 18,000 years. It was determined that *F. grandifolia* moved at the rate of 150 m per year and up to 6 km per generation, a rate much faster than nut dropping under the tree canopy would predict. Webb (1987) also studied *F. grandifolia* dispersal, and she determined that Beech trees in Wisconsin likely dispersed over an area in which they no longer grow. Both studies conclude that animal vectors are the most likely dispersers, especially the Blue Jay and the now extinct Passenger Pigeon (*Ectopistes migratorius*) (Bennett 1985; Webb 1987). *Castanea* and *Quercus* also exhibit faster dispersal than explained by nut drop alone (Davis 1981; Webb 1986 both cited in Johnson & Webb 1989). Johnson and Webb (1989) argued that the role of the Passenger Pigeon in the dispersal of *Castanea*, *Fagus* and *Quercus* nuts was highly limited. They assert that plant establishment via Passenger Pigeons would have been unlikely because a pigeon facilitated dispersal strategy relies too heavily on chance factors. For example, the pigeon would regurgitate the nut, the nut would remain viable, the dropped nut would escape predation, the nut would fall into a favorable site in a mostly unfavorable climate and this would happen a sufficient number of times to be effective. Instead, Johnson and Webb argue that the Blue Jay was and is the primary disperser of *Castanea*, *Fagus* and *Quercus* trees because jays
exhibit a number of behaviors during caching that are conducive to plant establishment (Johnson and Webb 1989). This is reinforced by the fact that Blue Jays are today considered the main dispersal agents of *Quercus* in postagricultural and successional habitats (Harrison & Werner 1984; Crow et al. 1994).

Though the Blue Jay’s caching behavior has been documented, the recovery of caches by the same individual that made the cache has not. Individual recovery of caches has been documented in six other species of Corvids: European Jays (Bossema 1979), Eurasian Nutcrackers (Balda 1980), Clark’s Nutcracker (Vander Wall 1982), Gray Jays (Bunch & Tomback 1986) Pinyon Jays and Scrub Jays (Balda & Kamil 1989). In order to further investigate the Blue Jay as the primary nut disperser in eastern North America, it is necessary to determine the role of spatial memory for cache sites plays in the recovery of hidden food stores by Blue Jays. This study should also help to evaluate the adequacy of the Blue Jay as a test subject for future spatial memory studies.

In this series of experiments we examine the caching and retrieval behavior of captive Blue Jays. We tested six null hypotheses. They were as follows:

$H_0^1$: Caching Blue Jays are not recovering caches at success rates greater than predicted by a random model.

$H_0^2$: Non-caching Blue Jays are not recovering their caches at success rates greater than predicted by a random model.

$H_0^3$: Caching Blue Jays are not recovering caches at success rates...
greater than success rates of non-caching Blue Jays.

\( H_1^* \): Caches made by caching Blue Jays are not placed within 15 cm of room edges or objects in the experimental environment at rates higher than predicted by a random model.

\( H_0^* \): Order of cache recovery by caching Blue Jays is not correlated to the order of cache creation.

\( H_0^6 \): Order of cache recovery by caching Blue Jays is not influenced by nearest-neighbor-cache distances.

No statistical analysis for \( H_0^6 \) was performed and the results are presented here in a descriptive format. Additionally, the probing distributions of caching birds and non-caching birds around recovered and discovered caches is compared and the results are also presented in a purely descriptive format.
A Review of Avian Food Caching

Food hoarding, or caching, is defined by Vander Wall (1990) as "the handling of food to conserve it for future use." Food caching behavior is manifest in a wide variety of animals including arthropods, mammals and birds. Avian groups in particular have been well studied. Food hoarding is known in at least fifteen avian families, most notably families Corvidae, Paridae and Picidae (Vander Wall 1990). Vander Wall (1990) identifies at least ninety-five species of birds in which food hoarding has been observed and suggests the existence of many more.

The discussion presented herein will be primarily limited to the discussion of Corvids and Parids. Haftorn (1944; 1953; 1954; 1956 a-c all cited in Haftorn 1974; 1974) described the food storing habits of many species of Scandinavian and North American tits (Parus spp.). Tombrek (1977) described the caching of conifer seeds by Clark’s Nutcrackers (Nucifraga columbiana). Caching of acorns by Florida Scrub Jays (Aphelocoma coerulescens) is described by Woolfenden and Fitzpatrick (1984) and DeGagne et al. (1989). Grinnell (1936) described Western Scrub Jays caching acorns in the Kaweah River Valley in California. The caching of Quercus palustris acorns by Blue Jays (Cyanocitta cristata) in Blacksburg, Virginia was documented by Darley-Hill and Johnson (1981). Johnson and Adkisson (1985) recorded Blue Jays caching Fagus grandifolia nuts in Southeastern Wisconsin. Brown (1963) gave a detailed description of the act of caching by Gray-breasted Jays (Aphelocoma ultramarina), Scrub Jays, Steller’s Jay (Cyanocitta stelleri) and Blue Jays.
Cached Food as a Means of Extending Resource Availability

Temporal fluctuations in the availability of important food items, such as nuts and seeds, motivate food storing behavior (Vander Wall 1990). This is deemed especially true for species in temperate climates because birds in these environments are more likely to experience fluctuations in resource availability (Roberts 1979). Food items may be limited on a daily basis; for instance, prey are active only at certain times of the day or tides affect access to foraging grounds. Other items may be seasonally limited; for example, fruits, seeds and nuts which may be available only in the summer or late fall. It is therefore advantageous to cache temporally limited food items when abundant. Most food storing behavior takes place when resources are at peak availability (e.g., Tomback 1977; Johnson & Adkisson 1985). Caching temporally limited resources allows a bird to maximize its foraging efficiency. Gibb (1960) observed a Willow Tit (Parus montanus) caching upwards of 15 peanut halves provided at a feeding tray while non-storing species of tits at the same feeding tray were only able to obtain about two nuts per bird with an "eat as you go" strategy.

Food hoarding not only enhances immediate foraging efficiency, but can ensure an individual a reliable food supply during periods of food scarcity and can supplement readily available resources when provisioning fledglings and nestlings. Birds which hoard food for long or even short durations gain selective advantage over non-hoarding birds when competing for the same resources (Andersson & Krebs
The importance of hoarding is evident when the seasonal variation in the diets of several species is considered. For example, the amount of mast, i.e. acorns and beech nuts, in the Blue Jay’s diet peaks in November and December and again in February (Beal 1896). The peak times identified by Beal are times when mast items are unavailable directly from their natural sources and other food items such as invertebrates are at minimum abundance in the environment and in the Blue Jay diet (Beal 1896). In Florida, Scrub Jays consume acorns during all months of the year, but this vegetable matter decreases in dietary importance as invertebrate abundance increases in the late spring (DeGagne et al. 1989). Coal Tits (Parus ater) eat stored caterpillars at times well outside of their seasonal availability (Gibb 1960). Conifer seeds are the primary dietary item for Clark’s Nutcrackers from winter to mid-summer (Tormbach 1977), a period when the seeds are generally unavailable from the trees themselves. When other food sources are not abundant, hoarding species such as these can utilize cached items that non-hoarders cannot. Food storing enables both Coal Tits and Clark’s Nutcracker to survive seasonal weather conditions and food shortages that are intolerable to non-hoarding species.

Cache Predation

Cache predation compromises storing as a means to extend the availability of resources. Food storers must contend with predation from conspecifics and other vertebrate predators such as mice. Vander
Wall (1990) identified four ways in which caching animals can reduce losses: site selection, cache preparation, spacing of caches and aggressive cache defense. The first three of these strategies are applicable to the behavior of Corvids and Parids.

Selection of sites where cache predator densities are low is commonly utilized. Clark's Nutcracker frequently caches seeds on rocky slopes and wind-swept ridges where rodent densities are low (Vander Wall & Balda 1981). Nutcrackers also cache seeds in locations that become inaccessible to predators after seasonal snow falls. These food stores are also unavailable to the nutcrackers until spring thaw, but the caches are nonetheless protected (Vander Wall and Smith 1987). Blue Jays cache acorns in early successional habitats where predation from squirrels and other mammalian predators is likely to be low (Darley-Hill & Johnson 1981; Vander Wall & Smith 1987).

A cache which is concealed in a soil substrate has a higher probability of surviving than one that is not. For example, Bossema (1979) found in an experimental field test that 8.5 times more exposed acorns disappeared than those which were buried. By burying food items, caching birds can be relatively assured that the only cues available to others are olfactory (Vander Wall 1990). Burying caches substantially lowers the possibility that other birds, particularly conspecifics, will be able to locate the food items.

The scattering of cache sites over a broad area can also limit the ability of competitors to locate caches on a regular basis. Diurnal food hoarders like Corvids and Parids also have a difficult time directly
defending caches from nocturnal cache predators, so these birds must rely on cache spacing instead (Vander Wall & Smith 1987). Sherry et al. (1982) studied the cache spacing of Marsh Tits. The researchers made artificial caches at nearest neighbor distances (NND) equal to distances determined by Cowie et al. (1981) for wild Marsh Tits and Sherry et al. also made caches at smaller NNDs and greater NNDs. The results showed that the caches made at the smaller NNDs disappeared faster than those stored at the same NNDs as the Marsh Tits', and those seeds stored at greater NNDs did not survive any longer than the seeds stored by the tits. This suggests that the Marsh Tits are making their caches at the minimum separation distance required for maximum protection from seed predators. Bossema (1979) also examined cache spacing and found that captive "cache stealing" jays had a more difficult time finding experimentally scattered nuts than they did experimentally clumped nuts. Stapanian & Smith (1978) developed a model of optimal cache spacing for Fox Squirrels (Sciurus niger) but it is equally applicable to seed caching birds. The model states that intercache distances will increase to the point that discourages further searching for caches by predators that are successful at least once. An additional strategy that can be used in conjunction with spacing is making low density caches, i.e. placing a minimal number of items at each location. A cache predator may detect a cache but not recover the food item if the reward is too small.
Cached Food and Its Importance to Reproduction

Stored food is also crucial to the reproductive strategies of some birds. Individual Clark’s Nutcrackers store between 22,000 and 33,000 piñon pine seeds in the late summer and early fall (Vander Wall & Balda 1977). It is estimated that these stores represent up to three times the energetic requirements of an individual during the seasonal period of food scarcity. Excess stores enable nutcrackers to begin nesting in late winter or early spring (Tombback 1977) because the nutcrackers can provision young with the stored seeds (Mewaldt 1956). Pinyon Jays (Gymnorhinus cyanocephalus) are able to lay eggs as early as the beginning of March due predominantly to the harvesting and caching of pine seeds in the fall (Balda & Bateman 1972). Fledglings of these two species also benefit from seed stores. Clark’s Nutcracker fledglings are fed cached pine seeds that are high in protein and lipid concentrations (Botkin & Shires 1948 cited in Vander Wall 1990) until the midsummer months (Vander Wall & Hutchins 1983). Bossema (1979) reported that during the month of June, a time when fresh acorns are not available, approximately 88% of the vegetable matter diet of European Jay (Garrulus glandarius) fledglings consists of acorns.

Hypothesized Cache Recovery Mechanisms

In order for cached food to be beneficial to a bird in the ways described above, an individual must be able to recover the hidden items with a relative amount of success. Gibb (196c) and Haftorn (1974) suggested that birds hide food in sufficient quantities so that
some of the caches may be found by chance during subsequent foraging. This is known as the random search hypothesis. Under the random search hypothesis it is expected that all birds will have an equal chance of recovering cached food items. Andersson and Krebs (1978) argued that if the probability of finding a hidden store for all individuals competing for a resource is the same, then storing birds will have a lower fitness than conspecific "cheaters" that are not storing but are recovering caches. Contrary to the random search hypothesis, Bossema (1979) determined that captive non-caching European Jays cannot find the stores that others have made. Working with captive Clark's Nutcrackers, Vander Wall (1982) determined that cache recovery success rates for hoarding birds are too great to be explained by chance alone. This suggests that conspecifics do not have an equal chance of finding caches made by one another and that a process other than random searching must be at work.

Other suggested recovery methods include: random search of likely sites, olfaction, and use of microtopographical cues. Experimental evidence does not support the hypothesis that birds merely search sites where they are likely to have made caches. Sherry et al. (1981), working with captive Marsh Tits, determined that too many locations qualify as likely sites, so a random search of likely sites would be essentially equivalent to a random search of all sites. Cowie et al. (1981) conducted field experiments with Marsh Tits in which artificial supplementary caches were placed in areas where tits are likely to cache. The results showed that the tits recover their own
stores first, thereby suggesting that Marsh Tits find their cache locations by means other than randomly foraging in likely sites. Vander Wall (1982) determined with Clark's Nutcrackers that "'specific types of sites' do not appear to occur to a sufficient degree to make this recovery technique [random search of likely sites] practicable."

Studies involving Black-capped Chickadees (Sherry 1984a) also indicated that site preferences are not useful to explain cache recovery.

Olfaction has not proven to play a significant part in avian food recovery (Bossema 1979; Vander Wall 1982). Some mammals are able to recover hidden food items using olfactory cues (e.g. Howard & Cole 1967), but birds are unable to recover experimentally hidden food when the only available cues are olfactory ones (Vander Wall 1990). Bossema (1979) found that European Jays cannot find the caches of conspecifics at rates any better than chance. This suggests that European Jays are unable to smell the cached items or are at least not using olfactory information for recovery. Vander Wall (1982) found the same to be true for Clark's Nutcrackers. Bossema (1979) also found that European Jays are unable to locate experimentally hidden pieces of aromatic cheese. Gray Jays (Perisoreus canadensis) are successful at finding pungent artificial caches at rates no better than a random search paradigm would predict (Bunch & Tomback 1986). James and Verbeek (1983) did not find any statistically significant difference between the detection of experimentally cached odorless "false" clams and the detection of odiferous fresh clams by Northwestern Crows (Corvus
caurinus). These findings demonstrate that many Corvid species do not use olfactory cues to find cached food.

Microtopography has also been proposed as a possible recovery cue. It is speculated that soil disturbances made by a caching bird can leave cues that are used in recovery by both hoarders and non-hoarders alike. With increasing cache age, however, these cues become harder to see due to erosion and other substrate disturbances (Vander Wall 1982). Vander Wall (1982) conducted an aviary study with Clark's Nutcrackers and concluded that microtopography is not an essential component of recovery. Additionally, both Clark's Nutcrackers and Eurasian Nutcrackers (Nucifraga caryocatactes) have been observed recovering caches from beneath snow cover up to 130 cm deep (Reimers 1966; Holtmeier 1966 both cited in Tombback 1980; Tombback 1980). This is a prime example of a situation where any microtopography present or created during storing is likely no longer in existence. The employment of microtopography in cache recovery events has been virtually dismissed.

The conclusion of researchers based on all of the available evidence is that individual food caching birds remember the locations of their own caches. This strategy has obvious adaptive advantage because hoarding individuals are more likely to find hidden items than non-hoarding conspecifics (Andersson & Krebs 1978). Several studies have confirmed that individuals of many species of seed caching birds do remember the locations of their caches.
Bossema (1979) conducted several experiments with captive European Jays and concluded that individual jays remember their cache locations. This is evident in the behavior of a jay when it fails to find a cache in the perceived correct location; the jay will at first try other locations only to return to the first site and dig insistently in an attempt to find the cache (Bossema 1979). Similar behaviors have been observed for both Eurasian Jays (Balda 1980) and Marsh Tits (Shettleworth & Krebs 1982) in the same situation. Woolfenden and Fitzpatrick (1984) describe Florida Scrub Jays scattering sand "as if searching for cached acorns" with little apparent success. Whether or not these jays are persistently searching for an actual cache, however, has not been demonstrated.

Sherry et al. (1981) uniquely demonstrated the use of memory in the recovery of stored sunflower seeds by Marsh Tits. The researchers covered one of the bird’s eyes during caching trials and recovery trials for the control group but switched the cover to the other eye for the experimental group during recovery trials. The experimental group was unable to locate storage sites during recovery whereas the control group, in which there was no eye patch switch, had no difficulties. These results reflect a lack of interocular transfer of storage site information in the experimental group and indicate that visual information about the cache location is stored in memory (Sherry et al. 1981).

Vander Wall (1982) conducted a series of experiments on the spatial memory of captive Clark’s Nutcrackers. He determined that
seed caching individuals have success rates ranging from 52% to 78% when relocating their own caches, whereas non-caching individuals have success rates from 8% to 12% when searching for all of the caches made by the caching nutcrackers. The incongruity in performance levels is a clear indication that individuals are remembering the locations of their own caches (Vander Wall 1982).

Sherry (1984a) found that Black-capped Chickadees are capable of remembering the locations of their food stores. The chickadees relocated holes during retrieval trials in which they had stored food 24 hours earlier. This was accomplished without any cue from the food itself. Sherry accounted for any possible biases on the part of the chickadees for specific storage sites by conducting control experiments prior to caching trials in which it was observed that no one site was visited more frequently than any other site (Sherry 1984a).

Simple serial order recovery explanations provide potential basic mechanisms for recovery processes. It is possible that birds recover caches in sequential patterns, for example, they may recover seeds in the same order in which they were cached, a primacy effect, or they may recover them in reverse order, a recency effect (Vander Wall 1990).

If food storing birds rely on a progression of cognitive tasks to allow them to remember cache locations, then it is expected that a primacy effect would be observed (Vander Wall 1990). Cowie et al. (1981), studying wild Marsh Tits, found evidence that seeds were recovered in the same order in which they were stored. An examination of the research, however, discloses that only mean
sequence numbers are utilized; i.e. the exact sequence of recovery is not known, only data from two successive monitoring visits is compared and there is no differentiation between individual birds in the data (Cowie et al. 1981). Thus, this study does not provide strong evidence of a primacy effect.

A recency effect may play a part in recovery if birds suffer a decay in long term memory over time or if stored food may be more likely to be stolen by cache predators the longer it is stored (Vander Wall 1990). In either case, a bird that retrieves caches in reverse order is hypothesized to recover a maximal number of stored items because later made caches are remembered better and have a greater chance of having not been predated upon (Shettleworth & Krebs 1982; Sherry 1984a & b). Shettleworth and Krebs (1982) found evidence of a possible recency effect with captive Marsh Tits, but, as with Cowie et al. (1981), only two discrete groups of caches without individual sequences were examined.

Sherry (1984a) found no evidence of either a primacy or a recency effect when studying Black-capped Chickadees. His experiments examine actual cache sequences and predominantly show random order recovery. Only one out of twenty-four sequences examined reveal an order effect (Sherry 1984a). Similar results were found by Baker et al. (1988). Bossema (1979) found that European Jays do not appear to discriminate between caches of differing ages during recovery periods. No evidence of serial position effects, either primacy or recency, has
been found for either Clark's Nutcrackers (Kamil & Balda 1985; 1990) or Eurasian Nutcrackers (Balda 1980).

Macphail (1983) suggested that the lack of serial position effects in avian memory may be due to constraints of the avian memory system. For example, Staddon (1984) stated that time discrimination between particular events is inversely related to the event's age. In other words, it will be more difficult for an animal to differentiate closely occurring events that happened a long time ago as opposed to events that occurred only minutes before. Given the propensity of certain bird species to cache several items in rapid succession only to return days or months later, it seems unlikely that birds would recover caches in an order specifically correlated to the order of cache creation. This at least appears to be the case with both Corvids and Parids (Bossema 1979; Balda 1980; Sherry 1984a; Kamil and Balda 1985, 1990).

As an alternative to serial order effects, it has been suggested that birds first recover food from sites that are simply better remembered. Kamil and Balda (1985) found that captive Clark's Nutcrackers suffer a decline in retrieval performance over several recovery sessions. This decline is attributed to the high number of revisits to exploited cache sites and to chance as more caches are recovered since as more caches are located, there are fewer unexploited sites to be located. In a later study, Kamil and Balda (1990) studied the effects of forcing nutcrackers to recover their caches in random order. Birds in the free-recovery control group experience a decline in accuracy over four recovery sessions much like the birds in
Kamil and Balda’s (1985) previous study. Birds in the forced-order-recovery experimental group were only allowed to recover from one quarter of the floor surface per session. Despite having lower average accuracy than the control group, the nutcrackers experienced no performance declines over all of the sessions. Kamil and Balda (1985, 1990) concluded that nutcrackers recover seeds from better remembered sites first. The performance declines experienced by the nutcrackers in Kamil and Balda’s studies could, however, be attributed to the constraints of the experimental environment. The two studies only indicate the possible existence of better remembered sites, but do not shed any light on what makes a cache site better remembered.

A more complex recovery mechanism was proposed by Cheng (1989). Cheng’s vector sum model stated that a bird determines a vector from a landmark to a goal and then adds to that vector the vector from itself to the landmark when seeking to return to the goal (Cheng 1989). This model predicted that when a landmark was shifted in a particular direction that the bird would shift its search location in the same direction but never in the orthogonal direction (Cheng 1989). This model has been tested with pigeons (*Columba livia*) (Cheng 1989) and Black-capped Chickadees (Cheng & Sherry 1992). When landmarks were shifted either parallel or perpendicular in reference to a stationary edge, the basic tenets of the model held (Cheng 1989). When the landmarks were shifted diagonally, however, the birds did not respond as expected (Cheng & Sherry 1992). The results were similar for both pigeons and chickadees, suggesting that both species
process spatial information in much the same way. Cheng has since refined his model into the new "direction-averaging" model whereby it is predicted that a bird will search at a constant radial distance from a landmark in a direction that is an average of the directions that two conflicting cues present (Cheng 1994). Cheng's research on this model with pigeons has led him to replace the vector-sum model with the direction-averaging model (Cheng 1994). Further studies will be necessary to determine if this model is applicable outside of pigeons.

The Influence of Objects on Cache Recovery

The influence of objects in the environment on caching and recovery behavior is undoubtedly important. Bossema (1979) observed shifts in search patterns by European Jays during cache recovery that correlated with shifts in cue locations. He also examined the extent to which different types of objects influenced caching and recovery behavior. He found that caches were more often made near cues that were arranged horizontally rather than vertically. Conversely, during recovery trials most activity occurred about cues that were vertical not horizontal. Bossema suggests that both types are important, but the vertical cues are more important during recovery because European Jays must sometimes recover caches that are covered by snow (Bossema 1979).

Vander Wall (1982) conducted an experiment to test the influence of stationary objects on recovery behavior. Clark's Nutcrackers were allowed to cache nuts in an oblong room with objects
at either end. Before recovery, one end of the room was extended 20 cm in one direction and the objects in that end were moved accordingly, while the caches were not. During retrieval trials, the nutcrackers accurately located caches in the unshifted portion of the room and shifted their search pattern by 20 cm to locations that were correct relative to the altered portion of the room. Midway between both ends of the room, search patterns were shifted by about 10 cm. Vander Wall considered this to be evidence that locations of the nearest objects to a cache were important cues for recovery (Vander Wall 1982). Cheng (1989) also found that when objects near a goal are moved, pigeons alter their search pattern to a greater degree than when objects distant to the goal are moved.

**Differential Roles of Spatial Cues**

Spetch and Edwards (1987) began to define the differential roles of cues in avian memory systems. They identified both "local" and "global" cues. Local cues were defined as components of the environment immediately surrounding a goal, for example, the position of a specific location relative to other similar locations. Global cues were defined as components of the wide environment, for example, the position of a location as it relates to the entire experimental room. Spetch and Edwards' studies with pigeons suggested that both types of information are used and certain errors in search patterns are predictable when presented with conflicting cues. Spetch and Edwards suggest the presence of a hierarchical organization of spatial
information, whereby if the primary means of locating a site is obscured in some way, then the secondary information might be used (Spetch & Edwards 1987). This proposed hierarchical spatial system is similar to that in which migrating birds use several types of redundant navigational information (e.g. Emlen 1967a&b).

Herz et al. (1994) further tested the role of different cues using Black-capped Chickadees. The cues Spetch and Edwards termed "local" and "global", were renamed "proximal" and "distal" respectively. During experiments, the researchers allowed chickadees to cache seeds in the presence of both proximal and distal cues. The distal cues were then removed decreased in search accuracy during recovery trials was observed. A separate series of experiments was also conducted in which only distal cues were provided during caching. The distal cues were then rotated before recovery trials. In this second series of experiments the researchers found that chickadees searched in locations that were correct relative to the new cue locations. Herz et al. (1994) concluded that chickadees used distal cues in the environment to locate caches. In both experiments, caches were removed prior to recovery phases. Reduced recovery accuracy would be expected when it is not possible to recover anything.

In any case, the evidence from Spetch and Edwards (1987) and Herz et al. (1994) indicates that there is redundant usage of cues. It is not clear, however, to what extent birds differentiate between types of cues. If birds can indeed discriminate between cues from the wide environment and cues from the local environment, a room only 2 m²
(Herz et al. 1994), or even $2.4 \text{ m}^2$ (Spetch & Edwards 1987) for that matter, is unlikely to adequately measure differences in perception.

**Observational Learning**

As previously discussed in the context of non-spatial cues (odor, microtopography, etc.), cheaters in a food caching species are not likely to exist. It is possible, however, that an individual bird could observe another bird cache and subsequently pillage that conspecific’s cache. Vander Wall (1982) found some evidence of this in captive Clark’s Nutcrackers, but the data presented are sparse and the discussion of their implications are limited. Bunch and Tomback (1986) found that although captive non-caching Gray Jays that had seen other Gray Jays make caches could recover those caches. The observing jay’s success rates, however, were lower than if the jay had not seen the seen the cache created at all. Baker et al. (1988) also found that Black-capped Chickadees that had seen other chickadees make caches, could not locate caches any better than caches whose creation was not witnessed. This evidence is in agreement with Andersson and Krebs (1978) who argue that an observational cheating strategy would lead to a lower fitness for the hoarders and is therefore not likely to exist.

**Species Ecology and Spatial Memory**

All species of birds which hoard food are not equal in their abilities to retrieve it. Closely related species of birds can greatly differ in their spatial memory abilities. Balda and Kamil (1989) studied the
differences in caching behavior of Clark's Nutcrackers, Pinyon Jays and Scrub Jays. Balda and Kamil (1989) found that all three species located caches at levels greater than chance and that nutcrackers and Pinyon Jays performed significantly better than Scrub Jays. The differences were attributed to the ecological requirements of the three species. Balda and Kamil (1989) hypothesized that Clark's Nutcrackers had the highest success rates because of high dependency on cached seeds in the wild and Scrub Jays did the worst because of a lack of dependency on cached seeds for over-wintering. Pinyon Jays, which did well recovering caches in the experiments, are highly social Corvids. Pinyon Jays consistently cache and recover in large flocks and are consequently believed to "clump" cache sites together in the wild. Balda and Kamil (1989) attributed the observed high recovery rates of the Pinyon Jays to clumping behavior, surmising that it was necessary for an individual Pinyon Jay to remember spatial information about only a small location rather than the whole room. Balda and Kamil (1989) admit that their results are not hard evidence of species differences, and they suggest that the comparison of birds under a variety of more controllable experimental conditions be made.

Olson (1991) followed Balda and Kamil's suggestion when she tested for differences in spatial memory of Clark's Nutcrackers, Scrub Jays and pigeons. Pigeons were included so that data generated in these experiments could be checked against the existing literature on pigeons in order to detect any procedural inconsistencies. Olson used an operant to non-matching procedure in which subjects were required
to respond to a series of lighted keys in a specific sequence in order to receive a reward. She found significant differences in performance between Clark's Nutcrackers and Scrub Jays in two different types of tests. This, coupled with Balda and Kamil's (1989) results, suggests that there are indeed real differences between these two species in their capacity for spatial memory tasks. Both Olson (1991) and Kamil and Balda (1989) have suggested that performance differences are a result of the differences in each species' ecological niche, such as a seasonally harsh environment like the Rocky Mountains versus the mild climate of south Florida, and consequential reliance on stored food.

An indicator of a bird's dependency on stored food is its ability to remember cache locations for long periods of time. There would be no adaptive significance in remembering cache locations for extended periods of time if it were not necessary to do so. Balda and Kamil (1992) tested Clark's Nutcrackers at several retention intervals and found that the birds can remember cache locations for at least 285 days. This lengthy retention interval is consistent with observations of nutcrackers feeding on pine seeds in seasons when the seeds are unavailable from the primary source (e.g., Tombback 1977). Hitchcock and Sherry (1990) tested Black-capped Chickadees under similar conditions and found that after twenty-eight days the birds were unable to reliably recover caches. It has been estimated that the caches of the closely related Marsh Tit last approximately three days in the field before being lost to predators or recovered (Cowie et al. 1981;
Sherry et al. 1982). Further tests would be required to determine if birds only have the ability to remember cache locations as long as needed. It is possible that excess caches not recovered within a specific period of time are simply forgotten.

Food Caching as a Means of Plant Dispersal

It is this last possibility that has drawn a lot of attention. If excess caches are forgotten on a regular basis, then it is plausible to view food hoarding birds as efficient dispersers of plant propagules. Food caching birds exhibit many behaviors that are beneficial to the dispersal of plants. Dispersal of propagules has been largely uninvestigated with respect to Parids and their caching behavior. An interesting difference between the behaviors of Parids and Corvids is their use of three dimensional space. Though no members of either family exclusively cache above ground level or at ground level, Corvids generally utilize ground level cache sites more than Parids and for this reason, most research on plant dispersal by avian agents has concentrated on Corvids. It has been found that Corvids select the best quality seeds and nuts for hoarding. Ligon and Martin (1974) found that Pinyon Jays use visual, tactile and auditory cues to determine the quality of Pinyon pine seeds. Bossema (1979) examined several aspects of European Jay acorn selection and found that the jays collected more physically undamaged than damaged acorns, more sound than parasitized acorns and more acorns with normal shells than those with loose shells. These three tests demonstrated that the
Jays were using both visual and tactile cues to determine acorn quality. Johnson and Adkisson (1985) found that Blue Jays transported 100 percent sound *Fagus* nuts. This is in contrast to the only eleven percent of sound nuts that Johnson and Adkisson found on the source trees. Consequently, this evidence suggests that these Corvids select only the most viable nuts and seeds for caching. The Cached nuts and seeds are most likely selected on the basis of their quality as a food item; however, the factors which make them quality food items also make them exceedingly viable propagules.

Propagation of the tree requires that the hoarder transport the selected nuts to sites which are favorable for growth. The cache sites selected by European Jays coincide with small clearings, open areas and dense conifer plantation edges conducive to oak seedling growth (Bossema 1979). Blue Jays cache acorns and nuts in many successional and edge habitats that are the locations of oak (*Quercus*) and beech (*Fagus*) regeneration (Darley-Hill & Johnson 1981; Harrison & Werner 1984; Johnson & Webb 1989; Crow et al. 1994)

A favorable habitat is hardly enough for cache survival. It is also important for the cached item to be buried. As previously discussed regarding cache predation, being concealed in the ground is highly beneficial to cache survival (Bossema 1979). Burial of the seeds and nuts provides them optimal microclimates for germination. There are several accounts of Corvids and jays burying their caches (e.g. Vander Wall & Balda 1977; Tombback 1977; Bossema 1979; Darley-Hill &
Johnson 1981). Furthermore, the spacing apart of caches reduces competition between seedlings.

Summary

Food storing and recovery is a wide spread behavior in the Class Aves. Temporal changes in the supply of important or preferred food items necessitates food caching for many non-migratory species. Caching can enhance foraging efficiency such as in the Willow Tit (Gibb 1960), and it can ensure a supply of food when other food may be scarce such as in Clark’s Nutcracker (Tombback 1977). Hoarded supplies also allow some birds to nest earlier than others, e.g. Clark’s Nutcracker nesting in late winter (Tombback 1977) and they can be important food items for nestlings and fledglings (Mewaldt 1956; Bossema 1979). Examination of the seasonal diets of birds like the Scrub Jay (Woolfenden and Fitzpatrick 1984) has provided insights into these areas.

Caching birds also exhibit a number of behaviors to prevent other animals from obtaining their caches. They frequently select sites where seed predator densities are low (e.g Vander Wall & Balda 1981) or where the caches may become inaccessible to others as the seasons progress (e.g. Vander Wall & Smith 1987). They also bury caches to reduce the amount of readily visible cues to potential seed predators (Bossema 1979), and they space caches out in order to discourage random searching as a main foraging strategy for non-cachers (Bossema 1979; Sherry et al. 1982). It has also been shown that
merely observing a conspecific cache does not provide enough information to ascertain cache locations (Bunch & Tombback 1986; Baker et al. 1988). The use of olfactory cues, microtopography and the random search of likely sites for cache recovery has been all but dismissed for several species of birds, notably European Jays (Bossema 1979), Marsh Tits (Cowie et al. 1981), Clark's Nutcracker (Vander Wall 1982) and Black-capped Chickadees (Sherry 1984a). Food caching is an advantageous strategy because individuals can remember the location of their own caches.

It has been suggested that cache locations are remembered in an order correlated to their creation to facilitate recovery, but these expectations maybe groundless (Macphail 1983; Staddon 1984). Evidence has also been presented that suggests recovery may begin with better remembered sites first (Kamil & Balda 1985, 1990), but further study is needed. The role of objects in the environment and their influence on recovery has been examined. Caching birds will shift their search patterns in predictable ways when objects are moved between caching and recovery trials (e.g. Vander Wall 1982). There is some evidence of redundant cue usage during recovery (Spetch & Edwards 1987; Herz et al. 1994), but it is uncertain at what level birds are discriminating between different sets of cues.

Closely related species differ in their ability to remember the locations of their cache sites. Three species of Corvids were tested, and it was found that their abilities correlated with their dependence on stored seeds (Balda & Kamil 1989). Other species have been tested
in a variety of highly controllable experiments (Olson 1991) and similar 
were results obtained. The duration of cache site memories has also 
been tested for some species. The Black-capped Chickadee (Paridae) 
can remember cache locations for up to twenty-eight days (Hitchcock & 
Sherry 1990), and the Clark's Nutcracker can recall cache locations for 
at least 285 days (Balda & Kamil 1992).

The activity of caching by birds greatly affects the plants that are 
the source of the cached seeds and nuts. It appears that food caching 
birds are responsible for a great deal of range expansion of trees such 
as the piñon pine (Vander Wall & Balda 1977), certain Quercus species 
(Bossema 1979; Harrison & Werner 1984; Crow et al. 1994), and Fagus 
species (Johnson & Adkisson 1985; Johnson & Webb 1989). Extensive 
studies into the ecological interactions between bird and tree are few 
(e.g. Bossema 1979). Currently the extent to which an active symbiosis 
exists, in which the birds are caching with the partial intent of 
dispersal, or a passive symbiosis exists, in which plant dispersal is an 
incidental consequence of caching behavior, is not fully known and 
deserves further investigation.
Materials and Methods

Fifteen adult Blue Jays (Cyanocitta cristata) of unknown age and sex were captured in Blacksburg, Virginia. Each bird was fitted with a Fish & Wildlife Service band and an identifying pattern of color bands. The jays were maintained in aviary having two outdoor flight cages measuring 6.01 x 3.04 x 2.44 m (l x w x h). The diet consisted of striped and black sunflower seeds, dry dog food and water ad libitum. Occasionally shelled, roasted, and unsalted peanuts were provided.

The experimental room was located between the two flight cages in the aviary and had the same dimensions as the previously described flight cages. The long walls were covered with black plastic and the short walls were covered with a white wind-block fabric. A one-way-glass observation mirror measuring 92.5 cm x 61.7 cm was installed on one wall at a height of 1.5 m. Two natural branch perches were suspended by wire from the ceiling in opposite corners of the room. The floor was covered by light brown sand at a uniform depth of approximately 5-7 cm. The sand had dried vines and leaves of Virginia Creeper (Parthenocissus quinquefolia) and large pieces of gravel mixed into it. Two tree stumps (Pinus spp.), two cinder blocks, a large dogwood branch and a pile of shrub branches and leaves were placed on the floor. A grid made of flags constructed of 31.9 mm electro-galvanized roofing nails and approximately 51 mm of colored electrical tape was laid out on the floor creating 32 areas of 0.58 m² each. The flags were moveable, and it did not appear that the jays treated them any differently than the leaf litter. The lines created by the flags
corresponded to lines on maps of the aviary and assisted in charting Blue Jay activity.

In order to test hypothesis $H_0^1$: caching Blue Jays are not recovering caches at success rates greater than predicted by a random model, I intended to allow Blue Jays to freely cache and recover in the experimental environment and compare jay performance to a random model. Three Blue Jays, however, did not cache. Using the performance of the non-caching jays I was also able to test hypothesis $H_0^2$: non-caching Blue Jays are not recovering their caches at success rates greater than predicted by a random model and hypothesis $H_0^3$: caching Blue Jays are not recovering caches at success rates greater than success rates of non-caching Blue Jays.

All experiments were carried out between 28 November 1995 and 27 March 1996. Each Blue Jay was tested individually and only once. First, the bird was isolated and provided only water for 24 hours, from 1530 hours to 1530 hours the following day. Then the jay was allowed into the experimental room where 15 shelled peanut halves and water were provided. The jay remained in the experimental room until all peanut pieces were eaten, cached or a total time of 1 hour had elapsed. The approximate location and order of each cache was noted with a pencil on a map of the aviary, including details about leaf litter placement.

At this point, the individual performance of a Blue Jay determined into which group the bird was placed. A Blue Jay was assigned to the "caching" group if it cached nuts in the experimental
environment and it was assigned to the "non-caching" group if it did not. The jay was then returned to isolation. During this second isolation the jay was provided with small amounts of food to avoid exhaustion if insufficient amounts were consumed during the caching trial. At 0800 hours the following morning, the bird was returned to the experimental room, provided only with water. Each member of the caching group was also provided with its undisturbed caches. Members of the non-caching group were given artificial caches in locations that corresponded to cache locations of a Blue Jay in the caching group. Each jay was kept in the experimental room until all caches were recovered, 30 minutes of "on floor" time had elapsed or a total of 1 hour had elapsed. The locations and number of probes were recorded as well as order of cache recovery and number of sites probed on the same map that caching information had been previously recorded on. The bird was then returned to the living quarters and subsequently released. Each of the above experimental runs was recorded on VHS video tape using a stationary video camera. Additionally, the verbal data "floor" and "perch" were recorded on the audio track during the trials when the jay was changing locations in order to facilitate any necessary review of the video taped data.

A cache was defined as any concealment of peanuts either in the substrate of the floor or on other suitable objects. Concealment is considered essential because this demonstrates an effort to hide the food item rather than putting it aside for later consumption. Both of these behaviors were observed in the aviary.
A probe was defined as any penetration of the substrate surface not involved in general foraging, e.g. gleaning insects off the surface or pulling up earthworms. When probing, Blue Jays make a characteristic sideways sweep of the bill with the mandible and maxilla slightly parted through the substrate (pers. obs.).

A recovery was defined as a bird in the caching group retrieving a cache it had made during the previous afternoon's caching trial or a bird in the non-caching group retrieving an artificially created cache.

Success percentage was a measure of an individual blue Jay's ability to recover caches. Success percentage was calculated by dividing the number of caches recovered by the number of sites probed multiplied by 100. A success percentage of cache recovery for each bird was determined in order to compare the performance of each group to a random model of cache recovery and to compare each group of birds to one another.

A random model of cache recovery was generated using a modified version of the models provided by Baida (1980) and Vander Wall (1992) so that expected success percentages and expected numbers of sites probed could be generated for comparison with the data from the caching and non-caching groups of Blue Jays. Vander Wall (1992) presented the following formula to predict random success probabilities:

\[ S_r = \frac{C\pi(r_p + r_c)^3}{A} \]
where \( r_p \) is equal to the radius of a probe, \( r_c \) is equal to the radius of a cache, \( C \) is equal to the number of caches present and \( A \) is the total area available for caching. Balda (1980) defined the effective search area of a probe as the area directly contacted by the bill plus the area of a cache around the contact area. Effective search area simply assumes the bird will locate a cache correctly even if the probing bill just contacts the edge of the cache. In Vander Wall's equation, the effective search area of a probe is equal to \( \pi(r_p + r_c)^2 \). In the case of the Blue Jay, the direct contact area of the bill is estimated at 4 cm\(^2\). The mean length of shelled peanuts measured on the long axis is 18.1 cm. In the random model used for this study, the effective search area is a rectangular area measuring 35.20 cm\(^2\). If anything, this should result in over estimates of random search success and underestimates of expected number of sites probed. This generous estimate of effective search area was inserted into the above equation.

I generated expected random success percentages for each individual Blue Jay based on the number of caches made divided by the minimum number of discrete searchable sites available (5144) multiplied by 100 (Table 1). Using the values generated for random success, I was also able to determine the number of expected sites that would have to be probed to retrieve identical numbers of caches using a random search (Table 2). This was done for both the caching group and the non-caching group because the number of recoveries for each group differed. In this model, sites were replaced because jays
were occasionally observed returning to sites that had been already searched.

Comparisons of success percentages and number of sites probed between the caching group, the non-caching group and the random model were made using Mann-Whitney tests (Tables 6 & 7).

Three additional hypotheses were tested using data generated by birds in the caching group. They were: \( H_0^4 \): caches made by caching Blue Jays are not placed within 15 cm of room edges or objects in the experimental environment at rates higher than predicted by a random model, \( H_0^5 \): order of cache recovery by caching Blue Jays is not correlated to the order of cache creation and \( H_0^6 \): order of cache recovery by caching Blue Jays is not influenced by nearest-neighbor-cache distances.

In order to test \( H_0^4 \), the number caches near (within 15 cm) an object in the environment or a room edge was determined for each jay in the caching group. A random model was devised to determine the expected number caches near an object or a room edge if caches are randomly distributed in the experimental environment. The expected number of caches near an object or a room edge for each jay is equal to the proportion of the total floor area that is within 15 cm of an object or a room edge (.222) multiplied by the number of caches made in the experimental room. These two groups were compared using a Mann-Whitney test (Table 5).

In order to test \( H_0^5 \), an examination of the sequence relationships between caching and recovery to detect primacy or
recency was done using a composite Spearman rank correlation statistic created by the Virginia Tech Statistical Consulting Center. The statistic:

\[ r^c = \sum_{i=1}^{n} r_i \frac{n_i}{N} \]

measured relative order effects during recovery by considering the relative order of caching versus the order of recovery and weighting the individual Spearman rank correlations \((r_i)\) by the proportion of recovered caches for which each bird was accountable \((\frac{n_i}{N})\). The statistic, \(r^c\) was tested against a distribution generated by assuming complete randomness of recovery order over 50,000 iterations (Table 8). All subjects with only one recovery were dropped from the analysis because it is impossible to detect serial position effects when only one item is considered.

In order to examine \(H_0^6\), a predicted sequence of recovery for each bird in the caching group was generated. The sequence was based on nearest neighbor-distances to the previously recovered cache. No Blue Jay recovered caches in the exact predicted sequence. No statistical tests were available to test \(H_0^6\), instead the proportion of birds making the 'correct' second, third, etc. choices was determined and is presented here merely as descriptive data (Table 3).
Results

The 12 Blue Jays in the caching group made 79 caches with a mean of 6.58 caches per bird and a range of one to twelve. Each cache consisted of only one item per location. 24.05% of all caches were located above ground level, these usually were tucked into the bark of stumps or placed in crevices at the juncture between the wall and the ceiling. In nearly all cases (90.9%), the first cache was made above ground level (Table 4). In all subsequent caches, the mean percentage created above ground was 11.58%. Jays in the caching group recovered a mean of 3.08 caches during recovery sessions.

Hypothesis $H_0^1$ was rejected because caching Blue Jays recovered their own caches at success rates significantly greater than the success rates predicted by the random model ($P<0.0001$; Table 6) and Blue Jays in the caching group probed significantly fewer sites than predicted by the random model ($P<0.0001$; Table 7).

Hypothesis $H_0^2$ was not rejected because the success rates for non-caching jays were not significantly greater than those predicted by the random model ($P=0.4223$; Table 6) and jays in the non-caching group did not probe significantly fewer sites than predicted by using the random model ($P=0.6625$; Table 7).

Hypothesis $H_0^3$ was rejected because, the success rates for caching jays were significantly higher than the success rates for non-caching jays attempting to recover the same caches ($P=0.0077$; Table 6) and caching jays also probed significantly fewer sites than the non-caching jays ($P=0.0392$; Table 7).
The analysis of cache placement with regards to edges and objects in the environment, allowed $H_0^4$ to be rejected. Caching Blue Jays placed significantly more caches near edges and objects in the environment than expected by random (P=0.007; Table 5).

Hypothesis $H_0^5$ was not rejected because using the pooled correlation statistic it was determined that there is no significant evidence of either primacy or recency effects on cache recovery (P=0.2955; Table 8).

The examination of nearest-neighbor distances did not reveal any consistent tendency for caching Blue Jays to recover caches in any order analogous to predicted nearest-neighbor distance sequences. Though no statistical analysis is available to compare these sequences, it can be seen in Table 4 that the proportion of recovered caches that correspond to predicted sequences is very low.

In one instance, a non-caching bird recovered two caches that the respective caching bird had also recovered. We compared the spatial distribution of probes by these two birds around these caches. Though there is no statistical evidence to support any generalizations about caching and non-caching birds in this regard, there is an apparent difference in the distributions of probes between these two individuals (Fig. 1 a&b)
**Discussion**

Blue Jays in the wild are only partly migratory and year round residents need to have sufficient food supplies to overwinter in most areas in North America. By caching acorns and nuts, they are able to extend the availability of these resources. Blue Jays are clearly not using a random foraging strategy to locate caches. Their success rates for recovery are significantly higher than those predicted by random models (Table 6), and they probe at significantly fewer sites than predicted by random foraging models (Table 7). Caching birds are also significantly different from non-caching birds in both success percentages (Table 6) and number of sites probed (Table 7). Non-caching birds, however, neither recover caches at success rates above random (Table 6) nor probe at significantly fewer sites than expected by random search (Table 7).

The suggestions that odor or microtopography might be cues for recovery are not well supported by the data. All birds were given equal opportunity to retrieve caches, and artificial caches for the non-caching jays were made to resemble as closely as possible the caches made by the jays in the caching group. Given the disparity in performance between groups, it appears that the non-caching birds were not cueing on odor from the caches nor were they using microtopographic disturbance cues. Previous studies involving European Jays (Bossema 1979), Eurasian Nutcrackers (Balda 1980) and Clark's Nutcrackers (Vander Wall 1982) found similar results. All three studies concluded that odor emanating from caches and microtopography were not the
means by which caches were recovered. This conclusion is further reinforced for Blue Jays by the fact that non-caching jays did return to sites where caches had been previously discovered caching jays did not. If a cache has been recovered then it can no longer emanate odors and most pertinent microtopographic features which suggested the presence of an undisturbed cache will no longer exist. Thus, it is apparent that to Blue Jays, odor and microtopography are not important facets of recovery.

All jays that did not cache in the experimental enclosure were naive birds that had never been in the experimental room before the trial. Some naive birds, however, readily cached during their trials. The non-caching birds may have been juveniles, in which case they might not know be ready to use stored food during periods of food shortage.

Blue Jays cached significantly more food items near objects and room edges than expected by random (Table 5). Overall 67.1% of their caches were within 15 cm of a room edge or an object. Though this figure is consistent with other studies, e.g. 65% for Eurasian Nutcrackers (Balda 1980), the confines of the experimental environment make it difficult to extrapolate the information in this analysis to the natural environment. Walls and objects always nearby in the experimental environment.

An additional examination of cache placement found that 90.9% of first caches were created above ground (Table 4). Above-ground caches were routinely placed in crevices in the bark of the stumps, in
holes in the wall covering and also on ledges at the top of the walls. This figure is in stark contrast to the only 25.3% of all caches that were made above ground. The jays also were prone to caching in the same above-ground sites used by other jays. The only cases of caches made in identical locations by different birds were these above-ground caches. In the wild, Blue Jays procure several nuts from the source at once (Darley-Hill & Johnson 1981; Johnson & Adkisson 1985). The jays then fly to a suitable caching site, deposit the nuts in a pile and proceed to cache the nuts one by one (Darley-Hill & Johnson 1981). They also have been observed recovering and recaching food stores (pers. obs.). These behaviors are consistent with an optimal foraging strategy in which a bird takes maximum advantage of a source while it is available and makes adjustments to its "stockpile" after the source has been exhausted. It is likely that captive jays are storing in these inferior ready-made sites as a means of quickly distributing the available peanuts. Blue Jays in the wild have been observed moving their caches (pers. comm. Adkisson). Perhaps if the jays were given more time in the experimental room, these above ground caches would be moved to more secretive locations.

No significant evidence of either primacy or recency in Blue Jay cache recovery was found (Table 8). It is often suggested that caching birds may be dependent on the serial position effects of primacy or recency to recover caches, yet evidence of either primacy or recency in avian memory studies has been inconclusive. Cowie et al. (1981) determined that Marsh Tits in the wild likely recovered caches in the
same order of their creation. Shettleworth and Krebs (1982), however, found the opposite to be true when studying Marsh Tits in the laboratory. Other studies with different species have been inconclusive or found no effect (e.g. Balda 1980; Sherry 1984a; Kamil and Balda 1985). It is often difficult to accurately assess this phenomenon because it is either impossible to determine the exact sequence of recovery in the field, or birds do not recover all of their caches in the laboratory. In order to get around this problem, previous studies have usually only considered the differences between "earlier" and "later" caches. In my study I used a composite Spearman rank correlation statistic developed by the Virginia Tech Statistical Consulting Center to examine serial position effects. The composite Spearman rank correlation statistic is better than previous estimations of serial position effects because it allows for the maximum amount of information utilization. The relative order of storage is compared to the order of recovery thus eliminating the need for full recovery of all caches. The information from each bird is then pooled and weighted so that an assessment of the whole group rather than individuals can be made.

It has also been proposed that caching birds might recover caches in an order related to nearest-neighbor distances, in other words, a systematic selection of a path that minimizes travel time between caches (Vander Wall 1990). There is no evidence from the behavior the caching Blue Jays in this study to indicate that nearest-neighbor distances play any role in cache recovery. For each cache,
only a small proportion of birds chose the cache consistent with nearest-neighbor distance models (Table 3). This observation is consistent with Blue Jay behavior in the experimental room. Blue Jays retrieve a cache and retreat to a perch to consume it before retrieving another cache. Use of nearest-neighbor distances would be expected if the jay retrieved several caches prior to consumption rather than the observed one at a time. There is no information on the use of this strategy by Blue Jays in the wild.

Four caches were discovered by the birds in the non-caching group. Two of the four caches were located above ground in the same relatively exposed location and were quite likely located by seeing the cached item itself. The other two caches that were discovered were identical to caches recovered by birds in the caching group. This permitted a comparison between the probing patterns made to discover and to recover these caches. The dispersion of probes made by the non-caching bird showed a decrease in probing density at increasing radial distances around the cache location (Figure 1a). Sixty-nine of the probes made for cache number two were made after the discovery of the cache and all were located within 20 cm of the cache. In the case of the caching bird (Figure 1b), all probes were at the cache site, and all occurred prior to recovery. This suggests that non-caching Blue Jays are using a "win-stay" foraging strategy (Olton et al. 1981) because they are returning to the site of previous success in hopes of increasing the likelihood of further success. Caching Blue Jays on the other hand apparently use a "win-shift" strategy whereby they do not return to
probe further at the site of a previous success. The contrast in the behavior of these two birds indicates a difference in how information obtained during foraging is used by cachers and non-cachers. It also further supports the hypothesis that Blue Jays are using spatial memory to retrieve caches.

The phenomenon of cache site revisits that has been observed and studied in nutcrackers (Balda 1980; Kamil & Balda 1985; Kamil et al. 1993) was hardly in evidence in the caching group of Blue Jays. In only one instance during experiments was such a return to an emptied site recorded. During pilot studies, a caching Blue Jay placed two peanuts in one location, recovered both and subsequently continued to return to the site. Perhaps Blue Jays can remember cache locations but not the exact quantity of items stored in those locations. In most cases, however, this is of no relevance to Blue Jays since nearly all caches consist of one item in one location.
Conclusions

This study has provided new information about the food caching and recovery behavior of Blue Jays. It is apparent that caching Blue Jays remember the locations of their caches and that non-cachers are unable to find the caches of others with enough success to make it a viable foraging strategy. The importance of Blue Jays to deciduous tree dispersal can now be more fully understood. The success percentages reported here suggest that Blue Jays are quite good at recovering their caches. It is still, however, not known what percentage of cached nuts are recovered in the wild. Once this is determined it should be possible to determine if mortality of jays, forgetting by jays or masting by trees is most important to the dispersal of oaks, beeches and chestnuts.

The behaviors observed in this experiment also demonstrate that Blue Jays are ideal subjects for further spatial memory studies. Their relative lack of need for training, the habit of caching items singly, and their high success rates are all desirable qualities for examination of spatial memory. During this study and pilot studies Blue Jays were observed caching food in March and April. Since these birds were maintained outdoors under natural photoperiods, this suggest that food shortages and not photoperiods are most influential to Blue Jay caching behavior. If this is so then it would be possible to conduct experiments at all times of the year, another desirable quality.

Blue Jays are familiar and wide spread, but they have been mostly passed over for scientific study. It is only recently that we have
come to realize how much this species' continued success can tell us about avian ecology. It is hoped that this study will lead to further studies of Blue Jays and food caching which will provide us with more information about the role of spatial information in foraging strategies and about animal facilitated dispersal of plants.
Figures
Figure 1a. - Probing pattern of a non-caching captive Blue Jay for two discovered caches.

Figure 1b. Probing pattern of a caching captive Blue Jay for two recovered caches. (same as in 1a.)
Tables
Table 1. Success Percentages of caching and non-caching captive Blue Jays, and expected success percentages using random model.

<table>
<thead>
<tr>
<th>Random</th>
<th>Non-Caching</th>
<th>Caching</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.156</td>
<td>6.38</td>
<td>100</td>
</tr>
<tr>
<td>0.078</td>
<td>0</td>
<td>15.38</td>
</tr>
<tr>
<td>0.039</td>
<td></td>
<td>100</td>
</tr>
<tr>
<td>0.117</td>
<td>7.69</td>
<td>75</td>
</tr>
<tr>
<td>0.175</td>
<td></td>
<td>100</td>
</tr>
<tr>
<td>0.175</td>
<td></td>
<td>25</td>
</tr>
<tr>
<td>0.039</td>
<td></td>
<td>100</td>
</tr>
<tr>
<td>0.175</td>
<td></td>
<td>50</td>
</tr>
<tr>
<td>0.175</td>
<td></td>
<td>100</td>
</tr>
<tr>
<td>0.156</td>
<td></td>
<td>100</td>
</tr>
<tr>
<td>0.233</td>
<td></td>
<td>41.67</td>
</tr>
</tbody>
</table>

Mean 0.128     4.69     76.28
Table 2. Number of sites probed by caching and non-caching captive Blue Jays, and expected number of sites probed using random model.

<table>
<thead>
<tr>
<th>Caching</th>
<th>Expected (Caching)</th>
<th>Non-Caching</th>
<th>Expected (Non-Caching)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>1923</td>
<td>47</td>
<td>1923</td>
</tr>
<tr>
<td>26</td>
<td>5128</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>5128</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>2564</td>
<td>13</td>
<td>855</td>
</tr>
<tr>
<td>4</td>
<td>2285</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>571</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>5128</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>1714</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>2285</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>2564</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>246</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>6</td>
<td>22</td>
<td>926</td>
</tr>
</tbody>
</table>
**Table 3.** Proportion of cache recoveries by caching captive Blue Jays that adhere to predicted nearest-neighbor-distance paths.

<table>
<thead>
<tr>
<th>Recovery</th>
<th>Proportion Correct</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>2nd</td>
<td>0.375</td>
<td>8</td>
</tr>
<tr>
<td>3rd</td>
<td>0.125</td>
<td>8</td>
</tr>
<tr>
<td>4th</td>
<td>0.2</td>
<td>5</td>
</tr>
<tr>
<td>5th</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>6th</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>
Table 4. Cache placement by caching captive Blue Jays - Above ground vs. Ground.

<table>
<thead>
<tr>
<th>Cache</th>
<th>Proportion Above Ground</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.909</td>
<td>11</td>
</tr>
<tr>
<td>2</td>
<td>0.273</td>
<td>11</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>4</td>
<td>0.222</td>
<td>9</td>
</tr>
<tr>
<td>5</td>
<td>0.111</td>
<td>9</td>
</tr>
<tr>
<td>6</td>
<td>0.125</td>
<td>8</td>
</tr>
<tr>
<td>7</td>
<td>0.143</td>
<td>7</td>
</tr>
<tr>
<td>8</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>9</td>
<td>0.4</td>
<td>5</td>
</tr>
<tr>
<td>10</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>11</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>12</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>
**Table 5.** Comparison of the number of caches made within 15 cm of an object or room edge between caching captive Blue Jays and a random model. (Mann-Whitney)

<table>
<thead>
<tr>
<th># near edge or object</th>
<th>expected # near edge or object (random)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>1.77</td>
</tr>
<tr>
<td>1</td>
<td>0.887</td>
</tr>
<tr>
<td>2</td>
<td>0.444</td>
</tr>
<tr>
<td>4</td>
<td>1.35</td>
</tr>
<tr>
<td>8</td>
<td>1.99</td>
</tr>
<tr>
<td>5</td>
<td>1.99</td>
</tr>
<tr>
<td>1</td>
<td>0.444</td>
</tr>
<tr>
<td>4</td>
<td>1.99</td>
</tr>
<tr>
<td>3</td>
<td>1.99</td>
</tr>
<tr>
<td>8</td>
<td>1.77</td>
</tr>
<tr>
<td>11</td>
<td>2.66</td>
</tr>
<tr>
<td>1</td>
<td>0.222</td>
</tr>
</tbody>
</table>

The two groups are highly significantly different, P<0.01.
Table 6.  
Comparison of success percentages of caching and non-caching captive Blue Jays and the random model. (Mann-Whitney)

<table>
<thead>
<tr>
<th></th>
<th>Caching</th>
<th>Non-Caching</th>
<th>Expected (Random)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caching</td>
<td>**</td>
<td>**</td>
<td></td>
</tr>
<tr>
<td>Non-Caching</td>
<td>-</td>
<td>-</td>
<td>n.s.</td>
</tr>
<tr>
<td>Expected (Random)</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

** highly significant, P<0.01  
n.s. not significant, P>0.10
**Table 7.** Comparison of number of sites probed by caching and non-caching captive Blue Jays and the random model. (Mann-Whitney)

<table>
<thead>
<tr>
<th></th>
<th>Caching</th>
<th>Non-Caching</th>
<th>Expected (Random)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caching</td>
<td>-</td>
<td>*</td>
<td>**</td>
</tr>
<tr>
<td>Non-Caching</td>
<td>-</td>
<td></td>
<td>n.s.</td>
</tr>
<tr>
<td>Expected (Random)</td>
<td></td>
<td></td>
<td>-</td>
</tr>
</tbody>
</table>

** highly significant, P<0.01
* significant, P<0.05
n.s. not significant, P>0.10
Table 8. Composite Spearman rank correlation to test for serial position effects on cache recovery by caching captive Blue Jays.

<table>
<thead>
<tr>
<th>Bird</th>
<th>r</th>
<th>n/N</th>
<th>Partial Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>-0.5</td>
<td>0.0857</td>
<td>-0.0492</td>
</tr>
<tr>
<td>2</td>
<td>0.8</td>
<td>0.1143</td>
<td>0.0914</td>
</tr>
<tr>
<td>3</td>
<td>-1</td>
<td>0.0571</td>
<td>-0.0571</td>
</tr>
<tr>
<td>4</td>
<td>-0.5</td>
<td>0.0857</td>
<td>-0.0429</td>
</tr>
<tr>
<td>5</td>
<td>0.8</td>
<td>0.1143</td>
<td>0.0914</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>0.0571</td>
<td>0.0571</td>
</tr>
<tr>
<td>7</td>
<td>0.5</td>
<td>0.0857</td>
<td>0.0429</td>
</tr>
<tr>
<td>8</td>
<td>-0.2</td>
<td>0.1143</td>
<td>-0.0229</td>
</tr>
<tr>
<td>9</td>
<td>-0.4</td>
<td>0.1143</td>
<td>-0.0457</td>
</tr>
<tr>
<td>10</td>
<td>0.829</td>
<td>0.1714</td>
<td>0.1421</td>
</tr>
</tbody>
</table>

\[ r^c = 0.2134 \]
\[ (P=0.2955) \]

- \( r^c \): Composite Spearman Rank Correlation
- \( r \): Individual Spearman Rank Correlation
- \( n_i \): Individual # caches retrieved
- \( N \): Total # caches retrieved

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Literature Cited


Bennett, K.D. 1985. The spread of *Fagus grandifolia* across eastern North America during the last 18,000 years. *Journal of Biogeography, 12*:147-164.


Ehrlich, Paul R., Dobkin, David S. & Wheye, Darryl 1988. The Birder’s


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Wilson Ornithological Society, 1995-present

Professional Meetings
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1995 August 15-19, Attended 113th stated meeting of the American Ornithologists’ Union, Cincinnati, OH

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