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The development of caching behavior, cache site and cache item defense tactics, and cache site and cache item sharing in orphaned fledgling blue jays (*cyanocitta cristata*) at a songbird rehabilitation center

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The Development of Caching Behavior, Cache Site and Cache Item Defense Tactics, and Cache Site and Cache Item Sharing in Orphaned Fledgling Blue Jays (*Cyanocitta cristata*) at a Songbird Rehabilitation Center

by

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Dedicated to my best friend, lover,
husband, Saturday Night Scrabble buddy and
hot tub soul mate, Vicente.

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Abstract

One of the primary goals of songbird rehabilitators is to promote controllable factors that increase survivorship in orphaned songbirds upon to release. As caching serves an important function in corvid life, this study sought to determine if this behavior would develop with or without outside input. Eight orphaned blue jays (consisting of both hatchlings and nestlings) were brought into the care of the Bird Center of Washtenaw County, Inc. in Ann Arbor, Michigan. Birds were videotaped and observed for the development of caching behavior, cache item and cache site sharing, and cache defense tactics. Caching behavior and cache defense tactics all developed without parental or caretaker input, regardless of age at which birds were received. Cache site sharing and theft tolerance occurred with all cohorts but at varying frequency. This study recommends that blue jay release criteria include the development of food hoarding behavior.

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Chapter 1

Introduction

Food hoarding (synonymous with *caching* or *storing*) is defined as the discrete storage of a food item in a given location for future use (Morris, 1962; Vander Wall, 1990; Brodin, 2005). Vander Wall (1990) points out that this definition excludes the hiding of food in body parts, such as cheeks or crops, as this is merely a means of transportation or deferred digestion and not considered actual hoarding.

More than 100 species of crows, jays, nutcrackers, and magpies (family Corvidae) exhibit food hoarding behavior (Vander Wall, 1990; Pollok, Prior & Güntürkün, 2000; Brodin, 2005). This behavior is important for survival as it allows the bird to store food for future times when resources may not be readily available (Johnson & Adkisson, 1986; Brodin, 2005) and increases survival (Yoerg, 1991), as corvids have evolved physiological (Bock, Balda & Vander Wall, 1973; Vander Wall, 1990; Heinrich & Pepper, 1998) and behavioral (Roberts, 1979; Johnson & Adkisson, 1985; Kamil & Balda, 1985) adaptations specifically for caching.

Research on corvid food-hoarding behavior has examined multiple areas including cognition (Emery & Clayton, 2004), such as spatial memory (Kamil & Balda, 1985; Brodin, 2005; Clayton, et al., 2006); caching techniques (Johnson & Adkisson, 1985 & 1986); and the ecological impact of caching (Darley-Hill & Johnson, 1981; Vander Wall & Balda, 1981; Johnson & Adkisson, 1985; Kamil & Balda, 1985; Johnson & Adkisson, 1986; Johnson & Webb, 1989). Despite the breadth of these studies, the majority of previous research has focused on caching behavior in adult birds. To date, few data address the development of caching behavior in fledgling corvids, or the

development of related behaviors, such as cache site and cache item sharing or cache defense tactics.

Food hoarding behavior in orphaned fledgling blue jays (*Cyanocitta cristata*) has been minimally studied and much of the development of this behavior in these birds is little known, including associated behaviors, such as development and implementation of cache defense tactics, sharing and theft tolerance of cache items and cache sites.

Data on development of caching behavior, cache defense, and cache sharing would be of interest to songbird rehabilitators as well as to avian behavioral ecologists. It is understood among songbird rehabilitators that released orphaned songbirds are disadvantaged compared to wild-raised conspecifics. Orphaned songbird rehabilitation typically lacks contact or interaction with parents or kin, exposure to "normal" social behavior, and, most likely, exposure to adult conspecific song. Thus, the primary goal of songbird rehabilitators working with orphaned species is to maximize survivorship by minimizing detrimental factors that are controllable. Factors that wildlife rehabilitators have control over which can contribute to bird mortality upon release include inability to self-feed, human/predator habituation, lack of waterproofing, and poor health. Currently, assuming birds meet all other criteria for release (waterproof feathers, parasite-free, etc.), all orphaned songbirds are retained until they are able to feed themselves for seven consecutive days, as this is assumed to be the last survival-skill necessary for self-sufficiency and independence from the parents. Blue jays represent the ideal species for this study, as they are the species of corvid that songbird rehabilitators in Michigan are most likely to encounter during the bird-breeding season (unpublished data; based on intake forms from rehabilitators).

Collectively, the objectives of this study are to develop a set of criteria to be used when determining the developmental progress of orphaned blue jays for the purpose of increasing survivorship. To this end the primary goals of the study are as follows:

1) To learn whether or not the caching behavior of blue jays develops in the absence of an adult conspecific.
2) To characterize developmental benchmarks, noting the timing by which these behaviors manifest themselves.
3) To determine whether orphaned fledgling blue jays employ cache defense strategies to protect their established caches.
4) To record whether orphaned fledgling blue jays share cache items and/or cache sites.

General Methods

Eight hatchling and nestling blue jays (one hatchling pair from 2006 [cohort GH], two nestling pairs and two nestling singles from 2007 [each pair is thought to come from the same nest; the two singles were housed together to form a single cohort (cohort CD)]) were brought to the Bird Center of Washtenaw County, Inc. (henceforth, the Bird Center) rehabilitation center by people from Washtenaw County, Michigan. Each bird was aged (based on physical characteristics such as presence of pin feathers and amount of visible skin) and inspected upon entering the Bird Center for possible injury or illness, and treatment was administered, if needed. All jays were in excellent health upon arrival and during their stay at the Bird Center and did not require additional medical treatment.

Each jay cohort was housed in an artificial nest that satisfied the standards set by both International Wildlife Rehabilitation Council and National Wildlife Rehabilitators Association's *Minimum Standards for Wildlife Rehabilitation* (Miller, 2000). Artificial nests were designed to limit visual input of caregivers to the birds as to prevent habituation to humans. Artificial nests were composed of a large plastic bucket (about 25cm across and about 25cm deep) and lined with two sheets of Brawny® paper towel. A smaller and shallower plastic container (about 11.5cm across and 5cm deep to 16.5cm across and 10cm deep, depending on the size of the birds) was placed inside the plastic bucket, on top of the Brawny® paper towel lining and served to hold the birds. The inner container was lined with Brawny® paper towel and unscented, non-lotion Kleenex® facial tissue. The artificial nest was placed inside a mesh bag to help contain birds that began fledging. A single sheet of Brawny® paper towel was placed over the top of the artificial nest to help limit visual contact with human caretakers and, thus, habituation to humans. Blue jays were fed about 2 to 4 ml of Passerine Diet every 15 minutes as hatchlings and 4 to 8 ml (or until satiated) every 30-45 minutes as nestlings, from 7am until 9pm, seven days a week (birds were progressively fed less frequently and given more food as they aged). Food was warmed in a microwave to about 98.6°F. Afterwards, the food was thoroughly stirred and temperature was tested by dabbing some of the food onto the underside of the caretaker's wrist. Birds were fed with a plastic 2 ml eye dropper.

Once blue jays had fledged (defined, for the purposes of this experiment, as jumping to the top of the artificial nest three consecutive times), they were transferred to a basket that satisfied the requirements outlined in *Minimum Standards for Wildlife*

Rehabilitation (Miller, 2000). Fledgling baskets were rectangular Rubbermaid® laundry baskets (about 67.3cm long by 50.8cm wide by 31.1cm high). Sides of the baskets were scored with a razor blade, then hardware screening was secured to the inside walls of the basket with hot glue. A piece of hardware cloth measuring slightly larger than the top of the basket became the ceiling of the basket and was secured in place using 6-8 wooden clothespins. A wooden perch was inserted into the center of the basket and secured using two clothespins on the outside of the basket. Baskets were lined with four connected sheets of Brawny® paper towel, two sheets folded over on top of the other two. Jays were fed the Passerine Diet until satiated, every 45-60 minutes from 7am until 9pm, seven days a week. This continued until jays were self-feeding (defined as continuously rejecting the dropper for seven consecutive days by not opening their mouths when the dropper was presented to them, but still maintaining or gaining weight). Birds were on a 14:10 light schedule and provided with food and water *ad libitum* until they left the Bird Center for release cages. Once upgraded to a fledgling basket, birds were videotaped to monitor the development of caching behaviors, since the fledgling basket offers opportunities to cache that do not exist in the nestling artificial nest.

A video recorder was positioned next to the birds' basket to record a 45-minute session of behavior. Each basket was recorded every day. Times at which videos were recorded were random under the assumption that fledgling blue jay caching activity would be relatively constant throughout the day, as adult caching activity is (Johnson & Adkisson, 1985). A blind was permanently placed around each basket, preventing visual input from other cohorts or birds. The blind consisted of connected sheets of Brawny® paper towel and were suspended from all sides of the basket, except the side that faced

the video camera during recording sessions. The blind was held in place on the basket by the same clothes pins that kept the hardware screen ceiling in place. From this point, only members of the same cohort could visually influence each other's caching development. The only time the young blue jays could see other birds was when another bird had escaped from its basket at the Bird Center and either flew over or landed on top of the blue jays' basket. At that time, the escaped bird was pursued until caught and could not demonstrate caching behavior.

Cohorts were labeled with a numbered diaper pin that was directly attached to the basket screening. Jays that were brought to the Bird Center by the same person(s) at the same time were considered related and were placed in the same housing unit. Cohorts AB, EF and GH were all considered related, although genetic relatedness was not tested. Birds that came in at different times or were brought in by different people were considered unrelated, as was the case for cohort CD. In video scoring sessions, individual birds within the cohort were identified by unique spot patterns on the back and wings that were visible when birds turned their backs to the camera.

Videos were labeled prior to recording with the date, time, and basket number. Videos were watched by the researcher using a video player and television. A notebook was used to collect data. The date, time, and basket number were marked for that particular data-collecting event, and a chart was drawn in the notebook to mark specific behaviors that were being monitored. Behavior was scored according to criteria outlined in subsequent chapters. Individual birds were designated a specific color of ink in which their data would be marked. Each bird's ink color was noted for each data-collecting event.

Chapter 2

Development of Caching Behavior

Introduction

Adult blue jays, like most members of family Corvidae, store their caches in excavations in the ground over large areas and cover them with nearby debris, such as rocks, leaves, or grass (Roberts, 1979; Darley-Hill & Johnson, 1981; Johnson & Webb, III; 1989; Brodin, 2005). As scatter hoarders, a single blue jay will store a single item in a single place resulting in many small stores over a large area (Morris, 1962; Scarlett & Smith, 1991, Brodin, 2005). This activity is relatively constant for blue jays throughout the day (Johnson & Adkisson, 1985). Using their expandable upper esophagus, these birds are capable of transporting many more items, such as acorns, than would be possible without the aid of this adaptation (Johnson & Webb, III, 1989). While much research has been conducted on adult corvid caching behavior (Laskey, 1942 & 1943; Roberts, 1979; Harrison & Werner, 1984; Johnson & Adkisson, 1985; Johnson & Webb, 1989; Scarlett & Smith, 1991; Clayton, Griffiths, Emery and Dickinson, 2001; Emery & Clayton, 2004; Dally, Emery & Clayton, 2005; Clayton et al., 2006; von Bayern, de Kort, Clayton & Emery, 2007), little is known about the development of caching behavior in fledgling blue jays. Currently, caching behavior is not a specific release criterion for rehabilitated blue jays, or corvids in general. This amounts to an implicit assumption that caching behavior develops during rehabilitation without the presence of an adult conspecific to demonstrate it. If this assumption is false, then orphaned blue jays released into the wild may lack caching skills they need to survive. The goal of this study

was to learn *if* caching behavior manifests itself in young blue jays before they are sent to release cages, and if so, *at what age* does caching behavior become evident. The present study tests the hypothesis that the development of caching behavior persists in fledgling blue jays without demonstration. If data do not support the hypothesis, then development of caching behavior should not only be a release criterion specific to blue jays, and perhaps all corvids, but methods for teaching the skill to orphaned corvids should be implemented in corvid care.

Methods

Video recorded sessions were reviewed and quantified for the following behaviors, which, for the purposes of this study, are considered smaller components of caching behavior: *moves*, *removes*, *hides*, and *uncovers* cache items, as well as *creates/maintains* cache sites. The criteria used to determine what actions qualified for a particular behavior are as follows:

- *Moves: Picking up food and transferring food to another location, such as in a crevice, hole, or under an object (such as a food dish or under a piece of paper towel).*
- *Removes: Taking food from a cached location, such as a crevice, a hole, or from under an object*
- *Creates/Maintains: Formation and manipulation of cache locations by pecking at existing holes or crevices, ripping at and twisting pieces of screen, poking and rotating beak in holes*
- *Hides: Covering up a food-object with another object, such as paper towel or other debris*
- *Uncovers: Removing a food-object that had been covered with paper towel or other debris*

These behaviors were selected as action-components involved with caching. A chart was drawn in the data collection notebook with each behavior as a column heading. A tick mark in the jay's designated color was placed in the column for that particular behavior when it was observed. Jays' designated colors were noted in the data collection notebook for that particular day.

Ages of the jays were divided into four blocks of time. Time periods consisted of Age Block 1 (20 to 25 days), Age Block 2 (26 to 31 days), Age Block 3 (32 to 37 days) and Age Block 4 (38 to 44 days). The number of incidences that occurred for each action for each jay was averaged for each age block. Then the two individual averages for the cohort members were averaged to give an action average for the cohort during each age block.

Starting age was analyzed with a bird(pair) x behavior ANOVA. Development of each behavior was analyzed with a bird(pair) x time block ANOVA. SPSS 15.0 and JMP-IN (version 3.2) were used to conduct statistical analysis. Sigma Plot 14.0 and Microsoft Office Excel 2003 were used to construct graphs.

Results

A total of 24 days were recorded. One day was not recorded in 2007 for cohort AB due to an improperly charged battery. Two days were not recorded in 2007 for cohort EF due to an improperly charged battery. All fledgling blue jays developed caching behavior, regardless of the age at which they entered the Bird Center. Ages (measured in days) at which the various components of caching behaviors were first observed are shown in Table 2.1.

Table 2.1.

Age At Which the Components of Caching Behaviors Were First Observed. Age is measured in days.

Pair	Bird	Moves	Removes	Creates	Hides	Uncovers
1	A	29	33	24	29	29
	B	28	32	21	32	32
2	C	28	26	23	34	34
	D	32	33	27	33	34
3	E	34	31	24	34	35
	F	32	31	24	44	34
4	G	26	26	20	37	24
	H	24	24	20	27	26

Different behaviors were first observed at different ages ($F_{4,16}$=13.9582, $p<0.0001$), with cache site creation occurring first and hiding food occurring last (see Figure 2.1). Some pairs developed caching behavior earlier than others ($F_{3,16}$=13.2012, $p=0.0001$). Birds within pairs developed caching behaviors at similar times ($F_{4,16}$=1.4799, $p=0.2547$). Pairs developed behaviors in similar sequences over time (pair x behavior interaction $F_{12,16}$=0.9902, $p=0.4968$).

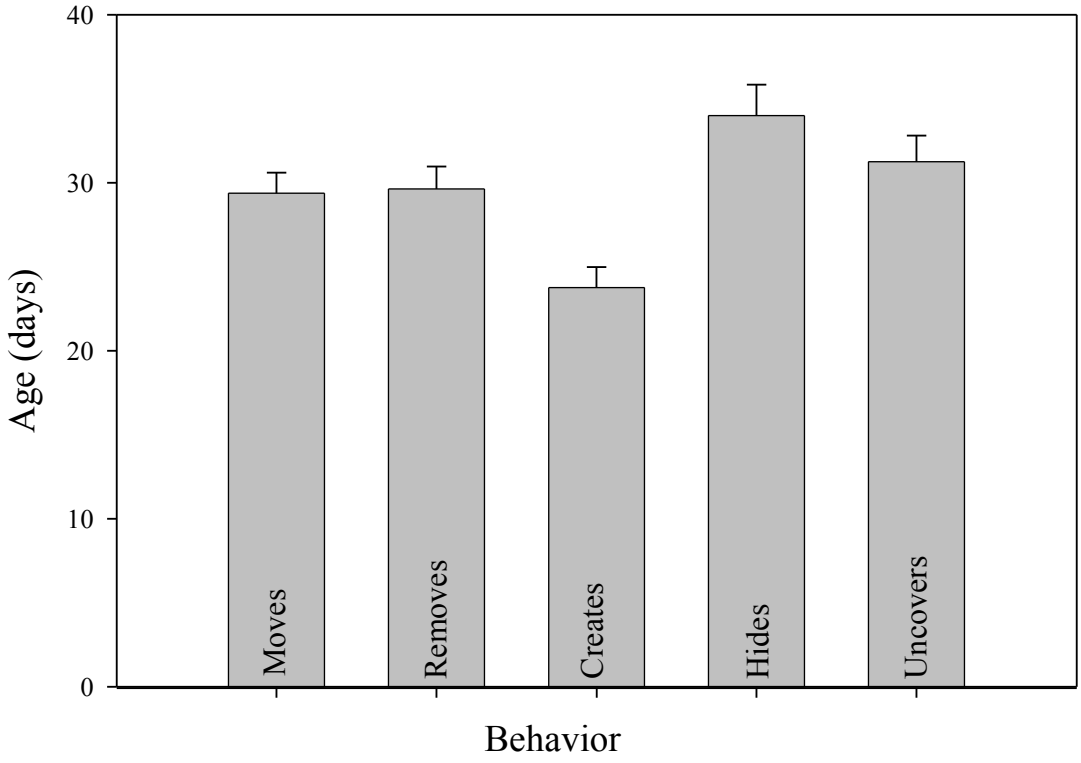

Figure 2.1 Average age at which each component of caching behavior was first observed. Age of jays was measured in days.

The average number of moves increased over time ($F_{3,9}$=10.1285, p=0.0030, see Figure 2.2). Different pairs developed this behavior at different times ($F_{3,12}$=13.983, p=0.0003) and changed over time at different rates ($F_{3,12}$=4.2801, p=0.0110, see Figure 2.2). Birds within pairs did not differ dramatically in their development of move activities ($F_{4,12}$=1.1626, p=0.3749).

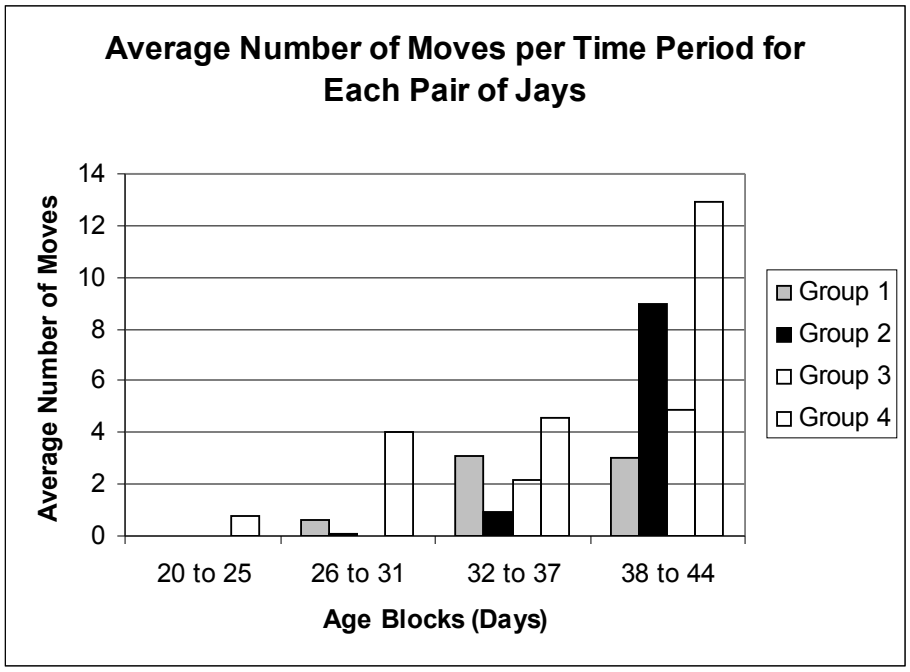

Figure 2.2 Average number of moves per pair of jays across four time periods of development. Time periods are the ages of the birds measured in days and put into blocks: 20 to 25, 26 to 31, 32 to 37, and 38 to 44 days. The number of moves incidences that occurred for each jay was averaged for each age block. Then the two individual averages for the cohort members were averaged together to give a moves average for the cohort during each age block.

The average number of removes increased over time ($F_{3,9}$=6.3349, p=0.0134, see Figure 2.3). Different pairs developed this behavior at different times ($F_{3,12}$=14.4247, p=0.0003) and changed over time at different rates ($F_{3,12}$=6.6765, p=0.0017, see Figure 2.3). Birds within pairs developed removes similarly ($F_{4,12}$=0.7113, p=0.5998).

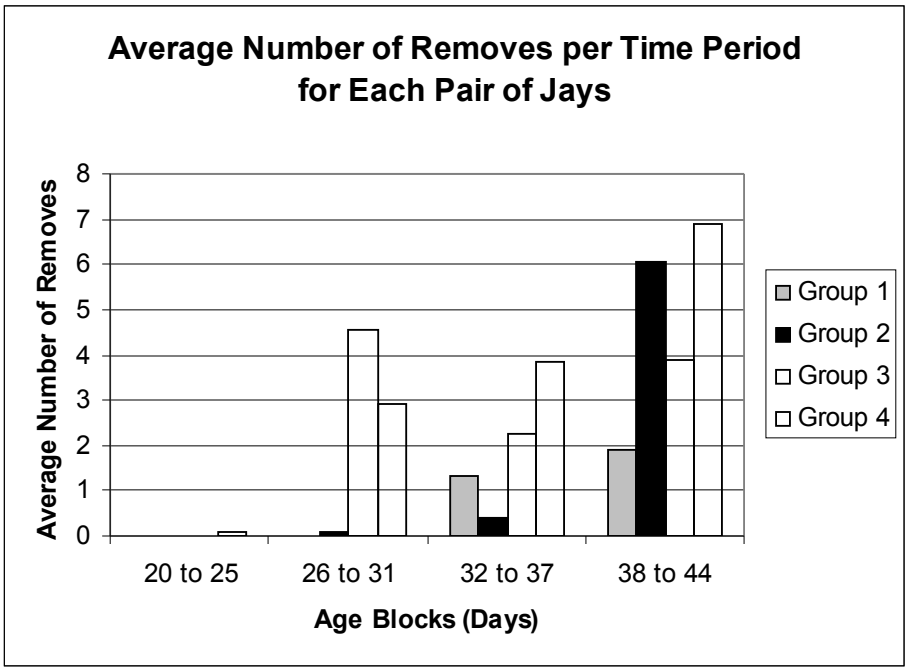

Figure 2.3 Average number of removes per pair of jays across four time periods of development. Time periods are the ages of the birds measured in days and put into blocks: 20 to 25, 26 to 31, 32 to 37, and 38 to 44 days. The number of removes incidences that occurred for each action for each jay was averaged for each age block. Then the two individual averages for the cohort members were averaged to give a removes average for the cohort during each age block.

The average number of creates increased over time ($F_{3,9}$=22.6944, p=0.0002, see Figure 2.4). Different pairs developed this behavior at different times ($F_{3,12}$=29.1272, p<0.0001) but changed over time at similar rates ($F_{3,12}$=1.3524, p=0.3067, see Figure 2.4). Birds within pairs developed creates similarly ($F_{4,12}$=1.1778, p=0.3690). A pairwise comparison was conducted to see the effect age had on *creates*/*maintains* behavior. Age blocks 2, 3, and 4 were analyzed for *creates*/*maintains* behavior. *Creates/maintains* only had a significant effect (F=38.5128, p=0.0084) from Age Block 3 (days 32 to 37) to Age Block 4 (days 38 to 44) meaning that birds displayed increasing cache site creating/maintaining activity from Age Block 3 to Age Block 4.

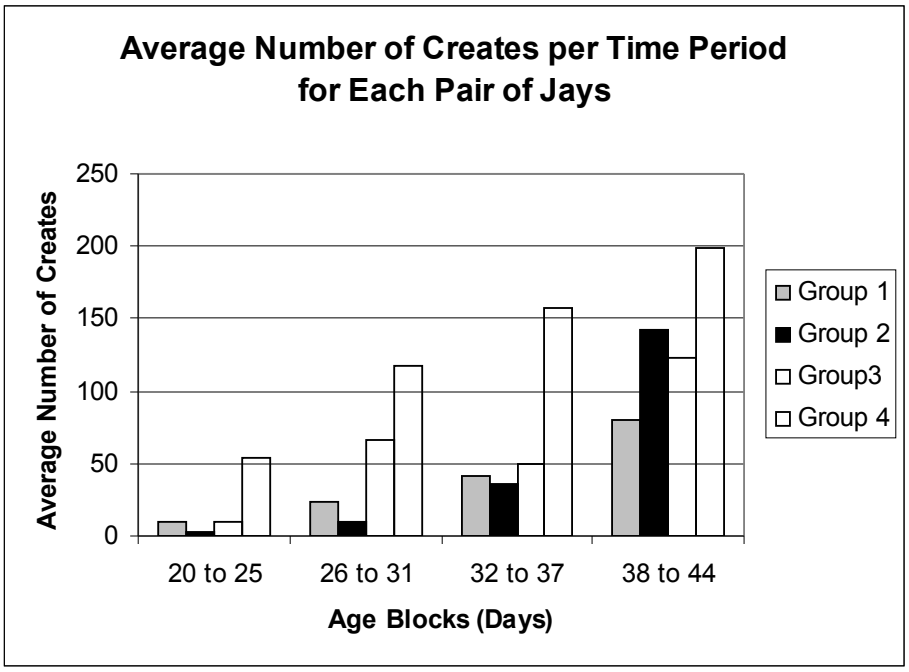

Figure 2.4 Average number of creates per pair of jays across four time periods of development. Time periods are the ages of the birds measured in days and put into blocks: 20 to 25, 26 to 31, 32 to 37, and 38 to 44 days. The number of creates incidences that occurred for each jay was averaged for each age block. Then the two individual averages for the cohort members were averaged to give a creates average for the cohort during each age block.

The average number of hides tended to increase over time although this change was not statistically significant ($F_{3,9}$=3.6490, p=0.0571, see Figure 2.5). Different pairs developed this behavior at similar times ($F_{3,12}$=0.7318, p=0.5527) and changed over time at similar rates ($F_{3,12}$=1.1654, p=0.3934, see Figure 2.5). Birds within pairs developed hides similarly ($F_{4,12}$=1.6358, p=0.2289).

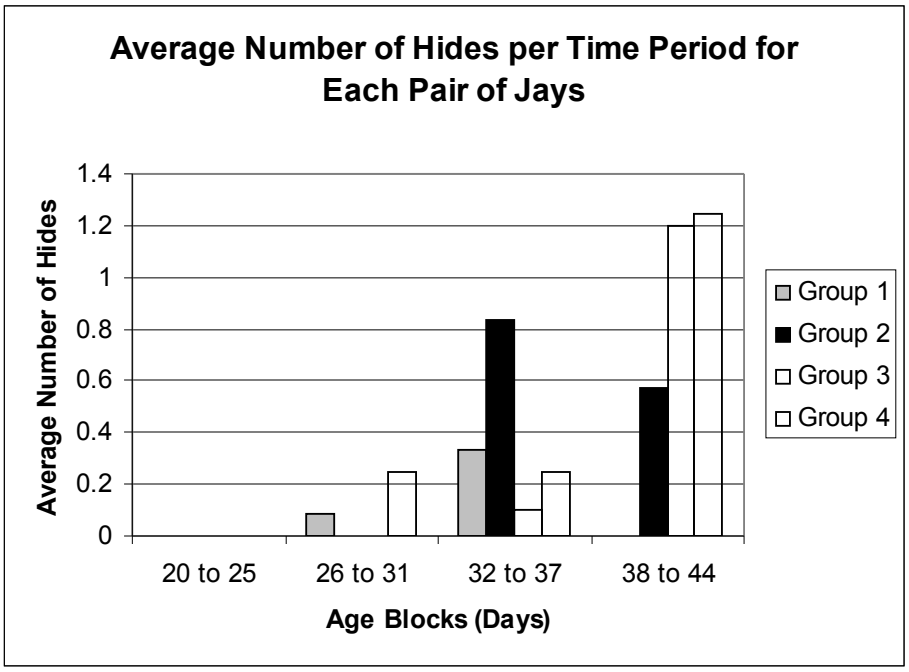

Figure 2.5 Average number of hides per pair of jays across four time periods of development. Time periods are the ages of the birds measured in days and put into blocks: 20 to 25, 26 to 31, 32 to 37, and 38 to 44 days. The number of hides incidences that occurred for each jay was averaged for each age block. Then the two individual averages for the cohort members were averaged to give a hides average for the cohort during each age block.

The average number of uncovers did not increase significantly over time ($F_{3,9}$=2.7927, p=0.1014, see Figure 2.6). Different pairs developed this behavior at similar times ($F_{3,12}$=0.9154, p=0.4626) and changed over time at similar rates ($F_{3,12}$=1.1086, p=0.4239, see Figure 2.6). Birds within pairs developed uncovers similarly ($F_{4,12}$=1.4228, p=0.2854).

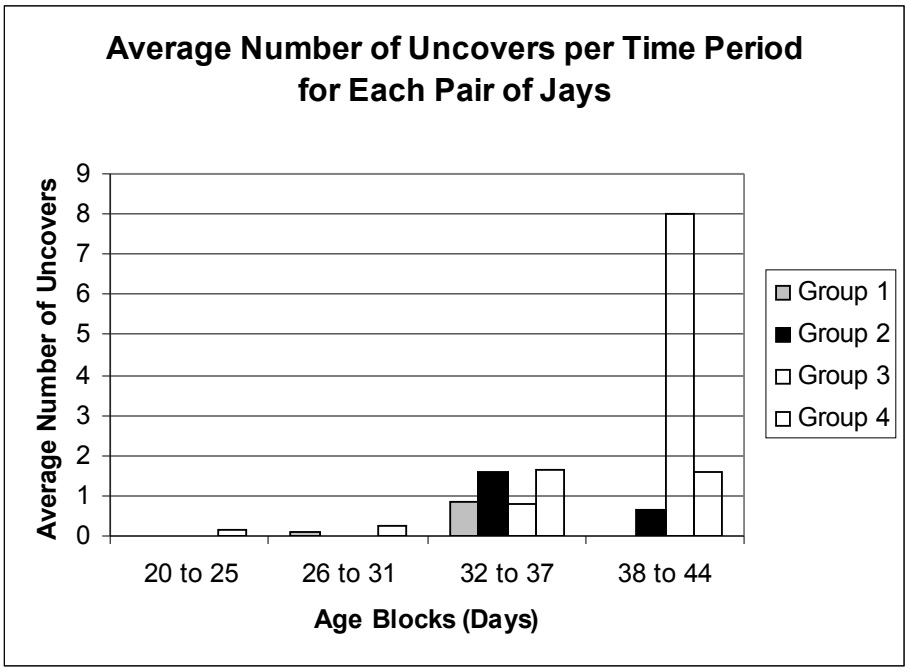

Figure 2.6 Average number of uncovers per pair of jays across four time periods of development. Time periods are the ages of the birds measured in days and put into blocks: 20 to 25, 26 to 31, 32 to 37, and 38 to 44 days. The number of uncovers incidences that occurred for each jay was averaged for each age block. Then the two individual averages for the cohort members were averaged to give an uncovers average for the cohort during each age block.

Discussion

The data from this experiment support the hypothesis that orphaned fledgling blue jays do not require demonstration to initiate the development caching behavior. Although the fledgling basket provided an environment more conducive for caching than did the nestling environment, it was not an ideal environment for blue jay caching. Blue jays store items in the ground (Johnson &Webb, 1989; Johnson & Adkisson, 1985; Scarlett & Smith, 1991; Laskey, 1942 & 1943) and the basket had a hard bottom in which jays were not able to store items, despite numerous observed attempts. Therefore, even in this environment, the manifestation of caching behavior still persists.

None of the cohorts failed to develop caching behavior. This evidence provides support for the hypothesis that caching behavior is a behavior birds learn to do on their own without being shown by an adult conspecific or caretaker. However, the cohort that provides the strongest support for the hypothesis that orphaned blue jays do not need to observe caching behavior for development to occur is the 2006 cohort (Cohort GH), which consisted of two birds who arrived at the Bird Center as hatchlings (eyes not yet open). Thus, these birds could not have seen parents or another animal displaying caching behavior.

Chapter 3

Development and Employment of Cache Defense Tactics

Introduction

Adult blue jays, like other members of Corvidae, display little territorial behavior towards conspecifics, and often a territory overlaps with other conspecifcs' territories (Stokes, 1979; Shank, 1986). Despite this, corvids are protective of their caches and implement various tactics to protect them from or deter pilfering (Heinrich & Pepper, 1998; Heinrich, 1999; Emery & Clayton, 2001; Bunyar & Kotrschal, 2002; Dally et al., 2005; Clayton et al., 2006). Corvids who have stolen cache items from a conspecific display greater caution and preference for privacy when caching items in the presence of conspecifcs (Clayton et al., 2006; Dally et al., 2005), such as waiting until an observing conspecific is distracted or conspecific viewing is obstructed (Clayton et al., 2006; Dally et al., 2005; Heinrich & Pepper, 1998; Heinrich, 1999), or recaching items sooner that were cached in the presence of an observing conspecific (Clayton et al., 2006; Dally et al., 2005; Emery & Clayton, 2001; Heinrich, 1999; Goodwin, 1955). Numerous studies have been conducted about cache defense behaviors in adult corvids and tactics that are employed to deter pilfering (Heinrich & Pepper, 1998; Bunyar & Kotrschal, 2002; Dally et al., 2005). Studies and observations about blue jay territorial behaviors (Stokes, 1979), as well as those of Steller jays (*Cyanocitta stelleri*; a close relative of the blue jay (*Cyanocitta cristata*)) have been described (Brown, 1963), but there is little to no published data regarding this in young blue jays. Therefore, it is not known whether or not fledgling blue jays utilize defense tactics to protect their own food hoards from

conspecifics. If they do in fact perform these behaviors, it is not known at what age these behaviors manifest themselves. Based on current housing criteria (blue jay housing criteria is the same as that for all songbirds) and preliminary observations, I hypothesized that young blue jays will not utilize cache defense tactics while in captivity. If the data do not support this hypothesis and it is found that orphaned fledgling blue jays do exhibit cache defense tactics while in captivity, then new housing criteria specific to blue jays should be considered as a means of reducing stress in captive blue jays.

Methods

For the purposes of this study, cache defense strategies employed by the cacher consisted of the following behaviors: *body posture*, *body block*, *attack*, *pursuit*, and *denial*. These behaviors were chosen as they have been used to describe typical territorial actions of wild blue jays or other members of the family Corvidae (Brown, 1963; Stokes, 1979; Heinrich and Pepper, 1998; Bugnyar and Kotrschal, 2002; Dally et al., 2005) and they could be easily quantified given the limited space the birds live in. These actions were associated with cache defense behavior only if the "cache defender's" aggressive behavior was preceded immediately by the "pilferer" raiding an established cache.

- *Body Posture: the "intruder" (or pilferer) exhibits body-fluff with raised crest, while the "territory-holder" (or cacher) exhibits a flattened crest, erect body posture and hops around the "intruder" (Stokes, 1979)*
- *Attacking: the cacher jumps on the pilferer and/or uses its beak to peck at the pilferer (Heinrich and Pepper, 1998)*

- *Body Blocking: the cacher places itself between the pilferer and the cache site preventing or discouraging the pilferer from gaining easy access to the cached item (Bugnyar and Kotrschal, 2002)*

- *Pursuit: the cacher proceeds to chase the pilferer after the pilferer has succeeded in taking a cached item either directly from the cacher or the cacher's cache site (Brown, 1963; Stokes, 1979; Bugnyar and Kotrschal, 2002).*

- *Denial: the cacher prevents or attempts to prevent the pilferer from taking a cached item (may also include tactics not previously described; Bugnyar and Kotrschal, 2002)*

Tapes were scored for the above cache defense strategies by marking a tick mark per event observed in the color of ink designated to that particular bird in the column with the heading pertaining to that specific behavior.

Ages of birds were put into blocks (Age Block 1: 20-25 days; Age Block 2: 26-31 days; Age Block 3: 32-37 days; and Age Block 4: 38-44 days). Starting age was analyzed with a bird(pair) x time block ANOVA. Development of each behavior was analyzed with a bird(pair) x behavior ANOVA. SPSS 15.0 and JMP-IN (version 3.2) were utilized for statistical analysis. Graphs were constructed using Sigma Plot 14.0 and Microsoft Office Excel 2003.

Results

A total of 24 days were recorded. One day was not recorded in 2007 for cohort AB due to an improperly charged battery. Two days were not recorded in 2007 for cohort EF due to an improperly charged battery. Orphaned fledgling blue jays do develop cache defense tactics without the presence of an adult conspecific. The average age of the onset of individual cache defense behaviors is shown in Figure 3.1. The chart

in Table 3.1 shows the observed starting ages (measured in days) for the various cache defense tactics that appeared in the individual birds.

Table 3.1.

Age At Which Each Cache Defense Tactic Was Observed in Each Bird. Age is measured in days. "NA" means the behavior was not observed during any of the recorded sessions.

Pair	Bird	Body Block	Pursuit	Attack	Denial
1	A	39	28	27	41
	B	24	28	24	28
2	C	34	34	36	34
	D	38	34	33	27
3	E	NA	41	41	29
	F	28	42	29	32
4	G	34	34	29	21
	H	31	29	21	24

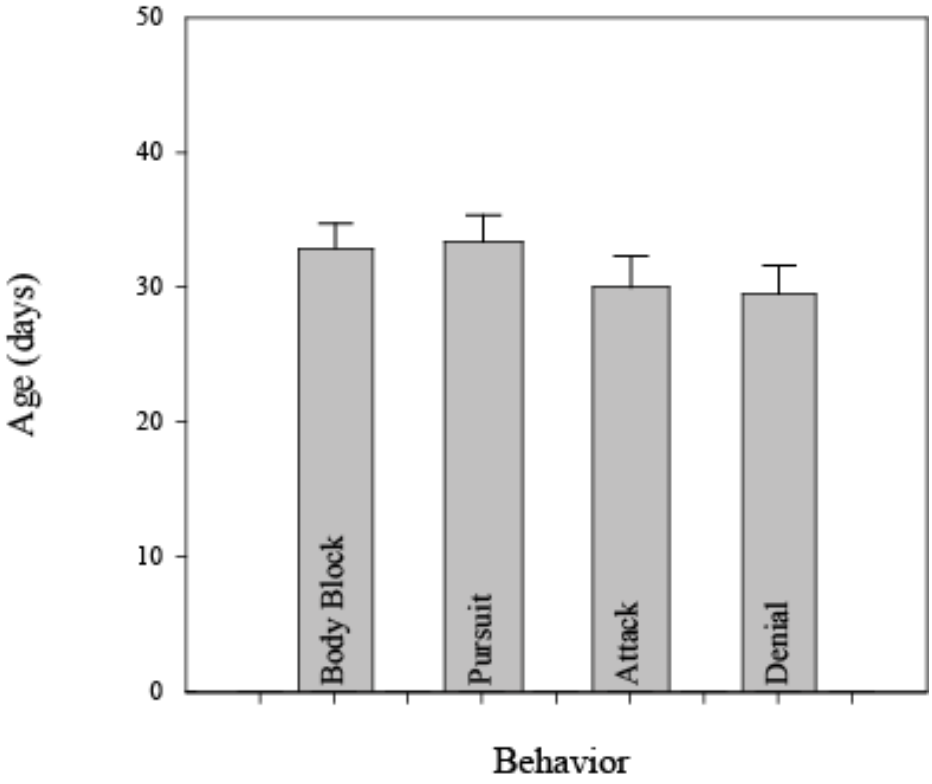

Figure 3.1 Average age when each of the cache defense tactics were first observed in orphaned fledgling blue jays. Age is measured in days.

None of the blue jays observed from 2006 or 2007 exhibited territorial/submissive body posture.

The average number of body blocks did not consistently increase over time ($F_{3,9}$=2.4162, p=0.1336, see Figure 3.2). Different pairs developed this behavior at similar times ($F_{3,12}$=0.2021, p=0.8930) and changed over time at roughly similar rates ($F_{9,12}$=0.6420, p=0.7435, see Figure 3.2). Birds within pairs similarly developed body blocks ($F_{4,12}$=1.6199, p=0.2327).

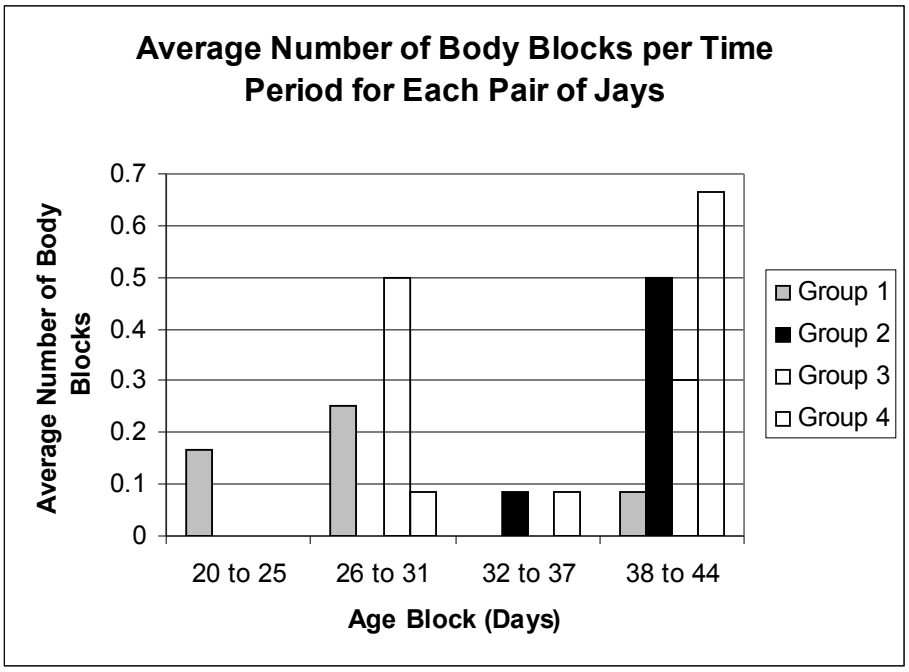

Figure 3.2 Average number of body blocks per pair of jays across four time periods of development. Time periods are the ages of the birds measured in days and put into blocks: 20 to 25, 26 to 31, 32 to 37, and 38 to 44 days. The number of body block incidences that occurred for each jay was averaged for each age block. Then the two individual averages for the cohort members were averaged to give a body blocks average for the cohort during each age block.

The average number of pursuits increased over time ($F_{3,9}$=5.1836, p=0.00236, see Figure 3.3). Different pairs tended to develop this behavior at different times ($F_{3,12}$=3.1357, p=0.0654) but changed over time at similar rates ($F_{9,12}$=1.7232, p=0.1873, see Figure 3.3). Birds within pairs developed pursuits similarly ($F_{4,12}$=1.3493, p=0.3082). A pairwise comparison was conducted to see the effect age had on pursuit. Age blocks 2 (26-31 days), 3 (32-37 days), and 4 (38-44 days) were analyzed, as the behavior did not develop during Age Block 1 (20-25 days). No significant effect was found for increasing pursuit activity related to any age block.

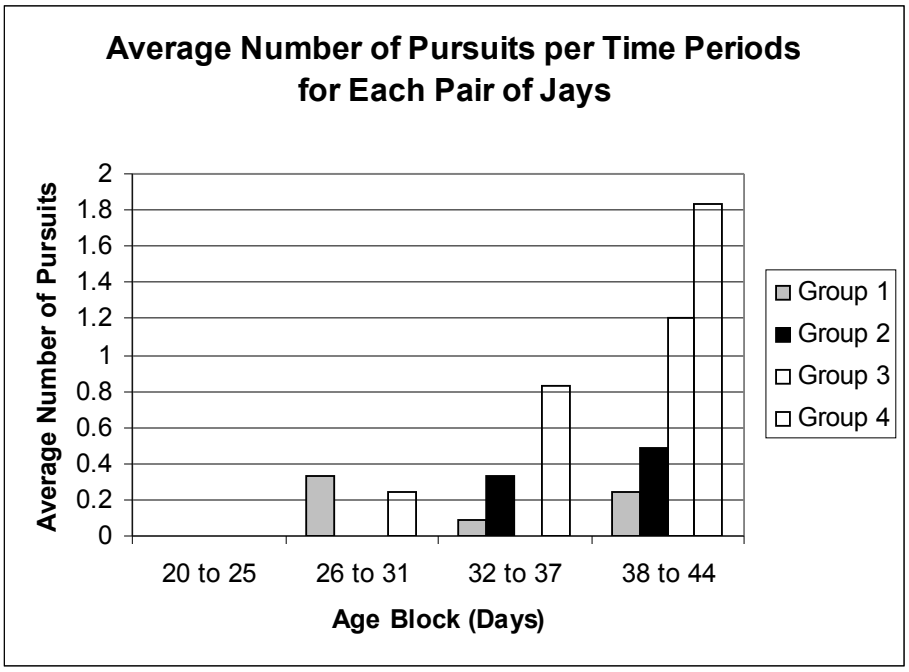

Figure 3.3 Average number of pursuits per pair of jays across four time periods of development. Time periods are the ages of the birds measured in days and put into blocks: 20 to 25, 26 to 31, 32 to 37, and 38 to 44 days. The number of pursuit incidences that occurred for each jay was averaged for each age block. Then the two individual averages for the cohort members were averaged to give a pursuits average for the cohort during each age block.

The average number of attacks did not increase over time ($F_{3,9}$=0.5397, p=0.6669, see Figure 3.4). Different pairs developed this behavior at different times ($F_{3,12}$=8.3589, p=0.0029) and changed over time at different rates ($F_{9,12}$=5.5434, p=0.0038, see Figure 3.4). Birds within pairs differed in their development of attack behavior ($F_{4,12}$=4.7845, p=0.0154).

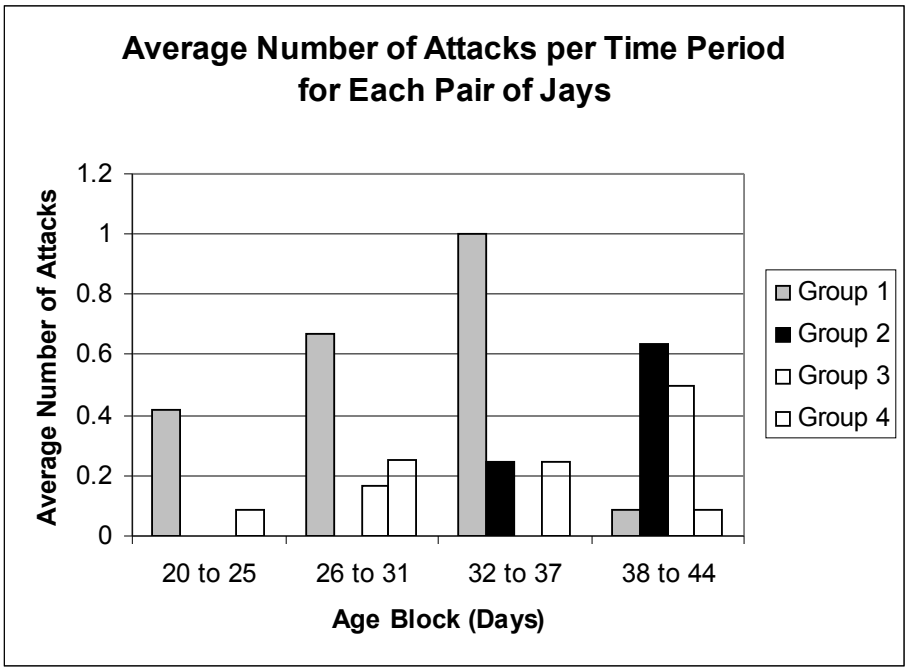

Figure 3.4 Average number of attacks per pair of jays across four time periods of development. Time periods are the ages of the birds measured in days and put into blocks: 20 to 25, 26 to 31, 32 to 37, and 38 to 44 days. The number of attack incidences that occurred for each jay was averaged for each age block. Then the two individual averages for the cohort members were averaged to give an attack average for the cohort during each age block.

The average number of denials increased over time ($F_{3,9}$=7.1325, p=0.0094, see Figure 3.5). Different pairs tended to develop this behavior at different times ($F_{3,12}$=3.4490, p=0.0516) but changed over time at similar rates ($F_{9,12}$=1.0509, p=0.4570, see Figure 3.5). Birds within pairs developed denial behavior on similar schedules ($F_{4,12}$=0.4431, p=0.7754). A pairwise comparison was conducted to see the effect age had on denial. Age blocks 2 (26-31 days), 3 (32-37 days), and 4 (38-44 days) were analyzed, as the behaviors did not develop during Age Block 1 (20-25 days) for any other pair other than Group 4 (Cohort GH from 2006). No significant effect was found for increasing denial activity related to any age block.

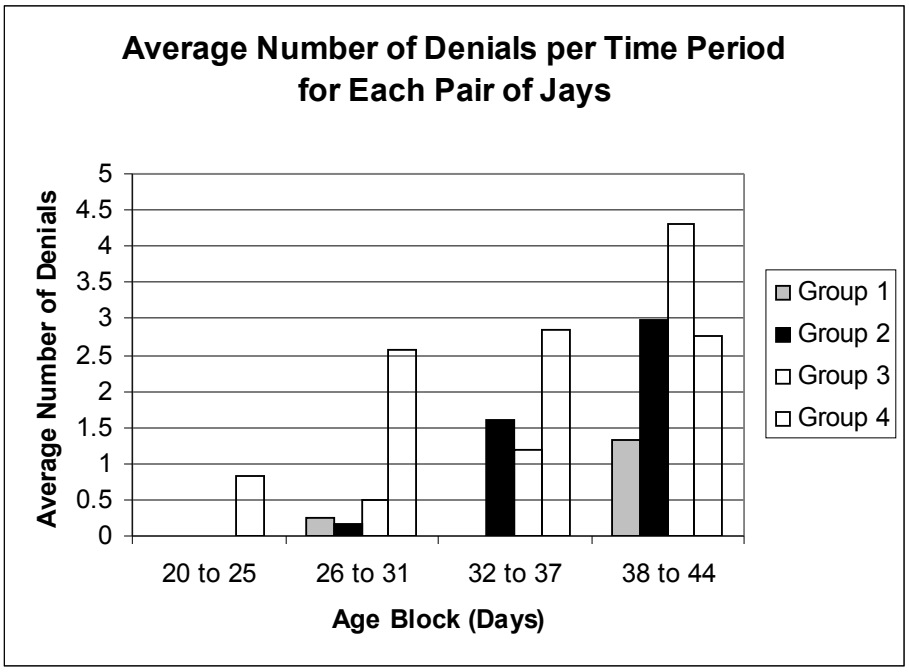

Figure 3.5 Average number of denials per pair of jays across four time periods of development. Time periods are the ages of the birds measured in days and put into blocks: 20 to 25, 26 to 31, 32 to 37, and 38 to 44 days. The number of denial incidences that occurred for each jay was averaged for each age block. Then the two individual averages for the cohort members were averaged to give a denial average for the cohort during each age block.

Discussion

None of the cohorts from 2006 or 2007 exhibited territorial or submissive body posture. This might mean that the jays were still too young to have displayed this behavior yet or that this behavior is learned via observation of adult conspecific. Further research should be conducted to determine when these behaviors develop in wild-raised fledgling blue jays.

Observations from this experiment provide evidence that orphaned fledgling blue jays do exhibit cache defense strategies while in captivity, thereby refuting the earlier stated hypothesis that orphaned fledgling blue jays will not exhibit cache defense strategies. Orphaned fledgling blue jays do indeed exhibit cache defense tactics against cohort members who attempt or succeed at pilfering a cache site. It has been statistically shown that the number of pursuits and denials by basketmates increases over time, suggesting that the young jays are becoming increasingly more territorial about their caches. Changes in housing standards for developing blue jays should be considered, although additional research should be conducted to determine what specific changes in housing standards would be most beneficial to blue jays.

Jays did steal from each other. This could be perceived as a benefit since corvids who are thieves themselves are more cautious to cache in secret than naïve corvids who do not exhibit a preference for caching in the presence of conspecifics or in secret (Dally et al., 2005). Housing fledgling blue jays with at least one other conspecific while in rehabilitation could reduce the number of naïve orphaned blue jays released back to the wild. Further research is needed to determine if the benefits of being a thief outweigh the risks exposing jays to additional stress of basketmates employing cache defense tactics.

Either way, new housing criteria specific for blue jays (and perhaps all corvids) should be considered.

Future studies could include the monitoring of re-caching of food, as this was a quantifiable behavior that was frequently observed but not recorded.

Chapter 4

Cache Site and Cache Item Sharing

Introduction

Food sharing (food given by one bird to another) is a common social behavior performed between related, paired, and non-related same-sex birds (de Kort, Emery & Clayton, 2003; de Kort, Emery & Clayton, 2006). Evolutionary theory explains this behavior performed between related or paired birds as being related to inclusive fitness or courtship feeding behaviors, respectively. However, apparent altruistic feedings between non-kin, same-sex birds garnered attention recently because such behaviors do not appear to result immediately in genetic endurance or proliferation. Instead, food sharing behaviors involving such circumstances are thought to improve survivorship by facilitating coalition formation, increasing social prestige and decreasing harassment (de Kort et al., 2003; Stevens & Hauser, 2004; von Bayern et al., 2007). In this context, food sharing behaviors would be rendered mutualistic interactions rather than altruistic (de Kort et al., 2003; Stevens & Hauser, 2004; de Kort et al., 2006; von Bayern et al., 2007).

Although food sharing behavior is commonly observed in adult blue jays, the same birds do not share cache sites. It is not known whether these behaviors occur in fledgling blue jays. The present experiment monitored behavior to determine if orphaned fledgling blue jays share cache sites and display food sharing behavior. Furthermore, this study will determine the age at which these behaviors occur and, importantly, the circumstances under which such behaviors occur (either prompted or unprompted by a begging basket mate). Since mutalistic sharing is a social behavior that occurs in many

birds (von Bayern et al., 2007), it is possible that young blue jays will not exhibit this behavior until after they have joined a flock and been exposed to normative social behaviors among wild-raised blue jays. In summary, the goal of this study is to discover *if* and *when* cache site and cache item sharing behavior manifest themselves in young blue jays. I hypothesized that orphaned fledgling blue jays will not share cache items or cache sites with cohort members. Although speculative, it could be hypothesized that because food sharing is a social behavior, baby blue jays will not develop it because they are not exposed to adult conspecifics or "normal" social interactions (beyond their cage mates) in a rehabilitation (artificial) setting compared to their natural environment (Brown, 1963; von Bayern et al., 2007).

Methods

For the purposes of this study, site sharing behavior is defined as the simultaneous display of caching-related behaviors (*moves, removes, creates, hides, uncovers*) by both basketmates the same cache site, provided that these behaviors do not result in theft or any cache defense behaviors (*body posture*, *body blocking*, *pursuit*, *attacking*, and *denial*). The start time was marked when both jays began a cache activity together, and the end time was marked when one or both birds discontinued the activity. Dependent measures include the frequency and duration of these behaviors.

Cache item sharing was defined as any of the following three behaviors: *tolerated theft*, *prompted giving,* and *active giving*. These behaviors required two participants, the beneficiary (i.e. the bird receiving the item) and the cacher (i.e. the bird that initially hid the item). The following criteria were utilized to identify cache item sharing:

- *Tolerated theft: The beneficiary takes a cache item directly from the cacher*

without consequence (the cacher does not body block, attack, pursue, or deny the other bird the item; de Kort et al., 2003)

- *Prompted Giving: The beneficiary begs for an item that the cacher has and the cacher gives it to the beneficiary (de Kort et al. , 2003)*
- *Active Giving: The cacher gives the beneficiary an item it does not beg for (de Kort et al., 2003)*

A tick mark was noted each time the cacher tolerated theft or shared items with the beneficiary. Only incidences involving items that were being or were cached were marked. The sharing of items not associated with cache sites (i.e. food taken directly from the food dish) was not scored.

Additional measures were taken concerning the number of seconds birds spent sharing a cache site. The onset of this behavior was demarcated when both jays started creating a cache site together, taking turns moving an item in and out of the same site, provided that such behaviors did not result in theft and were not interrupted by the exhibition of cache defense tactics. The end of this behavior was demarcated when one or both birds left the site *or* if one of the jays directed behavior to an object not associated with the cache site.

The dependent measures described above were compared as a function of age and between groups (i.e. bird pairs). Bird ages were separated into 4 blocks (Age Block 1: 20-25 days; Age Block 2: 26-31 days; Age Block 3: 32-37 days; and Age Block 4: 38-44 days). Starting age was analyzed with a bird(pair) x behavior ANOVA. Development of each behavior was analyzed with a bird(pair) x time block ANOVA. Statistical analyses were performed using SPSS 15.0 and JMP-IN (version 3.2). Graphs were constructed with Sigma Plot 14.0 and Microsoft Office Excel 2003.

Results

A total of 24 days were recorded. One day was not recorded in 2007 for cohort AB due to an improperly charged battery. Two days were not recorded in 2007 for cohort EF due to an improperly charged battery.

Orphaned blue jays were observed sharing cache sites and cache items with cohort members. The average age at which sharing first appeared in blue jays was at 29.63 days of age. The earliest age at which this behavior was displayed was 24 days and the latest age was 34 days of age. Table 4.1 shows the various ages at which the sharing of cache items occurs.

Table 4.1. *Age At Which Each Sharing/Tolerating Behavior Was First Observed. Ages are measured in days. "NA" means that the behavior was not ever observed for that individual bird.*

Pair	Bird	Tolerated Theft	Prompted Giving	Active Giving
1	A	28	29	29
	B	39	38	32
2	C	34	40	NA
	D	27	31	33
3	E	34	NA	NA
	F	33	NA	NA
4	G	25	NA	38
	H	24	NA	41

The youngest ages for beginning to share or tolerate theft was 24 and 25 days of age (jays G and H, respectively, for tolerating theft). The oldest ages were 47 and 42 days (jays D and H, respectively, for giving to a begging cohort member). Jays E, F, and G did not display prompted giving nor did they ever actively give to a cohort member who was not begging. Cohort EF spent far less time (37 seconds total) and had far fewer sharing events (three total) than any of the other cohorts, as seen in Table 4.2.

Table 4.2. *Summary of Observed Cohort Cache Site Sharing. Time is measured in seconds.*

Bird Pair/Cohort	Total Number of Observed Caching Events	Total Observed Time Spent Sharing a Cache Site	Average Time Spent per Sharing Event
Pair 1 (Cohort AB)	15	144	9.6
Pair 2 (Cohort CD)	33	285	8.64
Pair 3 (Cohort EF)	6	37	6.17
Pair 4 (Cohort GH)	72	538	7.47

Tolerance for basketmate theft of cache items varied across the 29-day period the blue jays were in the fledgling baskets. Not only was tolerance variable on a day-to-day basis, but so was giving cache items to a begging basketmate (initiated giving), as well as giving to a basketmate who was not begging (active giving), as seen in Figures 4.1, 4.2, and 4.3.

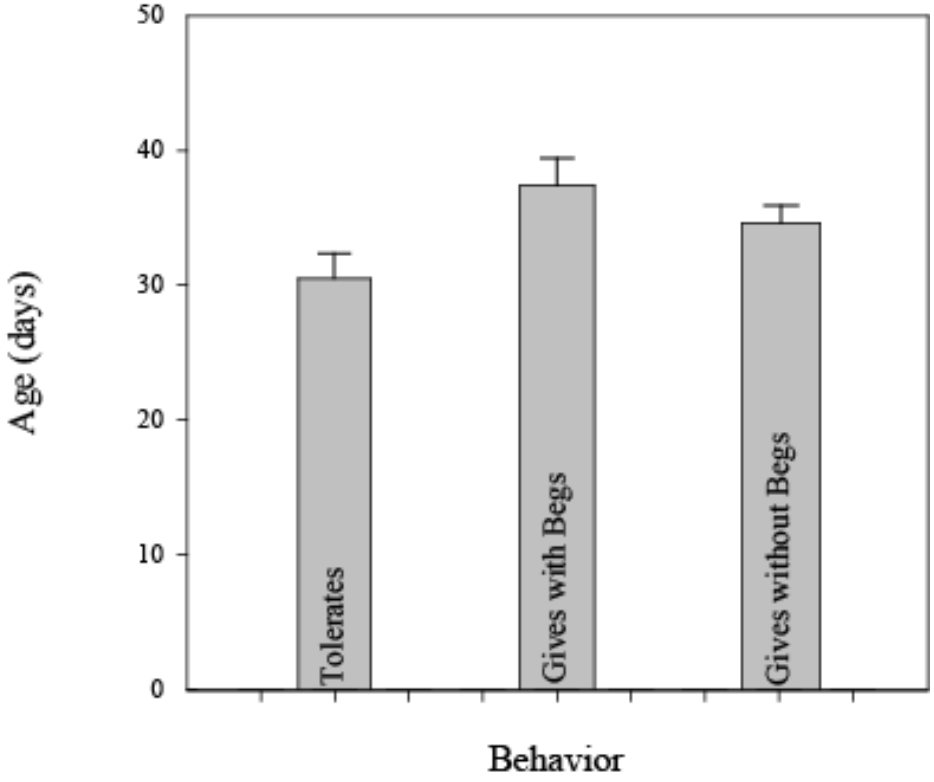

Figure 4.1 Average age of when each cache item sharing behavior was first observed in orphaned fledgling blue jays. Age is measured in days.

The average number of tolerance activities increased over time ($F_{3,9}$=6.7848,

p=0.0110, see Figure 4.2). Different pairs developed this behavior at different times ($F_{3,12}$=10.9399, p=0.0009) and changed over time at different rates ($F_{9,12}$=4.0900, p=0.0131, see Figure 4.2). Birds within pairs had similar development patterns of tolerance ($F_{4,12}$=2.0374, p=0.1529).

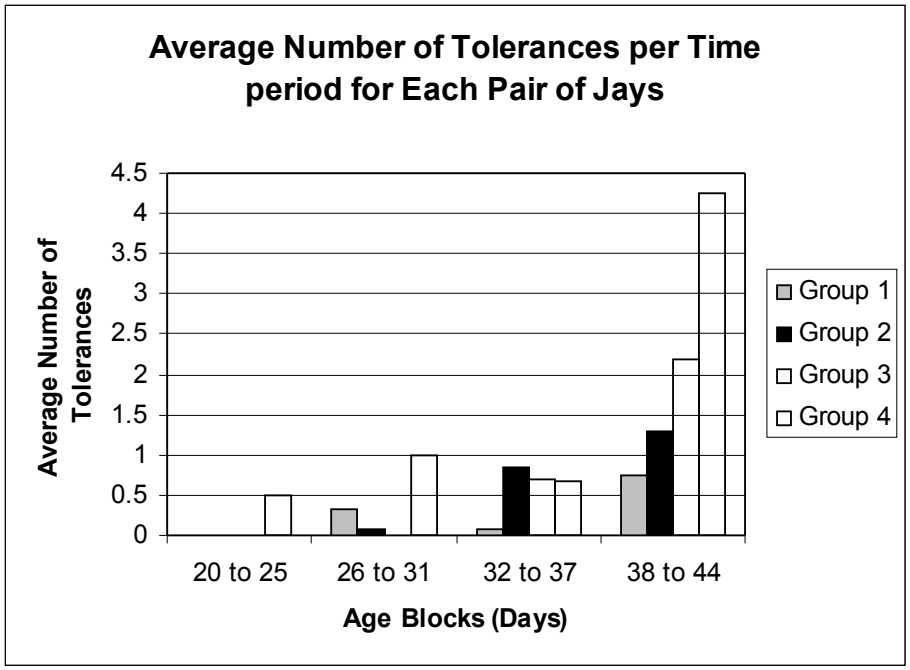

Figure 4.2 Average number of incidences of tolerated theft per pair of jays across four time periods of development. Time periods are the ages of the birds measured in days and put into blocks: 20 to 25, 26 to 31, 32 to 37, and 38 to 44 days. The number of tolerated theft incidences that occurred for each jay was averaged for each age block. Then the two individual averages for the cohort members were averaged to give a tolerated theft average for the cohort during each age block.

The average number of prompted giving activities did not increase consistently over time ($F_{3,9}$=2.1750, p=0.1608, see Figure 4.3). Different pairs developed this behavior at roughly similar times ($F_{3,12}$=1.7570, p=0.2087) and changed over time at similar rates ($F_{9,12}$=0.5743, p=0.7945, see Figure 4.3). Birds within pairs developed prompted giving similarly ($F_{4,12}$=1.8349, p=0.1870).

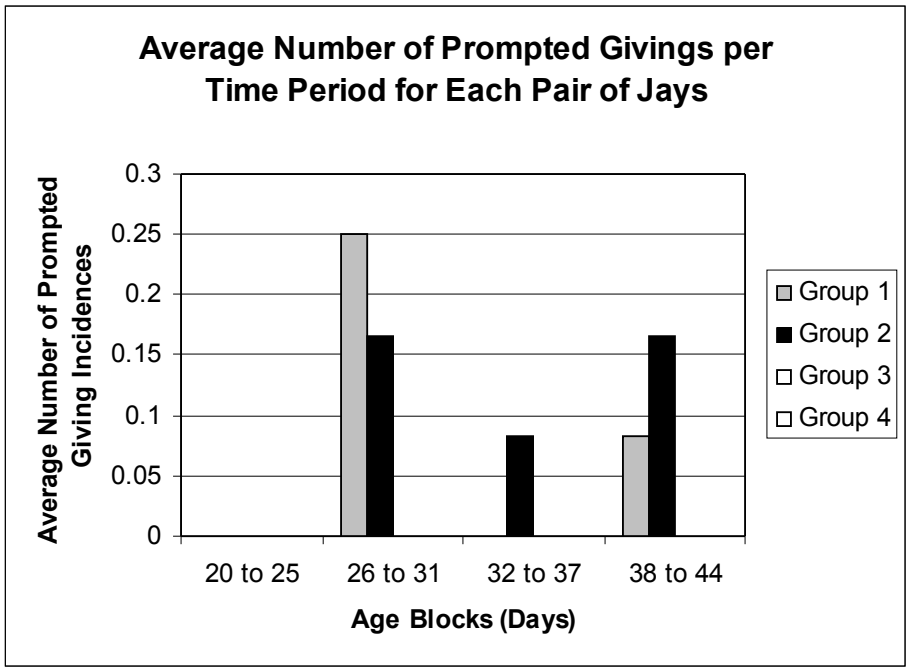

Figure 4.3 Average number of incidences of prompted giving activities per pair of jays across four time periods of development. Time periods are the ages of the birds measured in days and put into blocks: 20 to 25, 26 to 31, 32 to 37, and 38 to 44 days. The number of prompted giving incidences that occurred for each jay was averaged for

each age block. Then the two individual averages for the cohort members were averaged to give a prompted giving average for the cohort during each age block.

The average number of active giving activities did not increase consistently over time ($F_{3,9}$=2.7134, p=0.1074, see Figure 4.4). Different pairs developed this behavior at similar times ($F_{3,12}$=2.0014, p=0.1676) and changed over time at similar rates ($F_{9,12}$=0.8205, p=0.6095, see Figure 4.4). Birds within pairs had similar development patterns for active giving ($F_{4,12}$=0.3044, p=0.8695).

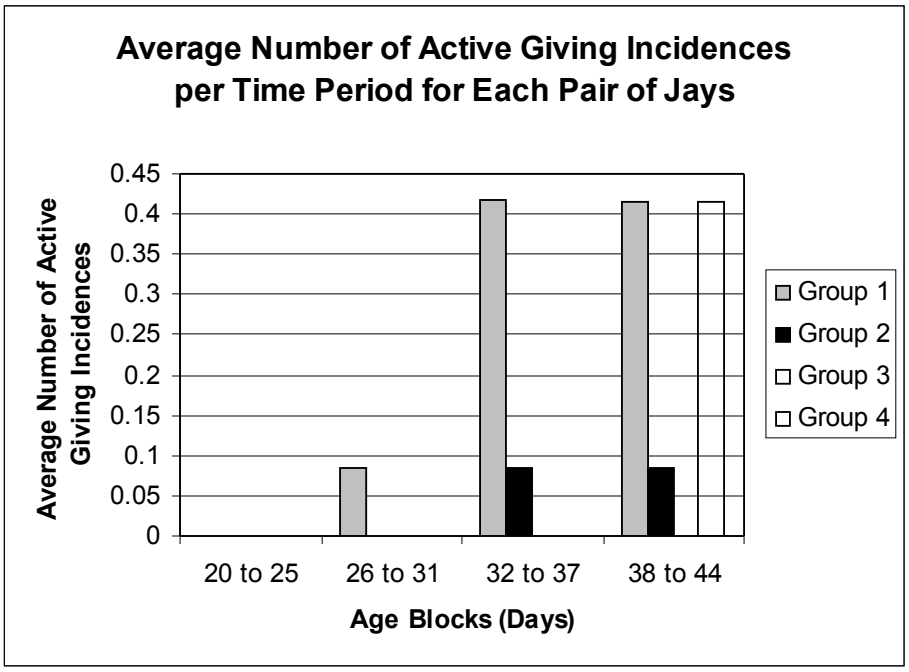

Figure 4.4 Average number of incidences of active giving activities per pair of jays across four time periods of development. Time periods are the ages of the birds measured in days and put into blocks: 20 to 25, 26 to 31, 32 to 37, and 38 to 44 days. The number of active giving incidences that occurred for each jay was averaged for each age block. Then the two individual averages for the cohort members were averaged to give an active giving average for the cohort during each age block.

Discussion

Data from this experiment do not support the hypothesis that orphaned fledgling blue jays fail to share cache sites, as all cohorts participated in creating or maintaining at least one cache site with their basketmate. This study represents the first time such behaviors have been described in fledgling blue jays. The present data were collected in an artificial environment to facilitate rehabilitation. Presently, there are little to no data describing this behavior in blue jays raised in their natural environment. Therefore, it remains unknown whether the expression of this behavior represents a by-product of captive rearing conditions. If this behavior is exclusive to captive-raised blue jays, it is not known how this behavior impacts juvenile blue jay survival upon release. The frequency with which fledgling blue jays shared cache items was less consistent between pairs. There were no discernable variables that would explain why some birds showed this and some did not. Initial hypotheses regarding this variability focused on the relatedness of basket mates. However, whether birds shared cache items with their basketmates was not contingent on whether the birds were related.

Chapter 5

General Discussion

Summary of Behavioral Results

This thesis represents the first time that the development of caching behavior has been described in fledgling blue jays. All jays developed all the components of caching behavior. These behaviors developed in the absence of adult conspecifics indicating that the presence of adult conspecifics was not necessary for its development. Furthermore, whether or not birds developed caching behavior was not contingent upon the ages at which they entered rehabilitation. All birds developed some form of cache defense tactics. All jays displayed some form of cache site sharing. In addition to sharing cache sites, all birds displayed tolerance behavior, which increased over time. Only half of the cohorts shared cache items when prompted to by a begging basketmate, and a little more than half (five out of eight) of the jays gave cache items to basketmates who did not beg for them. The average number of pursuit and denial activities increased over time. In the developmental time course of caching behavior, all birds displayed at least one component no later than age 30 days. This age may therefore represent a bench mark by which fledgling jays should begin to display behaviors related to caching. Despite the presence of all these cache-related behaviors, it was curious to note that none of the jays displayed submissive body postures. The theoretical and practical implications of these findings are discussed below.

Theoretical Implications

It's possible that increasing complexity of the jays' behavioral repertoire over the course of development may be a function of cognitive maturation and the development of higher levels of object permanence--the cognitive state in which an individual understands that an object continues to exist even after it is no longer visible (Piaget, 1954; Pollock et al., 2000; Zucca, Milos & Vallortigara, 2007). However, it is logical that an organism would undergo this maturation if it participates in food hoarding and has demonstrated excellent recall capacity for cache retrieval (Pollok et al., 2000; Clayton et al., 2001; Bugnyar & Kotrschal, 2002). Additional research would need to be done before it could be firmly established that blue jays are indeed developing higher levels of object permanence.

The increase in the number of pursuits and denials over time suggests that jays are becoming more territorial about caches with increasing age. It is not known if these developmental trends for captive-raised blue jays parallel those in wild-raised conspecifics or if these increases are a by-product of captive conditions. It is not known exactly why body posture behavior was not observed. It may be that jays do not utilize this tactic until they are much older, or it may be something that is learned through social interactions with other jays that perform body posture. It is not known at what age body posture develops in wild-raised blue jays.

It is interesting to consider the factors determining whether birds shared cache items with basketmates. Evolutionary theory regarding survivorship would predict that related birds are more likely to share cache items with begging basketmates than non-related birds; however, the current data do not support this hypothesis. Both of the non-

sharing cohorts are considered related (Cohort EF from 2007 and Cohort GH from 2006), whereas of the sharing cohorts, one was considered related (Cohort AB from 2007) and one was not (Cohort CD from 2007). Thus, it is not known why birds did not share cache items when prompted to by begging and the factors dictating food sharing behavior between birds remain to be determined.

However, one factor that may determine the occurrence of sharing behavior is the frequency of theft tolerance. It should be noted that among all the cohorts, the non-sharing cohorts (EF and GH) also displayed more tolerance behavior than the sharing cohorts (AB and CD). It may be that more tolerance results in fewer sharing events. A larger sample size and a correlation analysis between these variables would be required to be conducted to substantiate this claim.

A separate factor contributing to the presence of this behavior is gender. Since the sex of the birds was not determined (as presence of a brood patch or behavior during nesting period are the only reliable methods of sex determination in blue jays [outside of genetic testing], and neither would have been present in fledgling blue jays; Steel & Hinde, 1964; Tarvin &Woolfenden, 1997; Massaro, Davis & Davidson, 2006), this may have been a unique combination of sexes of all the cohorts. Sex may have influence on sharing activity, and further research could be conducted to find out.

Implications for Bird Rehabilitators

Caching behavior in blue jays is thought to be critical to survival, and a failure to develop this behavior during rehabilitation would potentially lead to increased mortality upon release into the wild. The present data provide a starting point for the identification

of developmental benchmarks that can be used by song bird rehabilitators for determining the developmental health of jays, and thus their suitability for release. Songbird rehabilitators should expect orphaned blue jays in their care to begin performing caching behaviors (e.g. screen separation from basket; holes punctured in screen; perch, food and other items accumulating outside the fledgling basket) at no later than 30 days of age. On average, these behaviors occurred in the following order 1) creates 2) moves/removes 3) uncovers/hides. Although jays did not display submissive posturing, this behavior is possibly acquired later during social interactions, and the degree to which this behavior affects survivorship is considerably less obvious.

Furthermore, songbird rehabilitators can expect to see some attacking behavior between basketmates; however, the occurrence of this behavior is subject to more variability between jays and does not appear to increase as jays age. Thus, the presence of attacking behavior may not be an accurate predictor of developmental health.

Blue jays share many behavioral characteristics with other members of the family Corvidae. For example, blue jays and Steller jays (*Cyanocitta stelleri*) both exhibit caching behavior, live in similar (although geographically distinct) habitats, reach sexual maturity at the same age, and have approximately the same lifespan. In the absence of data describing normal development in Steller jays, the present data could be applied to closely related species for the purposes of facilitating rehabilitation, until species-specific data are available. Further research should be conducted to see if the present findings extend to other members of the family Corvidae to determine if other species would also benefit from having similar housing and release criteria.

In summary, the present thesis has described a developmental time course in

orphaned, fledgling blue jays. Although interpretation of these data are hindered by experimental limitations (i.e. not controlling for gender, no follow-up to determine survivorship), they broaden the body of knowledge available to rehabilitators to determine the suitability of blue jays for release.

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