6-11-2021 2:00 PM

Food Caching Decisions in Canada Jays (Perisoreus canadensis)

Robert J. Martin, *The University of Western Ontario*

Supervisor: Sherry, David F., *The University of Western Ontario*
Co-Supervisor: Morbey, Yolanda E., *The University of Western Ontario*

A thesis submitted in partial fulfillment of the requirements for the Doctor of Philosophy degree in Biology

Recommended Citation
Martin, Robert J., "Food Caching Decisions in Canada Jays (Perisoreus canadensis)" (2021). *Electronic Thesis and Dissertation Repository*. 7823.
https://ir.lib.uwo.ca/etd/7823

Abstract

Food scarce periods pose serious challenges for birds, particularly when those periods coincide with demanding life history stages such as overwintering. For resident birds in the Northern hemisphere, resource scarcity typically occurs simultaneously with winter conditions. In order to combat these compounded stressors, some species cache food to ensure a reliable supply of resources. Food caching is the storing of food items for subsequent retrieval and consumption after some delay. Canada Jays (*Perisoreus canadensis*) are year-round residents of the North American boreal forest and some high elevation areas in the United States, and cache food to combat resource scarcity. Additionally, Canada Jays use cached food to supplement their offspring, making food caching essential for both adult and offspring survival. This thesis explores the decisions Canada Jays make during both the resource acquisition, *what food to cache*, and cache deposition, *where to cache that food*, stages of caching. I addressed four specific questions: 1) Do Canada Jays demonstrate cache-site preferences and if so, what information is used to assess site quality, 2) Do Canada Jays employ context-specific cache defense strategies based on risk of cache pilferage, 3) Can Canada Jays anticipate predictable food shortages and alter their behaviour to account for them, and 4) Do Canada Jays attend to the macronutrient contents of their caches, and do they manipulate these nutrients to improve their current or future state. To answer these questions, I maintained a population of captive Canada Jays, and developed specific foraging paradigms to assess their behaviour. I found that Canada Jays make decisions at both the resource acquisition and cache deposition phases of caching. I provide evidence that Canada Jays identify and exploit conifers as cache locations and suggest an empirical explanation for observed distribution trends. I also show that birds successfully employ context-specific cache defense strategies, and that Canada Jays modulate the macronutrient contents of their caches to meet specific macronutrient targets. Canada Jays did fail, however, to plan for food restriction on a short time scale. Overall, I suggest that Canada Jays employ a variety of behavioural tactics to ensure the security of their cached food.

Keywords

food caching, foraging, cache-rot, cache-preservation, cache-defense, cache-pilferage, future planning, macronutrients, Canada Jay, corvid, cache-site selection, cache-item selection, resource acquisition

Summary for Lay Audience

Many birds that spend the winter months in North America are faced with long periods of limited environmental food availability. For many of these species, ensuring a consistent supply of food during these times begins long before the winter. Food caching, or food storing, is the process of storing food throughout the environment so that it can be retrieved at a later time. For species that face food scarce winter conditions, food caching typically occurs in the fall when food is abundant. One species that relies of food caching to endure the winter months is the Canada Jay. Canada Jays live in North America year-round, and thus have to endure food scarce winters. Because cached food is essential to their survival, Canada Jays have likely developed behaviours in order to increase their caching success. That is, Canada Jays should make decisions that favour the future availability of their caches. In this thesis, I examined these decisions at two stages: 1) resource acquisition, or what food to cache, and 2) cache-deposition, or where to cache it. I examined the ability of Canada Jays to select cache sites that have known preservative properties, their ability to hide caches from potential cache-robbers, and their ability to predict future food restriction and to plan for it. I also examined their attentiveness to the nutrient contents of their caches and compared that to the nutrient contents of the food they chose to eat. In general, Canada Jays made decisions that benefited their survival. They readily identified and selected cache-sites known to preserve caches, and successfully hid cached food from potential cache-robbers. They also demonstrated an attentiveness to the nutrients they were both caching and consuming, and demonstrated an ability to ensure appropriate nutrients were being cached for later consumption. Canada Jays failed to plan for food restriction on a short time scale, however. Overall, these decisions and behaviours are a positive indication that Canada Jays are well suited to combat the challenging conditions associated with North American winters.

Co-Authorship Statement

All data chapters were completed under the supervision of Drs. David F. Sherry, and Yolanda E. Morbey. Dr. Sherry provided funding for and will co-author all chapters. All works benefited from informal feedback from Drs. Y.E. Morbey, E.A. MacDougall-Shackleton, and W.A. Roberts, as well as from members of the Advanced Facility for Avian research, as well as the Guglielmo, Hobson, Morbey and Sherry Lab Groups.

A version of Chapter 2 will be submitted for publication. Dr. David F. Sherry and Matthew Fuirst are co-authors. RJM co-conceived of the project, designed, constructed and carried out the experiment, analyzed the data and wrote the manuscript. MF co-conceived of the project, contributed to experiential design and setup, and provided comments on manuscript drafts. DFS provided input on experimental design, made comments on manuscript drafts, and provided funding for the project. Order of authorship; RJM, MF, DFS.

A version of Chapter 3 has been submitted for publication to *Animal Behaviour* and is currently under review [ANBEH-D-21-00018]. Dr. David F. Sherry will be a co-author. RJM conceived of the project, designed, constructed and carried out the experiment, analyzed the data and wrote the manuscript. DFS provided input on experimental design, made comments on manuscript drafts, and provided funding for the project. Order of authorship; RJM, DFS.

A version of Chapter 4 has been submitted for publication to *Biology Letters* and is currently under review [RSBL-2021-0210]. Drs. David F. Sherry and William A. Roberts, and Glynis K. Martin will be co-authors. RJM co-conceived of the project, designed, constructed and carried out the experiment, analyzed the data and wrote the manuscript. GKM assisted in experimental setup, data collection and provided comments on manuscript drafts. WAR co-conceived of the project, provided input on experimental design and gave feedback on manuscript drafts. DFS provided input on experimental design, made comments on manuscript drafts, and provided funding for the project. Order of authorship; RJM, GKM, WAR, DFS.

A version of Chapter 5 will be submitted for publication. Drs. David F. Sherry and Morag F. Dick will be co-authors. RJM conceived of the project, designed and carried out the experiment, analyzed the data and wrote the manuscript. MFD provided insight into physiological mechanisms responsible for observed behaviours, input into statistical analysis and provided comments on manuscript drafts. DFS provided input on experimental design, made comments on manuscript drafts, and provided funding for the project. Order of authorship; RJM, MFD, DFS.

All chapter statuses are current as of the time of submission. All chapters have been edited and adapted to meet the formatting requirements of this thesis.

Acknowledgments

First and foremost, I want to thank Dr. David Sherry. Over the past six years I could not have asked for a more supportive and engaged supervisor and mentor. I would not be near the scientist I am today without the time and effort you dedicated to my development. Your lab has always been a welcoming place, and I will be forever grateful that I was able to be a part of it.

To my co-supervisor Dr. Yolanda Morbey and to my advisory committee, Drs. Beth MacDougall-Shackleton and Bill Roberts. Thank you for your input and advice. I hope this thesis does justice to the time and effort you all have put in to make me a better researcher and is evidence of the way each of you have shaped my thinking about science.

Matt Fuirst, Glynis Martin and Drs. Morag Dick, Bill Roberts and David Sherry, my co-authors. Thank you for contributing to my scientific growth and the success of my research.

Working at AFAR has exposed to numerous special people. First, Francis Boon. I relish my self-proclaimed title, ‘biggest nuisance to Francis’. Thank you for everything you have done to make this research possible. Also, I want to apologize for the heart attack I very nearly gave you when you thought we were just playing a casual game of squash. My bad. Second, to Michela Rubeli. The work you do keeps the building open. Nothing would happen without your dedication. Third, the members of the Guglielmo, Hobson, and both MacDougall-Shackleton labs over the years: thank you for creating such an amazing place to work, learn and spend my time. Lastly, to my amazing volunteers and work study students; this would not have been possible without you.

To the members of the Sherry Lab, past and present: thank you, all of you. Caroline Strang, aside from David you have had the biggest influence on my scientific views. I thank you for many things, but for now I will be (sarcastically) bitter that you were not here to bring me brownies and diet coke while I was writing. Maddie Brodbeck.

You experienced this whole journey right along with me. I could not have done it without you, and frankly, I would not have wanted to (would've skipped fried octopus though).

Arzie Chant, Carol Curtis and the rest of the Department of Biology staff, thank you for everything you do. Please know that the students appreciate your work. Thank you to the Biology faculty that I have crossed paths with over the years. And thank you to Dr. Nina Zitani and the Western Biology Zoological Collections for the use of your specimens.

I have been surrounded by a fantastic group of people that deserve thanks. Dylan Baloun, Jessica Deakin, Lauren Witterick, Kevin Young, Jackson Kusack and Andrew Beauchamp: thank you for writing supports, life chats, grad club beers (and ciders), and always being available to talk about things, science of otherwise. The last 6 years would have been vastly less enjoyable without all of you.

To the medical staff at Victoria and University Hospitals, especially Dr. Nikolaos Tzemos, thank you for your dedication to me, my future and your pursuit of answers. You ensured that what could have been a life changing traumatic event turned into little more than an inconvenience. I will never be able to thank you enough for the quality of care I received.

To my family, especially my parents Rebecca and Scott Martin. Thank you for being supportive even if you didn't fully understand why anyone would want to be a 'bird shrink' as it was often put. I am thankful for your love and support. For Steve and Tracy in particular: Purple and Proud.

Lastly, Dr. Emily Ready. At this point you could have been grouped with the special folks above, family, but you deserve thanks warranting your own section. I owe you for too many things to list, so for now I will resort to thanking you for always unconditionally supporting me, and also for not leaving me while I was writing this document.

Thank you all.

Table of Contents

List of Figures

List of Appendices

List of Abbreviations and Symbols

ANOVA	Analysis of Variance
BF	Balsam fir, *Abies balsamea*
CP	Crude protein
DM	Dry matter
EH	Eastern Hemlock, *Tsuga canadensis*
GFN	Geometric Framework of Nutrition
HSD	Honestly significant differences
L:D	Light-Dark
LMM	Linear mixed model
HC	High Carbohydrate diet
HP	High Protein diet
HPHC	A diet pair, High Protein and High Carbohydrate diets
HPI	A diet pair, High Protein and Intermediate diets
I	Intermediate diet
IHC	A diet pair, Intermediate and High Carbohydrate diets
NPE	Non-protein energy
n.s.	Not significant
RM	Red Maple, *Acer rubrum*
RP	Red Pine, *Pinus resinosa*
TE	Total energy
SEM	Standard error of the mean
WB	White Birch, *Betula papyrifera*; also Paper birch
WS	White Spruce, *Picea glauca*

Chapter 1

1. General Introduction: Food caching decisions by Canada Jays (*Perisoreus canadensis*)

1.1 Introduction

The overarching objective of this thesis is to better understand the decisions that individuals make during food caching. For the purposes of this thesis, a *decision* will be the action an individual takes as a result of some mechanism when faced with two or more simultaneous options (described in McFarland, 1977). Another way, the *decision* will be the behavioural output of an individual when faces with a choice, regardless of the underlying machanism. In particular, questions regarding the cache-site selection, *the where* (Chapters 2-4), and cache-item selection, *the what* (Chapter 5), phases of caching behaviour are considered (Figure 1.1).

In Chapter 2 I empirically test the hypothesis that Canada Jays' (*Perisoreus canadensis*) distributional overlap with spruce trees (Strickland et al., 2011) is the result of an active cache-site preference for these trees. Further, I explore potential environmental cues that may aid individuals in making these decisions. Chapter 3 assesses Canada Jays' behavioural responses to the presence of a potential cache-robber. This chapter explicitly examines the cache-protection strategies employed by Canada Jays, focusing particularly on cache-site selection. In Chapter 4 I explore the ability of Canada Jays to plan ahead and anticipate restricted food availability. I directly evaluate the ability of Canada Jays to select caching locations with predictable future food restriction and test the conclusions reached for a notable result, apparent future planning, found in Western Scrub-Jays (*Aphelocoma californica*; Raby et al., 2007). Chapter 5 evaluates the macronutrient content of items that Canada Jays choose to cache. I assess the macronutrient contents of food both consumed and cached, and compare the nutrients consumed to those that were cached.

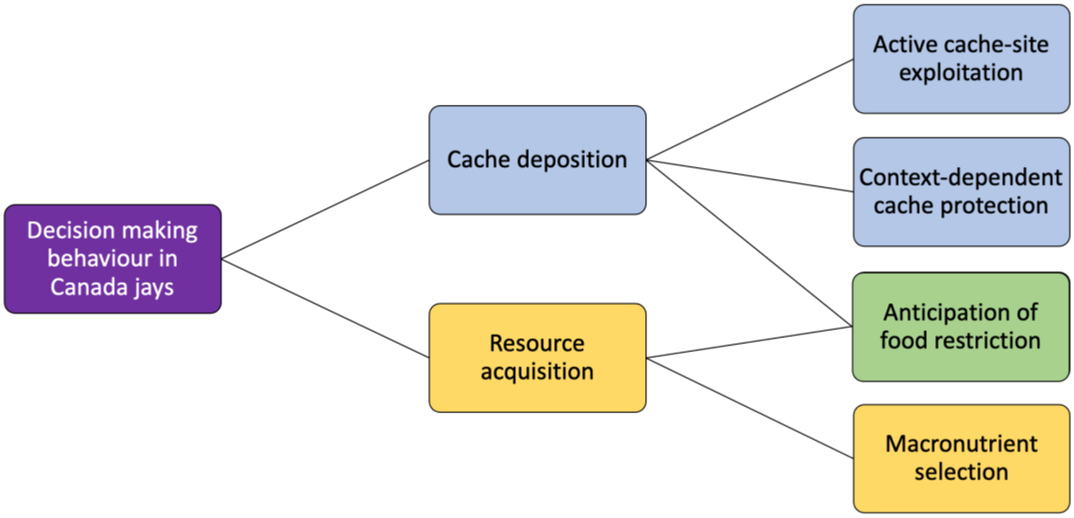


Figure 1.1 Schematic of thesis organization. The four topics in the right-most column represent Chapters 2-5 and are categorized by which caching phase they explore. Anticipation of food restriction explores the intersection of cache deposition and resource acquisition.

1.2 Food Caching

Food caching is a behavioural strategy employed by a wide variety of animals, particularly birds and mammals (reviewed in Smith & Reichman, 1984; Sutton et al., 2016). It involves the acquisition and storage of food for later retrieval and consumption. Food caching serves a multitude of purposes, though all are related to food security (Andersson & Krebs, 1978; Smith & Reichman, 1984; Vander Wall, 1990; Sutton et al., 2016).

1.2.1 Food Caching as an Adaptive Behaviour

For a behaviour to be adaptive, the fitness benefit of that behaviour must be greater than the benefit of competing behaviours. For food caching to be adaptive then, individuals of caching species must obtain a greater fitness benefit by caching than not. This has been modelled as follows (adapted from Andersson & Krebs, 1978):

$$F_H > F_N$$

where:

$$F_H = \ Gp - c$$

$$and$$

$$F_N = \ p_r mG$$

where *F* is the fitness benefit conferred to either the caching individual (*H*) or the non-caching individual (*N*), *G* is the benefit obtained by consuming one item (cached or otherwise), *p* is the probability that a cached item remains viable when retrieved, p_r is the probability that non-cached food is available and recovered, *m* is the multiplication factor for non-hoarded food (the difference in food availability between caching and recovery periods) and *c* is the cost incurred when caching the item.

The net fitness benefit can be affected by any number of parameters, either by modulating those parameters in the model directly or by modulating factors that influence these parameters. These variations and alternatives have been modelled extensively (e.g. Andersson & Krebs, 1978; Jorge et al., 2011; Sutton et al., 2016; and reviewed in Brodin, 2010), however caching remains a viable and adaptive strategy as long as caching continues to offer greater fitness benefits than not caching.

1.2.2 A Caching Timeline

Caching behaviour can be subdivided into six temporally distinct components: 1) *resource acquisition*, selecting and obtaining resources for caching; 2) *food handling*, the manipulation of acquired resources in preparation for caching; 3) *cache deposition*, the selection of a cache site and deposition of the acquired resource; 4) *caching interval*, the time between cache deposition and cache retrieval; 5) *cache retrieval*, the recovery of cached items; and 6) *consumption*, consuming the recovered item (Figure 1.2). While the simplest of caching timelines is linear – a resource is acquired, handled, deposited, left for a period of time, recovered and consumed – other sequences occur. In particular, many species are known to cache and re-cache food, forgoing *consumption* after *cache retrieval* and returning instead to *cache deposition* (e.g. Emery & Clayton, 2001; Seiwa et al., 2002; Burns & Van Horik, 2007).

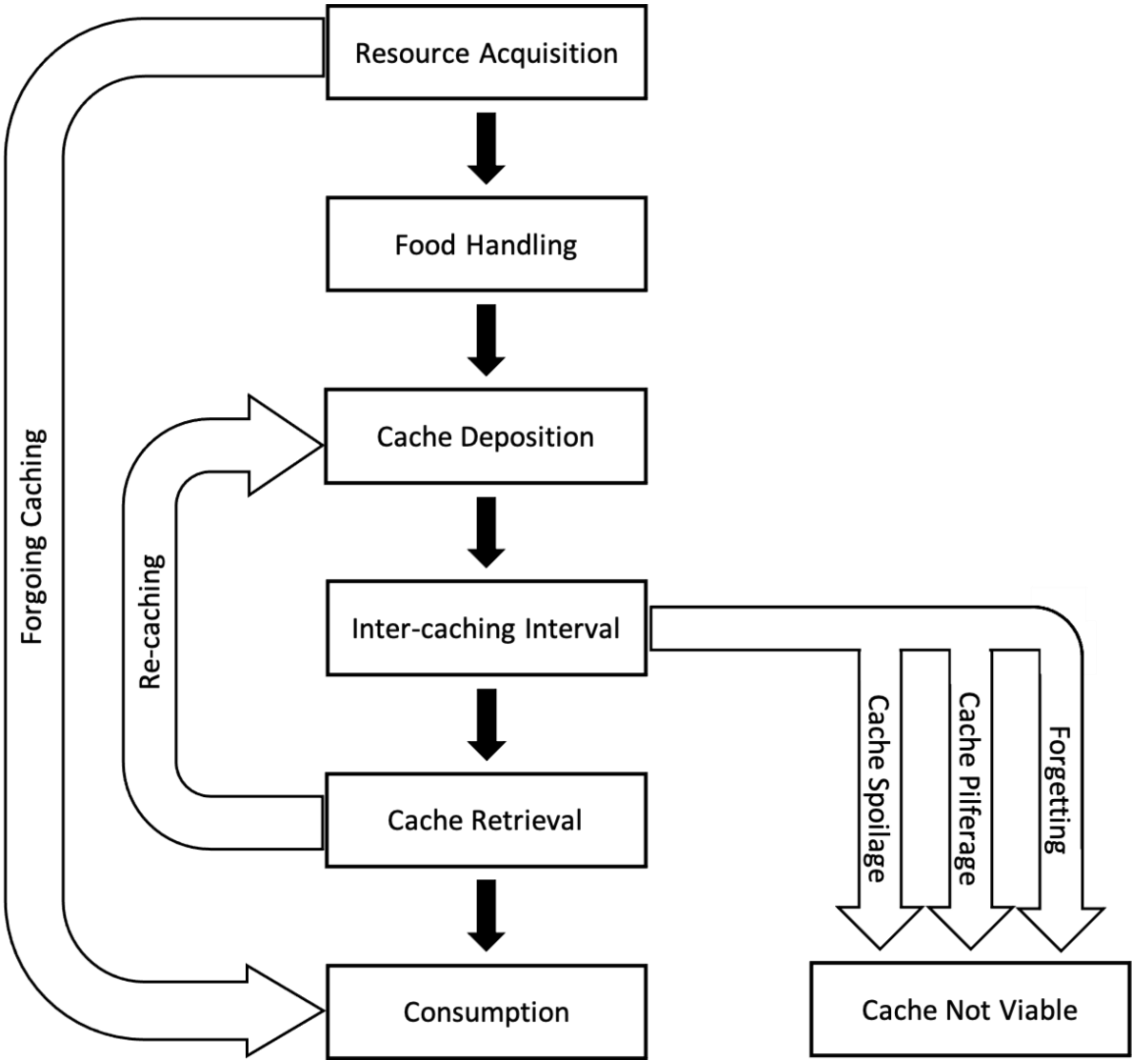


Figure 1.2 A schematic flow chart illustrating the timeline of caching. The typical caching timeline is shown with filled black arrows, while alternative pathways are shown with labeled open arrows.

1.2.2.1 Resource acquisition

Resource acquisition is the process of selecting and obtaining resources for caching. Though seeds, probably selected for their dense energy contents and low perishability, are the most commonly cached items, a wide variety of foods are cached, encompassing all the major categories of terrestrial food (Smith & Reichmann, 1984). The variety of food items cached reflects the diverse nutritional requirements of caching species. For example, large carnivores cache their kills (e.g. Elgmork, 1982; Balme et al., 2017) while some insects cache pollen and nectar (Strassman, 1979). In addition to food type, food availability plays a role in resource acquisition variation when individuals have access to two or more food sources (e.g. Hadj-Chikh et al., 1996; Waite, 2001).

1.2.2.2 Food handling

Food handling in the context of caching behaviour only deals with the manipulation of food in preparation for cache deposition. Handling time can vary greatly between species. Some animals store items as they are acquired, for example seeds stored unaltered and able to germinate if not consumed (e.g. Vander Wall, 1997). Other animals dedicate substantial amounts of time to manipulating their resources prior to caching (e.g. Dow, 1956). In addition to simply making food appropriate for caching (resizing, transporting) food handling is employed to increase the longevity of cached food items (e.g. Jansen et al., 2006), or to deter cache-pilferage (e.g. Jenkins & Devenport, 2014).

1.2.2.3 Cache deposition

Cache deposition is the process of first selecting a cache-site and subsequently depositing acquired resources in that location. Variation in *cache deposition*, particularly in selecting a cache site, can be influenced by a multitude of factors. For example, American Martens (*Martes americana*) are known to cache in close proximity to their resting sites (Henry et al., 1990), presumably for easy future access to food, while Leopards (*Panthera pardus*) are known to cache food arboreally in order to avoid cache losses to non-climbing competitors (Balme et al., 2017). Other species have been shown to select for a variety of environmental conditions and microclimates (e.g. Florida Scrub-Jay, *Aphelocoma coerulescens*, Fuirst et al., 2020).

1.2.2.4 Caching interval

The *caching interval* is the period of time between cache deposition and cache retrieval. Caching intervals vary greatly depending on the types of food cached, the requirements of the caching animal, and the ability of the caching animal to retrieve cached items. For example, highly perishable food items like animal carcasses are typically cached for relatively short durations, hours to days, while more stable foods like seeds and nuts are frequently cached for much longer durations, months to years (Vander Wall, 1990; Sutton et al., 2016). Additionally, the *caching interval* is the time of most risk for cached food items. Caches are frequently left unprotected (Vander Wall, 1990), subjected to environmental conditions that can negatively impact cache quality (Sutton et al., 2016), and are subject to potential cache-pilferage (Smith & Reichmann, 1984; Dally et al., 2006).

1.2.2.5 Cache retrieval

Cache retrieval refers to the recovery of previously cached items. Because of the variation in caching behaviour generally, variation in cache retrieval also exists. For example, animals that make few, large caches, like Red Squirrels (*Tamiasciurus* *hudsonicus*), often centrally locate their hoards (Vander Wall, 1990) making them relatively easy to relocate and retrieve food from. Animals, however, that make hundreds of individual caches, like Black-capped Chickadees (*Poecile atricapillus*), depend on enhanced spatial memory to retrieve their caches (e.g. Sherry, 1984).

1.2.2.6 Consumption

Consumption ends the caching cycle. Once an item is consumed, it can no longer be cached, or re-cached, and the individual gains the benefit of having stored that resource. In instances where animals are not caching discrete items like surplus killings by large carnivores or when larder hoarders remove only a portion of their caches upon retrieval, *consumption* only refers to the portion eaten. Any remaining resources remain not yet retrieved and are therefore not consumed. In species where offspring are provisioned from cached food, this provisioning is also an example of consumption. The resource has been consumed, and the caching individual should gain the benefit of that consumption, albeit indirectly.

1.2.3 Variation in Caching Behaviour

Although caching behaviour follows a relatively uniform timeline (described above), variation both within and between species can, and does, occur in all components. Largely however, caching species are categorized dependent on their *cache-deposition* behaviours, and the duration of their *caching interval*.

1.2.3.1 Larder vs scatter hoarding

Caching species are often dichotomously classified as either *larder hoarders*, animals that cache many food items in one or few locations, or *scatter hoarders*, animals that cache individual food items in many locations. Examples of larder and scatter hoarders occur in both birds and mammals, while virtually all other caching taxa (arthropods mainly) are solely larder hoarders (Vander Wall, 1990). Though often dichotomized, many caching species utilize some combination of larder and scatter hoarding behaviour (e.g. Eastern Chipmunk, *Tamias striatus*, Clarke & Kramer, 1994), leading some to argue that this dichotomy best describes particular behaviours, and should not be used to categorize species (Vander Wall, 1990).

Both larder and scatter hoarding provide cache protection benefits, albeit differently. Larder hoarders benefit from having few, large groups of resources to protect and can engage in defending these resources (Vander Wall, 1990). Alternatively, scatter hoarders benefit from the reduced likelihood that large scale cache loss can occur in a single event. Hypothetically, if a potential cache-pilferer locates the hoard of a larder hoarding species and successfully evades the defending individual, the cache-pilferer gains access to the entire hoard. The pilferer in this case has the potential to do significant damage to the overall food reserves of the caching individual. In the same scenario, where a potential pilferer encounters a scatter hoarding individual’s resources, the pilferer is virtually guaranteed access to the cache as it is likely undefended, but that cache represents much less of the caching individual’s food supply, thus a lesser detriment overall. Scatter hoarding, however, is not without risk. The distribution of caches across a territory increases the likelihood that a potential pilferer will encounter some by chance unbeknownst to the caching individual (Vander Wall et al., 2005; Cao et al., 2018), who may then expend energy attempting to retrieve a pilfered cache. Additionally, though enhanced spatial memory has evolved in many scatter hoarding species (Sherry, 1984, 1985; Sherry et al., 1992; Pravosudov & Roth, 2013), some percentage of caches still are forgotten, or overlooked and are never recovered (Vander Wall & Balda, 1977; Price & Jenkins, 1986; Hitchcock & Sherry, 1990; Tomback & Linhart, 1990).

1.2.3.2 Long vs short term caching

The duration of the *caching interval* is another behavioural indicator, typically used to categorize caching species. While often dichotomized into long-term and short-term caching species, caching intervals more accurately reflect a spectrum, the ends of which are the extreme long and short durations seen in nature. A variety of factors influence the duration of the *caching interval*, including the type of food security strategy (preventing seasonal food scarcity vs avoiding competition), the types of food cached (perishable vs non-perishable) and the location of caching (reviewed in Sutton et al., 2016).

Although notable exceptions exist, species that cache highly perishable food, such as animal remains or fleshy fruits and berries, typically fall on the short-term end of the caching spectrum, while species that cache less-perishable items like seeds and nuts typically exhibit longer caching intervals (Sutton et al., 2016). Species caching to avoid future seasonal food scarcity also tend to exhibit longer caching intervals than species caching to either avoid competition for resources in the present, or to gain reliable food access in close proximity to their nesting sites (Vander Wall, 1990), though exceptions to this pattern exist (e.g. some parids; Cowie et al., 1981; Hitchcock & Sherry, 1990).

1.2.3.3 Other notable variation

As previously mentioned most variation used for categorizing species relates to either the deposition or duration of caching behaviours. Variation, however, occurs in each of the 6 temporal components. Animals vary the resources they acquire based on nutritional requirements, the location of caches – particularly for scatter hoarders, the mechanism of retrieval (search strategy) and the method and degree of consumption (reviewed in Vander Wall, 1990). Much of this variation is the result of individuals actively making decisions regarding individual caching bouts and will be discussed in future sections.

1.2.4 Food Caching and Climate Change

Climate change is affecting food caching species in a variety of ways. In large part this stems from the variation observed in caching behaviour across taxa. Sutton and colleagues (2016) developed a framework to be used in evaluating these impacts on populations, with the goal of predicting which caching behaviours exposed caching species to the greatest risk. Unsurprisingly, the two most influential factors seem to be the perishability of the food cached, and the *caching interval*. Additionally, Sutton and colleagues (2016) identified cache location as an important contributor, with caches made at arboreal sites prone to greater cache degradation than those on the ground.

A variety of other factors can also influence caching species and can also be influenced by climate change. For example, range shifts can force species out of familiar territory, a potentially important factor in caching propensity for some rodents (Miller & Viek, 1944; Vander Wall, 1990; but see Jenkins & Peters, 1992), or can introduce new competitors into the caching species' existing range (e.g. Hitch & Leberg, 2007). Climate changes can also impact the effectiveness of strategies employed to stunt cache degradation. For example, some species rely on deep freezes to preserve caches (e.g. Canada Jay, Sutton et al., 2019), while others utilize snow in hunting and disguising cached prey (e.g. Canada lynx, *Lynx canadensis*; Nellis & Keith, 1968).

1.3 Cognition in Non-human Animals

Cognition, as defined by Shettleworth (1998), refers to the mechanisms involved in collecting, processing, storing and acting on information. In other words, cognition can broadly be thought of as the processing of information. Animal cognition (or animal intelligence historically) has long been of interest (e.g. Romanes, 1883), but is suggested to have arisen as a distinct field of study in the 1970s (Wasserman, 1993; Shettleworth, 1998). Since then, scientists have dedicated significant resources to understanding various aspects of animal cognition exploring basic cognitive functions like associative learning (e.g. Dickinson, 2012), more complex functions like episodic memory (e.g. Crystal, 2010), or future planning (e.g. Raby et al., 2007) and many other processes including learning and memory, discrimination, perception, social cognition and decision making (see Shettleworth, 1998).

1.3.1 Decision Making

Decisions are made constantly by animals. These decisions include choices regarding feeding, nesting, reproduction and vigilance. As these decisions are often between mutually exclusive behaviours (e.g. resting and feeding), they shape the daily activities of individuals and in turn, the general behavioural patterns that we attribute to species. Underlying these observable decisions are cognitive and physiological processes, representing decision making. Decision making in animals has been broadly studied by behavioural ecologists. Empirical studies of decision making, and the resulting decisions, began in the 1960s (Logan, 1965a, 1965b), and researchers have continued asking questions about animal decision making using both experimental (e.g. Jaramillo & Zador, 2014; Rojas-Ferrer & Morrand-Ferron, 2020) and theoretical (e.g. Conradt & Roper, 2003, 2005) methods. It has been suggested that decision making in animals adheres to the rules of *decision theory* and is heavily influenced by the environmental constraints of natural selection (McFarland, 1977). In other words, decision making in animals is essentially a series of cost-benefit analyses, where the variables and outcomes are influenced by the fitness consequences of each choice.

1.3.2 Foraging Decisions

Foraging is a context in which decision making has been thoroughly explored. Like decision making in general, foraging decisions have been explored by researchers using both experimental (Zimmerman, 1983; Shochat et al., 2004) and theoretical (McNamara & Houston, 1985; Houston et al., 2011) techniques. The rise, and subsequent exploration, of optimal foraging theory (see Stephens & Krebs, 1986; Kamil et al., 2012) is one example of the breadth to which foraging decisions have been studied.

Optimal foraging theory, at its core, suggests that decision makers should choose the most profitable outcome (MacArthur & Pianka, 1966; see also Kamil et al., 2012). While a variety of factors can influence the complexity of these decisions, they can be simplified by considering an example. A squirrel nests halfway between two patches of food. One patch offers large nuts and the second offers small nuts. If we assume that the squirrel is equally capable of opening and consuming both sizes of nut and that the larger the nut the greater the energy reward, then we can intuitively see that the squirrel should forage at the patch offering large nuts when faced with a choice. This can be modelled using the following equation:

$$\frac{E_1}{h_1} > \frac{E_2}{h_2}$$

where E is the energy gained by consuming the nut, h is the time spent travelling to and consuming the nut and the numerals denote which patch is being foraged at. In this example, patch one's rate of return (E/h) is greater than that of patch two. In this example, $E_1 > E_2$, and $H_1 = H_2$ creating a simple and intuitive scenario, but all four variables can be adjusted to reflect the realities of the scenario we are trying to model.

Like most models, this equation can be altered to generate predictions about particular contexts. If we modify the example above so large nuts are not continuously available but small nuts are, we might wonder if foraging on small nuts would become more profitable. We could modify the equation as follows:

$$\frac{p_1 E_1}{h_1} > \frac{p_2 E_2}{h_2}$$

where *p* is the probability that nuts will be available. By modulating *p*, we can make predictions about what animals faced with similar situations should do. These predictions are then testable.

Optimal foraging theory can be applied to any number of foraging scenarios, so long as there is a decision that must be made. Of particular interest in this thesis is the application of optimal foraging to decisions that are made by caching individuals. Although not always explicitly discussed, optimal foraging underpins decisions made at various points throughout the caching timeline illustrated above. That is, animals make caching decisions based largely on the fitness benefits that those decisions confer.

1.3.3 Caching Specific Decisions

Decisions must be made during each component of the caching timeline. At some stages the decisions are obvious, while at other stages decisions may be more subtle. For example, most species consume more than a single type of food so which type to consume is a choice that must be made in the resource acquisition phase. Conversely, during the food handling phase, animals may be forced to make decisions about the degree to which they manipulate food items, taking into account things like environmental conditions and increased predation risks, as well as potentially deferring handling time to the consumption phase. Caching decisions and the variety of factors affecting decision making while caching have been well documented (see Vander Wall,

1990) in all phases of caching, however, for this thesis I will focus on two particular components of the caching timeline: *resource acquisition*, and *cache deposition*.

1.3.3.1 Decisions during resource acquisition

Deciding what food to consume is a decision all animals must make regularly. For caching species, this decision is complex in that animals must decide not only what to consume, but also what to cache. Existing research surrounding decisions made during resource acquisition is plentiful. Researchers have shown that animals make acquisition decisions based on food perishability (e.g. Hadj-Chikh et al., 1996), abundance (e.g. Solheim, 1984), energy content (e.g. Kostrzewa & Krauze-Gryz, 2020), and a host of other factors (see Vander Wall, 1990), however, decisions based on the nutrient requirements of individuals remains largely unexplored.

Research in non-caching, migratory birds suggests that species make consumption decisions based on nutrient content, especially prior to migration, a physiologically challenging event (Parrish, 1997; Marshall et al., 2016). This feeding pattern, known as dietary shifting, is an example of animals making foraging decisions in the present that potentially affect their future states. While this phenomenon has not been observed in caching species, it raises interesting questions because caching species could utilize dietary shifting to mitigate the effects of their own physiological challenges. For example, similar trends to those seen in non-caching species could exist where caching species alter their dietary preference in order to gain some future advantage, surviving winter for example. Alternatively, caching species could demonstrate similar shifting patterns in their cached food resources, acting now in order to improve their future outcomes through caches, either directly, or indirectly.

As mentioned previously, evidence exists that animals make decisions about what to consume and what to cache, but those decisions have been historically attributed to differences in perishability (Reichman, 1988) or handing time (e.g. Jacobs, 1992). In this thesis I examine these resource acquisition decisions in the context of nutrient preference and nutrient requirements in caching species (Chapter 5).

1.3.3.2 Decisions during cache deposition

Once an individual has acquired resources, it must then decide where to put them. The primary goal of these decisions is food security; assuring a reliable source of food through periods of scarcity (investigated in Chapter 4). This obviously varies greatly across species, particularly between larder and scatter hoarders. While larder hoarders make limited decisions about where to cache food (stemming from the limited number of individual caches they make), scatter hoarders make hundreds, if not thousands of deposition decisions each season (Vander Wall, 1990).

These decisions can be influenced by a wide variety of factors and can play an important role in the long-term viability of caching behaviour. Mounting evidence suggests that many species use particular characteristics of caching locations in order to combat cache perishability and cache degradation. For example, caching birds have recently been shown to exploit arid or shaded microclimates in order to limit the degradation of caches over time (Fleck & Woolfenden, 1997; Kulahci & Bowman, 2011;

Neuschulz et al., 2015), and some studies have gone further, demonstrating that these site preferences are learned (Fuirst et al., 2020) implying that active decision making is involved. Additionally, many studies have shown that other aspects of cache sites (e.g., substrate, Kelley & Clayton, 2017), can be important in mitigating threats from potential pilferers (reviewed in Dally et al., 2006), and can play an important role in cache deposition (explored in Chapter 3).

1.4 Canada Jays

The subject of this dissertation is the caching behaviour of the Canada Jay (formerly Gray Jay). Canada Jays are an ideal species in which to test hypotheses and ask questions about caching decisions. They are highly motivated to cache, even in captivity. This is likely due to their high dependence on cached food to survive winter (Strickland & Ouellet, 2020). Additionally, Canada Jays are corvids, and related species have been the subjects of much recent research regarding decision making, and cognition in caching species (e.g. Kelley & Clayton, 2017; Fuirst et al., 2020; Vernouillet et al., 2021).

1.4.1 Diet and Foraging

Canada Jays are omnivorous, long-term scatter-hoarders. They consume a wide variety of food items including berries and plant matter, arthropods, carrion, eggs and nestlings, and fungi (Strickland & Ouellet, 2020). Canada Jays will also consume human food including bread, meat, cheese and dried fruit (Dow, 1965; Derbyshire et al., 2019; Strickland & Ouellet, 2020). Similarly, Canada Jays cache an equally wide variety of foods, including those that are perishable. Additionally, unlike many scatter hoarding species that cache predominantly in the ground, Canada Jays cache arboreally (reviewed in Sutton et al., 2016).

Canada Jays cache tens-of-thousands of food items per season (Strickland & Ouellet, 2020), and have been reported caching over 1000 food items in a single 17 h day (Waite, 1991), a rate of over 1 cache per minute. While food caching is employed by all Canada Jays, the behaviour appears to vary geographically. Populations in Alaska and the Yukon have been observed caching throughout the summer, while populations at the southern edges of the range in Manitoba and Ontario are typically not observed caching until late summer or early autumn. All populations seem to continue food caching until food is no longer abundant, and caching behaviour appears to peak in autumn, when temperatures cool and humidity drops (Strickland & Ouellet, 2020).

1.4.2 Distribution and Habitat

Canada Jays maintain stable year-round territories. Canada Jays inhabit every province and territory in Canada, Alaska and parts of New England and the Western United States, though typically at higher altitudes in warmer regions (Figure 1.3; Strickland & Ouellet, 2020). Canada Jay territories vary in size depending on resource and habitat quality but can range from approximately 27 – 146 ha (Strickland & Norris, 2015). The species has a close distributional relationship to spruce trees (*Picea* spp.) but can also be found among other conifer species (Strickland & Ouellet, 2020). At the southern edge of the Canada Jay range in Ontario, populations are most abundant when Black Spruce (*P. mariana*) and White Spruce (*P. glauca*) are present (Strickland et al., 2011; Strickland & Ouellet, 2020). At higher elevations, populations tend to coincide with clusters of Engelmann Spruce (*P. engelmannii*; Strickland & Ouellet, 2020). This distributional overlap is thought to be the result of the postulated preservative properties of spruce resins aiding in cache preservation (Sechley et al., 2015), however, no empirical evidence for this assumption exists. I explore this relationship and show how Canada Jays could impact this overlap through their caching decisions (Chapter 2).

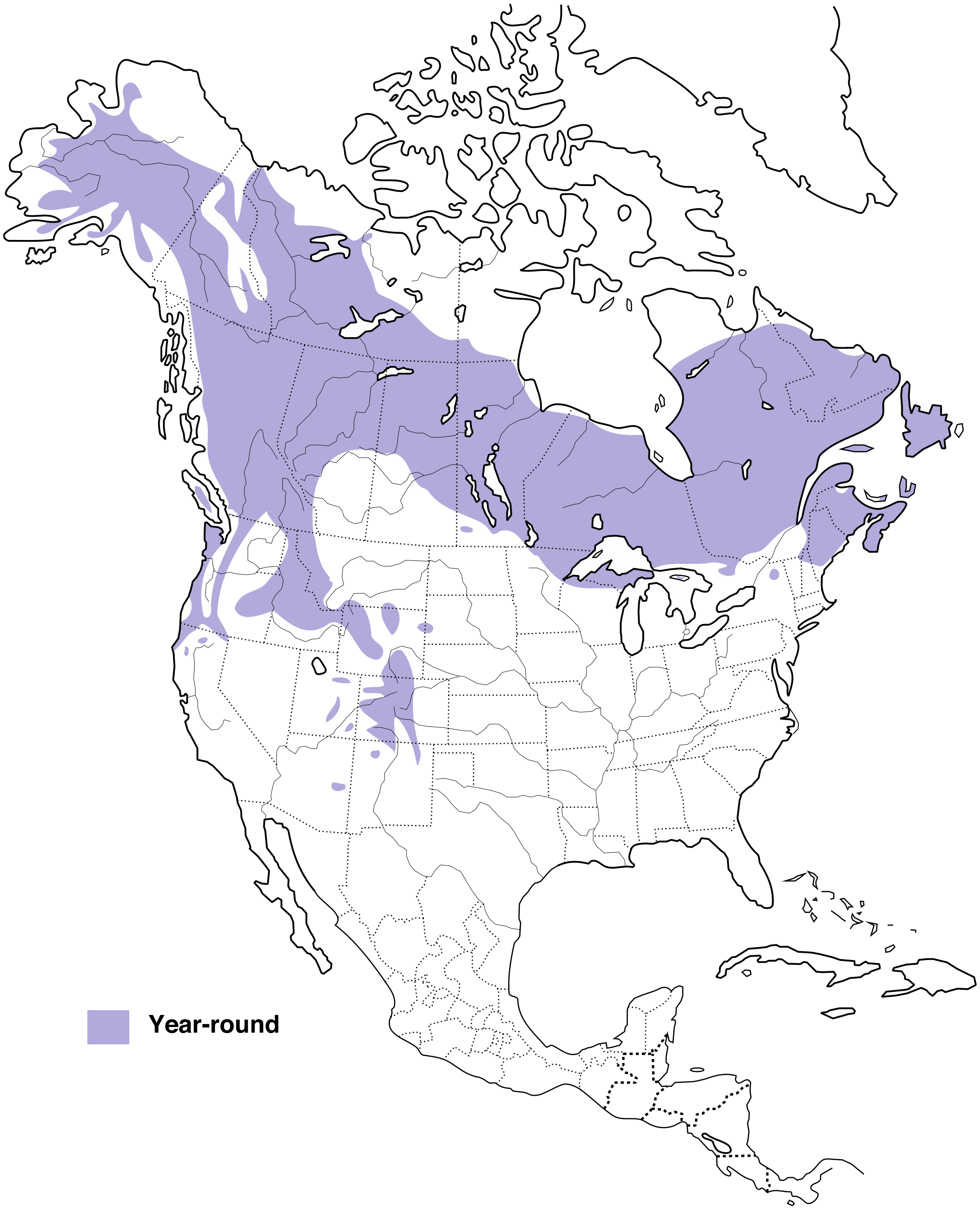


Figure 1.3 Canada Jay range map. Shaded area indicates the year-round range of the Canada Jay. Reproduced with permission from Birds of the World (see Appendix I).

1.4.3 Reproductive Timing and Breeding

Canada Jays reproduce atypically early in the year. Pairs initiate nest building between mid-February and mid-March, though initiation in early February has been reported (Strickland & Ouellet, 2020). First eggs are laid from mid-March to mid-April, and hatch roughly 20 days post-laying (Strickland & Ouellet, 2020). Notably, this phenology means the offspring are hatched and need provisioning significantly before lakes and waterways have thawed, before most migratory birds have returned, and before the vast majority of food is available (Strickland & Ouellet, 2020).

1.4.4 Canada Jay Caching

Canada Jays cache a wide variety of items, including foods that are perishable (Strickland & Ouellet, 2020), and to accommodate this engage in extensive food handling prior to caching. Canada Jays manipulate food items into boluses, saliva covered balls of prepared food (Dow, 1965). As previously mentioned, Canada Jays cache arboreally, thus these boluses are then deposited discreetly in trees throughout an individual's territory, hidden by bark, foliage or other substrates (Dow, 1965; Waite, 1991; Strickland and Ouellet, 2020).

Canada Jays, like many northern boreal birds, are reliant on their caches for winter survival (Strickland & Ouellet, 2020). Cached food provides birds with the resources required to survive the otherwise food scarce winter. Additionally, Canada Jays also provision their offspring using cached food (Derbyshire et al., 2019), though the extent to which cached food is used for provisioning is not known (Derbyshire et al., 2019; Strickland & Ouellet, 2020).

Despite Canada Jays having been studied for decades – the Algonquin Provincial Park population has been studied continuously since the 1960s (Derbyshire et al., 2015; Sutton, 2020) – caching specific research remains limited. Most existing research is dedicated to population level understanding of habitat use and population trends (Strickland et al., 2001; Derbyshire et al., 2015; Waite & Strickland, 2006, Sutton et al., 2019, 2020a, 2020b).

There are two notable exceptions in which Canada Jay caching has been the explicit focus of research. First, captive Canada Jays were used to confirm expectations that, similar to other food caching passerines (e.g. Black-capped Chickadees, Sherry, 1984), Canada Jays retrieved their caches using memory (Bunch & Tomback, 1986). Second, a group of Canada Jays in Alaska were used to study the economics of Canada Jay caching in the late 1980s and early 1990s (Waite, 1991) regarding cache distribution and rate maximization. Experimental manipulations of caching scenarios showed that Canada Jays behaved in a manner consistent with optimal theoretical models.

1.4.5 Impact of Climate Change

Canada Jays are extremely susceptible to the negative population level effects of climate warming (Waite & Strickland, 2006; Greenlee, 2012; Sutton et al., 2019, 2020a; and reviewed in Sutton, 2016). This risk seems to be heightened by multiple compounding factors. For example, Canada Jays cache a wide variety of perishable food items. As a long-term caching species, Canada Jay caches are subjected to varying environmental conditions (e.g. moisture, temperature) that lead to cache degradation (Sechley et al., 2015; Sutton et al., 2019). Weather and climatic factors can also cause range shifts (Greenlee, 2012), range contractions (Waite & Strickland, 2006), and a decrease in habitat quality (Strickland et al., 2011) and/or reproductive success (Sutton et al., 2020a). These negative trends independently have the potential to drive population level effects on Canada Jays, but when experienced simultaneously, it becomes evident that Canada Jay populations, particularly those at the Southern edge of the range, are becoming increasingly vulnerable.

1.5 Dissertation Objectives and Structure

In this thesis I address four distinct questions, each corresponding to one of four data chapters (Chapters 2-5), and each with the goal of better understanding the caching decisions of Canada Jays. More specifically, questions regarding cache-site and cache-item selection were explored.

In Chapter 2 I empirically test the assumption that Canada Jay's distributional overlap with spruce trees (Strickland et al., 2011) is the result of an active cache-site preference for spruce trees. Evidence suggests that for birds, some conifers may aid in cache preservation through protective properties in resin. However, due to the challenges involved with following birds to their caching locations, cache-site preferences are not easily studied. I investigated eight captive Canada Jays' ability to both identify and exploit conifer tree species. Further, I examined potential cues that birds may use in order to identify and select these potentially beneficial sites. I found strong evidence to suggest that birds can quickly identify conifer tree species, and subsequently exploit those cache locations preferentially. Furthermore, I found evidence that birds use structural but not olfactory cues when making caching decisions, suggesting that visual information is essential to both the identification of conifer trees and to cache-site selection decisions. These findings indicate that jays make rapid, fine scale assessments of their environments, discriminating among trees of different species, and use this information to select cache sites.

In Chapter 3 I assess Canada Jays' behavioural responses to the presence of a potential cache-robber, a model Blue Jay. Cache-robbers present a unique threat to food-caching individuals, including Canada Jays (Burnell & Tomback, 1985; Rutter, 1972). Accordingly, caching species are predicted to have evolved a variety of cache protection strategies in order to limit the potential risk of cache-robbery. I assessed the cache protection strategies, caching behaviour and movement patterns of captive Canada Jays in a variety of caching contexts that varied in potential risk of cache-robbing. I found that depending on perceived risk, Canada Jays flexibly employed a variety of non-mutually exclusive cache protection strategies including *cache depression*, caching *out-of-sight*, and *spacing* their caches. These cache protection strategies likely reduce the risk of cache-robbing and increase the probability of caches remaining available for recovery and consumption.

In Chapter 4 I explore the ability of Canada Jays to plan ahead and anticipate restricted food availability. In the past 20 years, research in animal cognition has challenged the belief that complex cognitive processes are uniquely human. At the forefront of these challenges has been research on mental-time-travel and future planning in jays. I tested whether Canada Jays were capable of future planning, using a procedure which had previously produced evidence of future planning in Western Scrub-Jays (Raby et al., 2007). "Future planning" in this procedure consists of birds distributing food caches in a way that makes food subsequently available in locations where the birds have experienced periods of predictable food restriction. Canada Jays showed no evidence of future planning in this sense and instead placed caches in a location where food was usually available, the opposite of the behaviour described for Western Scrub-Jays. I suggest potential explanations for these differing results and a re-evaluation of "complex cognition" as an explanation of caching behaviour in jays.

In Chapter 5 I evaluate the macronutrient content of items that Canada Jays choose to cache and consume. Food scarce periods pose serious physiological challenges for birds, especially in energetically demanding conditions. For Canada Jays, a decrease in available resources during winter adds further physiological stress to the energetic demands of life at low temperatures. Canada Jays also rear their young prior to spring green up, making food caching not only essential for adult winter survival, but also potentially important for meeting the requirements of growing offspring in late winter and early spring (Derbyshire et al., 2019; Strickland & Ouellet, 2020). In this study I examined the diet choices of Canada Jays immediately prior to winter, and the macronutrient composition of the foods Canada Jay consumed and cached at this time. I found that birds made no changes to their macronutrient intake prior to winter and that the ratio of macronutrients in food Canada Jays cache is the same as in the food they consume. These similarities in macronutrient ratios between cached and consumed foods suggest that the birds are foraging to simultaneous, but distinct, minimum energy and protein targets. It also suggests that these simultaneous targets define the foraging decisions of individuals when presented with dietary choices and should be important for diet generalist species.

In Chapter 6 I summarize and synthesize the results of the preceding four chapters, as well as previous research on these topics. I address the overall significance of my results and discuss the applications of my findings to future research and to the conservation of boreal caching species.

1.6 References

Andersson, M., & Krebs, J.R. (1978). On the evolution of hoarding behaviour. *Animal Behaviour*, *26*, 707-711.

Balme, G.A., Miller, J.R., Pitman, R.T., & Hunter, L.T. (2017). Caching reduces kleptoparasitism in a solitary, large felid. *Journal of Animal Ecology*, *86*(3), 634-644.

Brodin, A. (2010). The history of scatter hoarding studies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1542), 869-881.

Bunch, K.G., & Tomback, D.F. (1986). Bolus recovery by Gray Jays: an experimental analysis. *Animal Behaviour*, *34*(3), 754-762.

Burnell, K.L., & Tomback, D.F. (1985). Steller's Jays steal Gray Jay caches: field and laboratory observations. *The Auk*, *102*(2), 417-419.

Burns, K.C., & Van Horik, J. (2007). Sexual differences in food re-caching by New Zealand robins *Petroica australis*. *Journal of Avian Biology*, *38*(3), 394-398.

Cao, L., Wang, B., Yan, C., Wang, Z., Zhang, H., Geng, Y., Chen, J., & Zhang, Z. (2018). Risk of cache pilferage determines hoarding behavior of rodents and seed fate. *Behavioral Ecology*, *29*(4), 984-991.

Clarke, M.F., & Kramer, D.L. (1994). Scatter-hoarding by a larder-hoarding rodent: intraspecific variation in the hoarding behaviour of the Eastern Chipmunk, *Tamias striatus*. *Animal Behaviour*, *48*(2), 299-308.

Conradt, L., & Roper, T.J. (2003). Group decision-making in animals. *Nature*, *421*(6919), 155-158.

Conradt, L., & Roper, T.J. (2005). Consensus decision making in animals. *Trends in ecology & evolution*, *20*(8), 449-456.

Cowie, R.J., Krebs, J.R., & Sherry, D.F. (1981). Food storing by marsh tits. *Animal Behaviour*, *29*(4), 1252-1259.

Crystal, J.D. (2010). Episodic-like memory in animals. *Behavioural Brain Research*, *215*(2), 235-243.

Dally, J.M., Clayton, N.S., & Emery, N.J. (2006). The behaviour and evolution of cache protection and pilferage. *Animal Behaviour*, *72*(1), 13-23.

Derbyshire, R., Norris, D.R., Hobson, K.A., & Strickland, D. (2019). Isotopic spiking and food dye experiments provide evidence that nestling Canada Jays (*Perisoreus* *canadensis*) receive cached food from their parents. *Canadian Journal of Zoology*, *97*(4), 368-375.

Derbyshire, R., Strickland, D., & Norris, D.R. (2015). Experimental evidence and 43 years of monitoring data show that food limits reproduction in a food-caching passerine. *Ecology*, *96*(11), 3005-3015.

Dickinson, A. (2012). Associative learning and animal cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1603), 2733-2742.

Dow, D.D. (1965). The role of saliva in food storage by the Gray Jay. *The Auk*, *82*(2), 139-154.

Elgmork, K. (1982). Caching behavior of brown bears (*Ursus arctos*). *Journal of Mammalogy*, *63*(4), 607-612.

Emery, N.J., & Clayton, N.S. (2001). Effects of experience and social context on prospective caching strategies by scrub jays. *Nature*, *414*(6862), 443-446.

Fleck, D.C., & Woolfenden, G.E. (1997). Can acorn tannin predict scrub-jay caching behavior?. *Journal of Chemical Ecology*, *23*, 793-806.

Fuirst, M., Greer, J., & Bowman, R. (2020). Ontogeny of food-caching site preferences in young Florida Scrub-Jays: evidence of learning or changing social status?. *Journal of Field Ornithology*, *91*(3), 241-253.

Greenlee, E.S. (2012). *The Effects of a Warming Climate on the Migratory Strategies of a Putatively Non-Migratory Bird, the Gray Jay (Perisoreus canadensis)*. [Doctoral dissertation, The Ohio State University].

Hadj-Chikh, L.Z., Steele, M.A., & Smallwood, P.D. (1996). Caching decisions by grey squirrels: a test of the handling time and perishability hypotheses. *Animal Behaviour*, *52*(5), 941-948.

Henry, S.E., Raphael, M.G., & Ruggiero, L.F. (1990). Food caching and handling by marten. *The Great Basin Naturalist*, *50*(4), 381-383.

Hitch, A.T., & Leberg, P.L. (2007). Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology*, *21*(2), 534-539.

Hitchcock, C.L., & Sherry, D.F. (1990). Long-term memory for cache sites in the Black-capped Chickadee. *Animal Behaviour*, *40*(4), 701-712.

Houston, A.I., Higginson, A.D., & McNamara, J.M. (2011). Optimal foraging for multiple nutrients in an unpredictable environment. *Ecology Letters*, *14*(11), 1101-1107.

Jacobs, L.F. (1992). The effect of handling time on the decision to cache by grey squirrels. *Animal Behaviour*, *43*(3), 522-524.

Jansen, P.A., Bongers, F., & Prins, H.T. (2006). Tropical rodents change rapidly germinating seeds into long-term food supplies. *Oikos, 113*(3), 449-458.

Jaramillo, S., & Zador, A.M. (2014). Mice and rats achieve similar levels of performance in an adaptive decision-making task. *Frontiers in systems neuroscience*, *8,* 173.

Jenkins, J.R., & Devenport, L.D. (2014). Seed preparation diminishes cache loss in least chipmunks. *Journal of Mammalogy, 95*(2), 276-283.

Jenkins, S.H., & Peters, R.A. (1992). Spatial patterns of food storage by Merriam's kangaroo rats. *Behavioral Ecology, 3*(1), 60-65.

Jorge, M.L.S., Brown, J.S., & van der Merwe, M. (2012). Handling time and the evolution of caching behavior. *Behavioral Ecology, 23*(2), 410-417.

Kamil, A.C., Krebs, J.R., & Pulliam, H.R. (Eds.). (2012). *Foraging behavior*. Springer Science & Business Media.

Kelley, L.A., & Clayton, N.S. (2017). California Scrub-Jays reduce visual cues available to potential pilferers by matching food colour to caching substrate. *Biology Letters, 13*(7), 20170242.

Kostrzewa, A., & Krauze-Gryz, D. (2020). The choice and handling of supplemental food by red squirrels in an urban park. *Behavioural Processes*, 104153.

Kulahci, I.G., & Bowman, R. (2011). Recaching decisions of Florida Scrub-Jays are sensitive to ecological conditions. *Ethology*, *117*, 700-707.

Logan, F.A. (1965a). Decision making by rats: Delay versus amount of reward. *Journal of Comparative and Physiological Psychology*, *59*(1), 1-12.

Logan, F.A. (1965b). Decision making by rats: Uncertain outcome choices. *Journal of Comparative and Physiological Psychology*, *59*(2), 246-251.

MacArthur, R.H., & Pianka, E.R. (1966). On optimal use of a patchy environment. *The American Naturalist, 100*(916), 603-609.

Marshall, T.J., Dick, M.F., & Guglielmo, C.G. (2016). Seasonal dietary shifting in yellow-rumped warblers is unrelated to macronutrient targets. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 192*, 57-63.

McFarland, D.J. (1977). Decision making in animals. *Nature*, *269*(5623), 15-21.

McNamara, J.M., & Houston, A.I. (1985). Optimal foraging and learning. *Journal of Theoretical biology*, *117*(2), 231-249.

Miller, G.A., & Viek, P. (1944). An analysis of the rat's response to unfamiliar aspects of the hoarding situation. *Journal of Comparative Psychology, 37*(4), 221.

Nellis, C.H., & Keith, L.B. (1968). Hunting activities and success of lynxes in Alberta. *The Journal of Wildlife Management, 32*(4), 718-722.

Neuschulz, E.L., Mueller, T., Bollmann, K., Gugerli, F., & Böhning-Gaese, K. (2015). Seed perishability determines the caching behaviour of a food-hoarding bird. *Journal Animal Ecology, 84*, 71-78.

Parrish, J.D. (1997). Patterns of frugivory and energetic condition in Nearctic landbirds during autumn migration. *The Condor, 99*(3), 681-697.

Pravosudov, V.V., & Roth II, T.C. (2013). Cognitive ecology of food hoarding: the evolution of spatial memory and the hippocampus. *Annual Review of Ecology, Evolution, and Systematics*, *44*, 173-193.

Price, M.V. & Jenkins, S.H. (1986) Rodents as seed consumers and dispersers. In D.R. Murray (Ed.), *Seed Dispersal* (pp. 191-235). Academic Press, Sydney, Australia.

Raby, C.R., Alexis, D.M., Dickinson, A., & Clayton, N.S. (2007). Planning for the future by Western Scrub-Jays. *Nature*, *445*(7130), 919-921.

Reichman, O.J. (1988). Caching behaviour by eastern woodrats, *Neotoma floridana*, in relation to food perishability. *Animal Behaviour*, *36*(5), 1525-1532.

Rojas-Ferrer, I., & Morand-Ferron, J. (2020). The impact of learning opportunities on the development of learning and decision-making: an experiment with passerine birds. *Philosophical Transactions of the Royal Society B, 375*(1803), 20190496.

Romanes, G.J. (1883). *Animal intelligence*. D. Appleton.

Rutter, R.J. (1972). The Gray Jay: A bird for all seasons. *Nature Canada*, *1*(4), 28-32.

Sechley, T.H., Strickland, D., & Norris, D.R. (2015). Linking the availability of cached food to climate change: an experimental test of the hoard-rot hypothesis. *Canadian Journal of Zoology*, *93*(6), 411-419.

Seiwa, K., Watanabe, A., Irie, K., Kanno, H., Saitoh, T., & Akasaka, S. (2002). Impact of site-induced mouse caching and transport behaviour on regeneration in Castanea crenata. *Journal of vegetation science*, *13*(4), 517-526.

Sherry, D. (1984). Food storage by Black-capped Chickadees: Memory for the location and contents of caches. *Animal Behaviour, 32*(2), 451-464.

Sherry, D. F. (1985). Food storage by birds and mammals. In S. Rosenblatt, C. Beer, M-C. Busnel, & P.J.B. Slater (Eds.), *Advances in the Study of Behavior* (pp. 153-188). Academic Press.

Sherry, D.F., Jacobs, L.F., & Gaulin, S.J. (1992). Spatial memory and adaptive specialization of the hippocampus. *Trends in neurosciences*, *15*(8), 298-303.

Shettleworth, S. J. (1998). *Cognition, evolution and behaviour*. Oxford University Press.

Shochat, E., Lerman, S.B., Katti, M., & Lewis, D.B. (2004). Linking optimal foraging behavior to bird community structure in an urban-desert landscape: field experiments with artificial food patches. *The American Naturalist*, *164*(2), 232-243.

Solheim, R. (1984). Caching behaviour, prey choice and surplus killing by Pygmy Owls *Glaucidium passerinum* during winter, a functional response of a generalist predator. *Annales Zoologici Fennici*, 21, 301-308.

Stephens, D.W., & Krebs, J.R. (1986). *Foraging theory*. Princeton University Press.

Strassman, J.E. (1979). Honey caches help female paper wasps (*Polistes annularis*) survive Texas winters. *Science*, *204*(4389), 207-209.

Strickland, D., Kielstra, B., & Norris, D.R. (2011). Experimental evidence for a novel mechanism driving variation in habitat quality in a food-caching bird. *Oecologia*, *167*(4), 943-950.

Strickland, D., & Norris, D.R. (2015). An example of phenotypic adherence to the island rule?–Anticosti Gray Jays are heavier but not structurally larger than mainland conspecifics. *Ecology and evolution*, *5*(17), 3687-3694.

Strickland, D. & Ouellet, H.R. (2020). Canada Jay (*Perisoreus canadensis*), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi-org.proxy1.lib.uwo.ca/10.2173/bow.gryjay.01

Sutton, A. (2020). *Demographic and Environmental Drivers of Canada Jay Population Dynamics in Algonquin Provincial Park, ON* [Doctoral dissertation, The University of Guelph].

Sutton, A.O., Strickland, D., Freeman, N.E., Newman, A.E., & Norris, D.R. (2019). Autumn freeze-thaw events carry over to depress late-winter reproductive performance in Canada Jays. *Royal Society Open Science*, *6*(4), 181754.

Sutton, A.O., Strickland, D., & Norris, D.R. (2016). Food storage in a changing world: implications of climate change for food-caching species. *Climate Change Responses*, *3*(1), 1-25.

Sutton, A.O., Strickland, D., Freeman, N.E., & Norris, D.R. (2020a). Climate-driven carry-over effects negatively influence population growth rate in a food-caching boreal passerine. *Global Change Biology*, *27*(5), 983-992.

Sutton, A.O., Strickland, D., Freeman, N.E., & Norris, D.R. (2020b). Environmental conditions modulate compensatory effects of site dependence in a food-caching passerine. *Ecology*, e03203.

Tomback, D.F., & Linhart, Y.B. (1990). The evolution of bird-dispersed pines. *Evolutionary Ecology*, *4*(3), 185-219.

Vander Wall, S.B. (1990). *Food hoarding in animals*. University of Chicago Press. Chicago, Illinois, USA.

Vander Wall, S.B. (1997). Dispersal of singleleaf pinon pine (Pinus monophylla) by seed-caching rodents. *Journal of Mammalogy*, *78*(1), 181-191.

Vander Wall, S.B., & Balda, R.P. (1977). Coadaptations of the Clark's Nutcracker and the pinon pine for efficient seed harvest and dispersal. *Ecological monographs*, *47*(1), 89-111.

Vander Wall, S.B., Hager, E.C., & Kuhn, K.M. (2005). Pilfering of stored seeds and the relative costs of scatter-hoarding versus larder-hoarding in yellow pine chipmunks. *Western North American Naturalist*, 65(2), 248-257.

Vernouillet, A., Casidsid, H.J.M., Kelly, D.M. (2021). Conspecific presence, but not pilferage, influences Pinyon Jays' (*Gymnorhinus cyanocephalus*) caching behaviour. *Learning & Behavior*, *49*, 23-35.

Waite, T.A. (1991). Economics and consequences of scatterhoarding in Gray Jays (*Perisoreus canadensis*). [Doctoral dissertation, The Ohio State University].

Waite, T.A. (2001). Intransitive preferences in hoarding Gray Jays (*Perisoreus canadensis*). *Behavioral Ecology and Sociobiology*, *50*(2), 116-121.

Waite, T.A., & Strickland, D. (2006). Climate change and the demographic demise of a hoarding bird living on the edge. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1603), 2809-2813.

Wasserman, E.A. (1993). Comparative cognition: Beginning the second century of the study of animal intelligence. *Psychological Bulletin*, *113*(2), 211.

Zimmerman, M. (1983). Plant reproduction and optimal foraging: experimental nectar manipulations in *Delphinium nelsonii*. *Oikos*, 57-63.

Chapter 2

2. Canada Jays (*Perisoreus canadensis*) identify and exploit coniferous cache locations using visual cues

2.1 Introduction

Food caching, the process of storing and subsequently recovering food for later consumption, is a strategy widely used by birds and mammals to survive periods of low food availability (Smith and Reichman, 1984; Sherry, 1985; Vander Wall, 1990). Food caching species can be broadly divided into two groups; *short-term* and *long-term* food-cachers (Vander Wall, 1990). Short-term food caching species typically cache and recover items to cope with immediate uncertainty or threats of pilferage and retrieve caches within hours to days of caching. Long-term food caching species, however, typically store for future needs, frequently leaving caches for periods of months before retrieval. The latter strategy is often employed in highly seasonal environments that experience long stretches of limited resources. These long-term caches are subjected to potentially harsh environmental conditions, putting them at a greater risk of degrading.

While most species cache non-perishable food items like acorns or seeds, this is not the case for all species (Vander Wall, 1990). Many vertebrates cache perishable food items such as fungi, fruits, arthropods, and vertebrate flesh (e.g. Chesemore, 1975; McCord and Cardoza, 1982; Strickland and Ouellet, 2020). A recent review by Sutton et al. (2016) discusses the susceptibility of caching species to climate change. As one might predict, long-term caching species which store perishable food items are among those most vulnerable.

Caching species use behavioural strategies which maximize cache preservation, including microhabitat preference, prey incapacitation, and physical manipulation of the environment (reviewed in Sutton et al., 2016). Previous studies have demonstrated that caching species have the ability to actively utilize aspects of their environment to aid in preserving caches. For example, Florida Scrub-Jays (*Aphelocoma coerulescens*) select for high-tannin acorns and will cache in and re-locate acorns to drier sites less vulnerable to degradation and germination (Fleck and Woolfenden 1997; Kulahci and Bowman 2011; Fuirst et al, 2020). Additionally, Spotted Nutcrackers (*Nucifraga caryocatactes*) also select cache-sites with similar favourable microclimatic conditions (Neuschulz et al, 2015). While these studies demonstrate that food-caching species exploit certain environmental characteristics, particularly lack of moisture, for food preservation, little information exists about species exploiting other aspects of the environment. In addition, many corvid species cache predominantly in the ground; food-caching animals that prefer arboreal sites likely select for different cache site characteristics.

Many migratory birds demonstrate preferences for particular plant species, often exploiting the resources these plants provide for foraging (e.g. Wood et al., 2012; Kirsch and Wellik, 2017; Morgan et al., 2018) or for breeding sites (e.g. Anderson and Shugart, 1974; Squires et al., 2018). The same is true of resident species (e.g. Narango et al., 2017; 2018), however, evidence of active environmental exploitation in a non-migratory caching species is more limited. Willow tits (*Poecile montanus*) prefer caching in conifer trees compared to deciduous trees, but these preferences are likely due to the physical characteristics of conifers in the winter (Lahti et al., 1998), and given the short-term caching nature of Willow tits, this preference likely has little to do with cache preservation and more to do with reducing risk of pilferage.

Canada Jays (*Perisoreus canadensis*) are resident species of the boreal and subalpine forests in North America and maintain year-round territories (Strickland and Ouellet, 2020). Canada Jays are a long-term food caching species which store perishable food items including berries, mushrooms, invertebrates, and carrion for overwinter survival and late-winter reproduction (Sutton et al., 2016; Strickland and Ouellet, 2020). Thus, cache perishability and preservation are vital factors that influence the viability of cached food for future consumption.

Evidence suggests that the breeding territories of Canada Jays are largely determined by habitat quality, particularly forest composition (Strickland et al., 2011). More specifically, habitat quality of Canada Jay territories has previously been defined by the proportion of conifers such as Black Spruce (*Picea mariana*), White Spruce (*Picea glauca*), and Balsam Fir (*Abies balsamea* (Strickland et al., 2011; Strickland and Ouellet, 2020). It has been suggested that the mechanism for this association is the ability of conifer species to preserve perishable food items better than deciduous trees do (Strickland et al., 2011; Sechley et al., 2015). This natural preservation, however, is only beneficial if jays can identify and exploit these locations' cache-sites when available. Unfortunately, because Canada Jay territories are large with a variety of geological features like lakes and rivers, it is extremely difficult to actively track jays to their caching locations, and so cache-site preferences have not been empirically examined in Canada Jays.

Here I used captive birds to experimentally test whether Canada Jays actively discriminate among tree species in their placement of caches in the laboratory. Additionally, I assessed the cues that individuals might use to make such assessments. My experiment tested Canada Jays' ability to identify and exploit conifer trees, which are proposed to be beneficial for the preservation of caches. Birds were allowed to freely cache perishable food items in a variety of experimental set-ups. I predicted that individuals would be able to identify and preferentially cache in conifers, particularly spruce, and avoid caching in deciduous trees. I also expected that Canada Jays would demonstrate the ability to identify preferred trees based on isolated olfactory and structural cues.

2.2 General Methods

2.2.1 Subjects

Eight adult Canada Jays were captured by Potter trap near Sudbury, Ontario, Canada (46.3946, -80.7982) during December 2018 and transported to the Advanced Facility for Avian Research, Western University, London, Ontario, Canada. Birds were housed individually or in pairs from capture until one week before the experiment in large, outdoor, free-flight rooftop aviaries. Aviaries ranged in size from 2.5 x 3.0 m to 3.0 x 3.5 m, all were 2.5 m in height. One bird was removed from Experiments Two and Three due to health concerns.

One week prior to the start of each experiment, I moved the birds indoors to individual cages (0.75 x 0.4 x 0.4 m) and set the light cycle to 10:14 h light:dark cycle (light onset 0700 h). Birds were physically, but not visually or acoustically, isolated from one another. Food and water were available *ad libitum* except as required by each experiment (described below). Food was a mixture of Mazuri Exotic Gamebird Starter (PMI Nutrition International, Brentwood, MO, U.S.A.), Mazuri Parrot Pellets (PMI Nutrition International), shell-less peanuts and sunflower chips, and was supplemented with a HARI PRiME vitamin, mineral and amino acid supplement (Rolf C. Hagen Incorperated, Baie d'Urfé, QC, Canada).

2.2.1.1 Ethical Note

All birds were handled and tested in accordance with the guidelines set out by the Canadian Council on Animal Care. Canada Jays were collected and housed under Ontario Ministry of Natural Resources Wildlife Scientific Collector's Authorization 1091668. This research was conducted under protocol number 2015-065 approved by the Western University Animal Care Committee.

2.2.2 Behavioural Observations

I tested birds in a free-flight observation room (2.7 x 2.7 m; Figure 2.1) which could be observed through a one-way mirror to allow live behavioural scoring. Remote doors on the opposite wall to the mirror allowed birds to enter and exit the room without being handled. During all trials cache sites were available in each of the four corners of the room. In Experiment One these cache sites were 4 sections of different tree species.

In Experiment Two, each corner contained a custom caching board with a different odour cue. In Experiment Three, the four corners contained artificial trees with different structural configurations. In all experiments the location of a particular cache site and its associated cues in a given trial was counterbalanced across all possible locations. Additionally, a table with food and water was always present in the center of the room. Food for all testing sessions was shredded cheddar cheese, which is a highly perishable food previously used in behavioural studies on Canada Jays (Sechley et al, 2014).

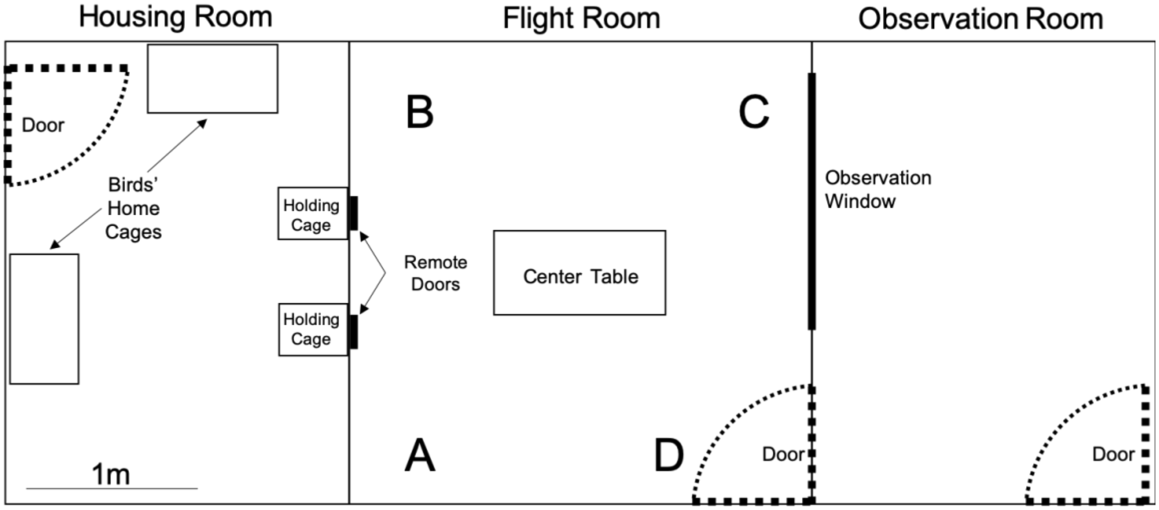


Figure 2.1 A scaled schematic of the experimental set up. Trials were run in a series of three conjoined rooms. Birds held in the Housing Room could be released into the Flight Room by an observer in the Observation Room operating the remote doors. Observers viewed trials through the one-way glass observation window. The symbols A, B, C, and D mark the locations of the stimuli, and a table with water and food were present in each trial. All doors remained closed during testing.

2.2.3 Training

Five days prior to the start of each experiment, the birds were allowed into the flight room in order to habituate. Four artificial trees were present in the room, one in each corner, along with the table containing food and water. Artificial trees consisted of a vertical 0.05 x 0.05 m wooden ‘trunk’ with 0.02 m diameter dowels protruding horizontally at varying heights. Each flight lasted 20 minutes, after which time the lights were turned off and birds were coaxed to return to their holding cages.

2.2.4 Behavioural Testing

All testing occurred between 0930 h and 1300 h (Figure 2.2). Birds were tested individually in two cohorts, each consisting of either three or four birds. At 0830 h, I transferred cohort 1 from their home cages into holding cages (0.4 x 0.3 x 0.3 m) where they were deprived of food for 1-2 h. Immediately prior to testing cohort 1 (0930 h), I transferred cohort 2 to holding cages and deprived them of food (resulting in 1.5-3 h of food deprivation). I tested cohort 2 immediately following the testing of cohort 1. Water remained available *ad libitum* in the holding cages. Because birds were tested one at a time, there were eight potential time slots each bird could be tested in. I changed the order of testing each day such that each bird tested in each of the possible time slots once. For Experiment One, there were eight possible slots, resulting in 8 trials per bird. For Experiments Two and Three, the slot originally occupied by the bird removed from the experiment was skipped, resulting in 7 trials per bird. The change in the order of testing was done to control for motivational differences, and so that food availability and length of deprivation was unpredictable to the birds.

A)

Day	**Time Slot**							
	Cohort One				Cohort Two			
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
1	1	2	3	4	5	6	7	8
2	6	7	8	5	2	3	4	1
3	3	4	1	2	7	8	5	6
4	8	5	6	7	4	1	2	3
5	5	6	7	8	1	2	3	4
6	2	3	4	1	6	7	8	5
7	7	8	5	6	3	4	1	2
8	4	1	2	3	8	5	6	7

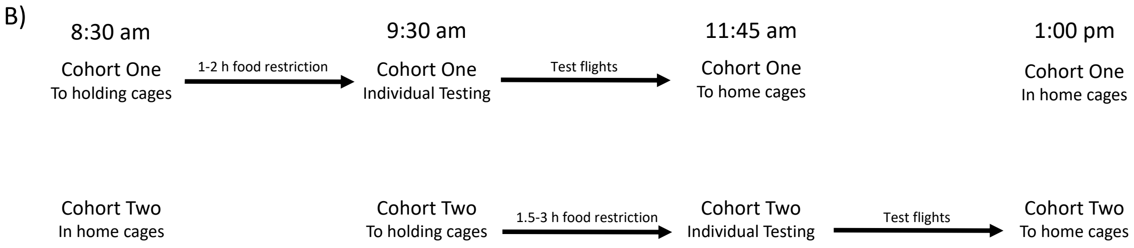


Figure 2.2 A schematic of the experimental design for all three experiments in this chapter. A) the daily order birds were tested in, and B) a flow chart showing how birds progressed through the procedure.

For each trial, a bird accessed the testing rooms through remote doors, controlled by the observer. While birds were in the flight room, an observer scored the location of the bird and any caching events. A caching event was defined as any time the bird deposited food in bolus form on any part of a tree and subsequently moved to a different location. Boluses deposited and immediately retrieved (without the bird moving) were not scored as caches. In addition, cheese left on flat surfaces, not in bolus form, were not scored as caches. Trials lasted 20 minutes, unless a bird remained stationary for five consecutive minutes at which point the trial was terminated. At the conclusion of a trial, the lights in the flight room were turned off, and the birds returned through the remote door to their holding cage unassisted. I returned the birds to their home cages after the completion of trials for their cohort.

2.2.5 Statistical Analysis

Alpha was set at 0.05 threshold for all analyses, and all analyses were performed using R Studio v1.1.456 (R Core Team, 2018). Linear mixed effects models were performed using the '*nlme*' package (Pinheiro et al., 2018), Poisson regressions were performed using the 'lme4' package (Bates et al., 2015), multiple comparisons were performed using the '*multcomp*' package (Hothorn et al., 2008) and all data was manipulated using the '*dplyr*' package (Wickham and François, 2018). All proportion data were arcsine transformed to correct for non-normality but for visual clarity untransformed proportion scores are presented in figures. Trials in which an individual did not interact with any of the stimuli are excluded from analysis for all exploration related measures (e.g., time spent, visits). For caching measures (e.g., total caches, cache proportion) only trials in which at least one cache was deposited were analyzed.

2.3 Experiment One: Site Identification and Exploitation

In this experiment I assessed jays' abilities to first identify and subsequently exploit beneficial cache locations. Birds were allowed to cache freely in any of four tree species available.

2.3.1 Methods

2.3.1.1 Observation room

Stimuli for Experiment One were sections of trees with distributions that overlap with the geographic range of Canada Jays in Ontario. I selected four sections from each of two coniferous species, Red Pine (*Pinus resinosa*), White Spruce (*Picea glauca*), and two deciduous species, Red Maple (*Acer rubrum*), and White Birch (*Betula papyrifera*; also referred to as paper birch) from Elginfield, Ontario (16 tree sections total). Tree sections were approximately 0.25 m in diameter and ranged in height from 1.7 to 2.7 m. Sections included intact portions of trees including the truck, branches and foliage, and were placed vertically with cut ends on the ground. For each testing day, a new spatial configuration of tree sections and new tree sections were used to control for both spatial preferences and possible preferences for particular tree sections.

2.3.1.2 Statistical Analysis

I used linear mixed effects models to analyze the number of visits to each tree species, the time birds spent in each tree species and location of birds' caches. For the time spent model, the proportion of time spent in a given tree species per trial was the response variable while for the cache location model, the proportion of caches per tree species in a given trial was the response variable. Trial number per bird was included as a within subjects factor, and individual was included as a random intercept.

To assess the exploitation of cache sites, I compared the caching rate per tree. Because caching rate was calculated as the number of caches made per ten minutes I used a Poisson regression. Tree type was included as a factor and individual was included as a random effect. I also assessed how likely an individual was to make a cache each visit to a particular tree using a second Poisson regression. The number of caches an individual made per 20 visits to a tree species was used as the dependent variable.

I used a one-way ANOVA to quantify differences in which tree species birds interacted with first on each trial. Data was collapsed across trials, as I had no reason to expect learning to occur due to the randomization of tree location and characteristics. The proportion of trials in which a bird interacted first with each species was included as the response variable.

2.3.2 Results

Birds interacted with at least one tree in all trials (n = 64) and deposited at least one cache during 81% of trials (n = 52).

2.3.2.1 First Tree Interaction

Canada Jays demonstrated a strong preference for which tree species they interacted with first ($F_{3,31} = 13.5$, $p < 0.0001$; Figure 2.3A). The random effects accounted for almost no variation, as both the marginal and conditional coefficients of determination were 0.57. Jays preferred the White Spruce over the Red Pine (Tukey's: $p = 0.0011$), Red Maple ($p < 0.0001$) and White Birch ($p = 0.0001$). All other comparisons were non-significant (Tukey's: $p > 0.05$ for all).

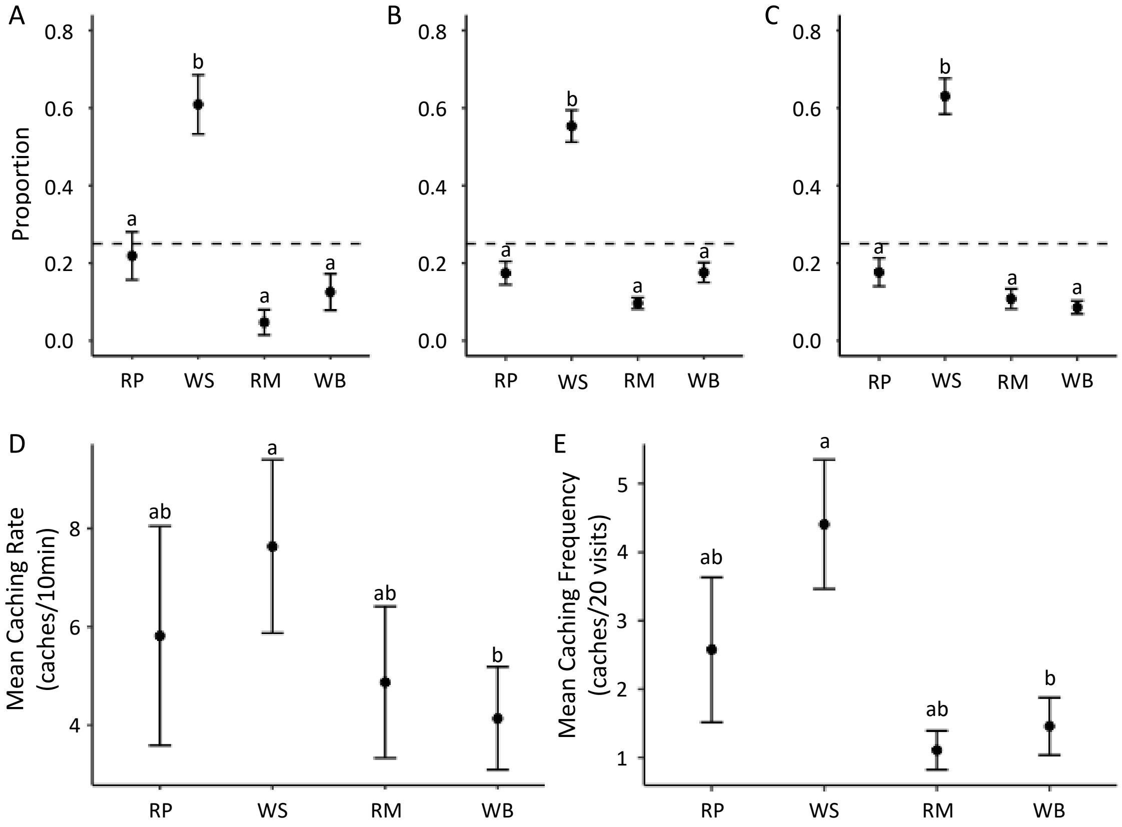


Figure 2.3 Top row: proportion of A) first visits, B) time spent and C) caches in branches of each tree species. Bottom row: mean number of D) caches deposited per 10 min block and E) caches deposited per 20 visits in branches of each tree species. Points represent group means (± SEM). Dashed lines represent the 0.25, chance level. Tree species are identified by two-letter abbreviations: RP, Red Pine; WS, White Spruce; RM, Red Maple; WB, White Birch. Lower-case letters that are not shared indicate a significant difference at $p < 0.05$.

2.3.2.2 Time Spent

Canada Jays also demonstrated a strong preference for the tree species in which they spent the most amount of time in ($F_{3,1} = 38.3$, $p < 0.0001$; Figure 2.3B). The marginal and conditional coefficients of determination were both 0.31. Jays spent the most time in the White Spruce (51.63% of all time) compared to Red Pine (20.01%; Tukey's: $p < 0.0001$), Red Maple (10.70%; $p < 0.0001$), or White Birch (17.66%; $p < 0.0001$) but showed no preferences between the other three trees (Tukey's: $p > 0.05$ for all remaining comparisons).

2.3.2.3 Cache Location

Canada Jays demonstrated a strong preference for tree species when caching ($F_{1,153} = 50.6$, $p < 0.0001$; Figure 2.3C). The marginal and conditional coefficients of determination were both 0.42. As with time spent, jays preferred to cache in White Spruce (63.08% of all caches) over Red Pine (17.64%; Tukey's: $p < 0.0001$), Red Maple (10.74%; $p < 0.0001$), and White Birch (8.54%; $p < 0.0001$) but showed no preferences between the other three trees (Tukey's: $p > 0.05$ for all remaining comparisons).

2.3.2.4 Caching rate and frequency

Tree species had a significant effect on the rate at which Canada Jays chose to cache in them ($\chi^2_3 = 9.56$, $p = 0.023$; Figure 2.3D). Canada Jays cached more frequently in the spruce tree over the White Birch (Tukey's: $p = 0.027$), however all other comparisons were not statistically significant.

Canada Jays' propensity to deposit a cache on a given visit also varied by tree species ($\chi^2_3 = 19.96$, $p < 0.0001$; Figure 2.3E). Canada Jays were more likely to make a cache on a given visit to the spruce tree rather than to either the maple (Tukey's: $p = 0.001$) or the White Birch ($p = 0.006$). Individuals were equally likely to deposit a cache when visiting either the spruce or pine trees.

2.3.2.5 Location of Inactivity

A total of twenty-five trials (39%) were ended due to inactivity, with each bird becoming inactive at least once. For 24 of these trials the inactivity occurred with the bird perched in a tree, while 1 ended with the bird on the ground. Of the 24 trials in which birds became inactive while perched, 18 (75%) occurred while the bird was in the White Spruce tree. The remaining trials were ended with birds perched in: Red Pine, 3; Red Maple, 1; White Birch, 2.

2.3.3 Discussion

Canada Jays were able to both identify and subsequently exploit beneficial conifer caching locations. Birds quickly identified and spent a disproportionate amount of time in the White Spruce tree, followed by the Red Pine. Additionally, Canada Jays cached at higher rates, and more frequently in the conifer species than the deciduous species.

The next step was to determine how birds are able to identify these locations. I tested whether the cue differentiating the preferred conifer species was olfactory.

2.4 Experiment Two: Olfactory Identification of Cache Sites

In this experiment I assessed birds' abilities to identify, and subsequently exploit cache sites based on olfactory cues. Because Canada Jays demonstrated a preference for conifer species in Experiment One, I used only conifer odours in this experiment.

2.4.1 Methods

2.4.1.1 Observation room

Stimuli for Experiment Two were custom made caching boards. Each board was 1.6 m x 0.25 m and contained 12, 0.5 cm diameter holes for caching. Caching holes were arranged in three columns, with holes in each column spaced 0.25 m apart. The lowest hole in the outer two columns was 0.80 m from the ground. Each hole had a perch 0.05 m below them. The lowest hole in the center column was at 0.68 m and holes in this column did not have perches. All caching locations were accessible to all birds.

Olfactory cues were provided by spraying one of four scented mixtures of water and commercially available essential oils (1% oil; Aliksir Essential Oils, Quebec, Canada) on each of four caching boards daily. Scented mixtures were shaken immediately before being sprayed and were sprayed until the caching board was visibly wet. Olfactory cues were easily detected by human researchers. Each scented mixture was applied to an individual board, resulting in four distinct scent caching boards.

I selected oils from four coniferous species as these species give off strong olfactory cues, and as a result of birds' demonstrated preferences for caching in conifer species (Experiment One). Scents selected for this experiment were white pine (*Pinus strobus*), White Spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and Eastern Hemlock (*Picea glauca*). For each testing day, a new spatial configuration of caching boards was used to control for spatial preferences.

2.4.1.2 Statistical Analysis

I used linear mixed effects models to analyze birds' tree species preferences for number of visits, time spent at each caching board and for cache location. In all models, trial number per bird was included as a within subjects factor, and bird id was included as a random intercept. I did not analyze the exploitation of site due to the low number of trials in which caches were deposited.

2.4.2 Results

Birds interacted with at least one caching board in 67% of trials (n = 32) and deposited at least one cache in 34% of those trials (n = 11). Canada Jays did not differ in the number of visits they made to a location ($F_{3,93} = 0.86$, $p = 0.47$; Figure 2.4A), the time they spent interacting with each of the scented caching boards ($F_{3,93} = 0.95$, $p = 0.42$; Figure 2.4B). Additionally, Canada Jays did not preferentially cache in any of the scented boards ($F_{3,30} = 0.88$, $p = 0.46$; Figure 2.4C). Random effects accounted for very little of the variation in any of the models. The marginal coefficients of determination were 0.01 for the number of visits, 0.02 for the time spent, and 0.06 for the proportion of caches. The conditional coefficients of determination were 0.30, 0.02, and 0.06 respectively.

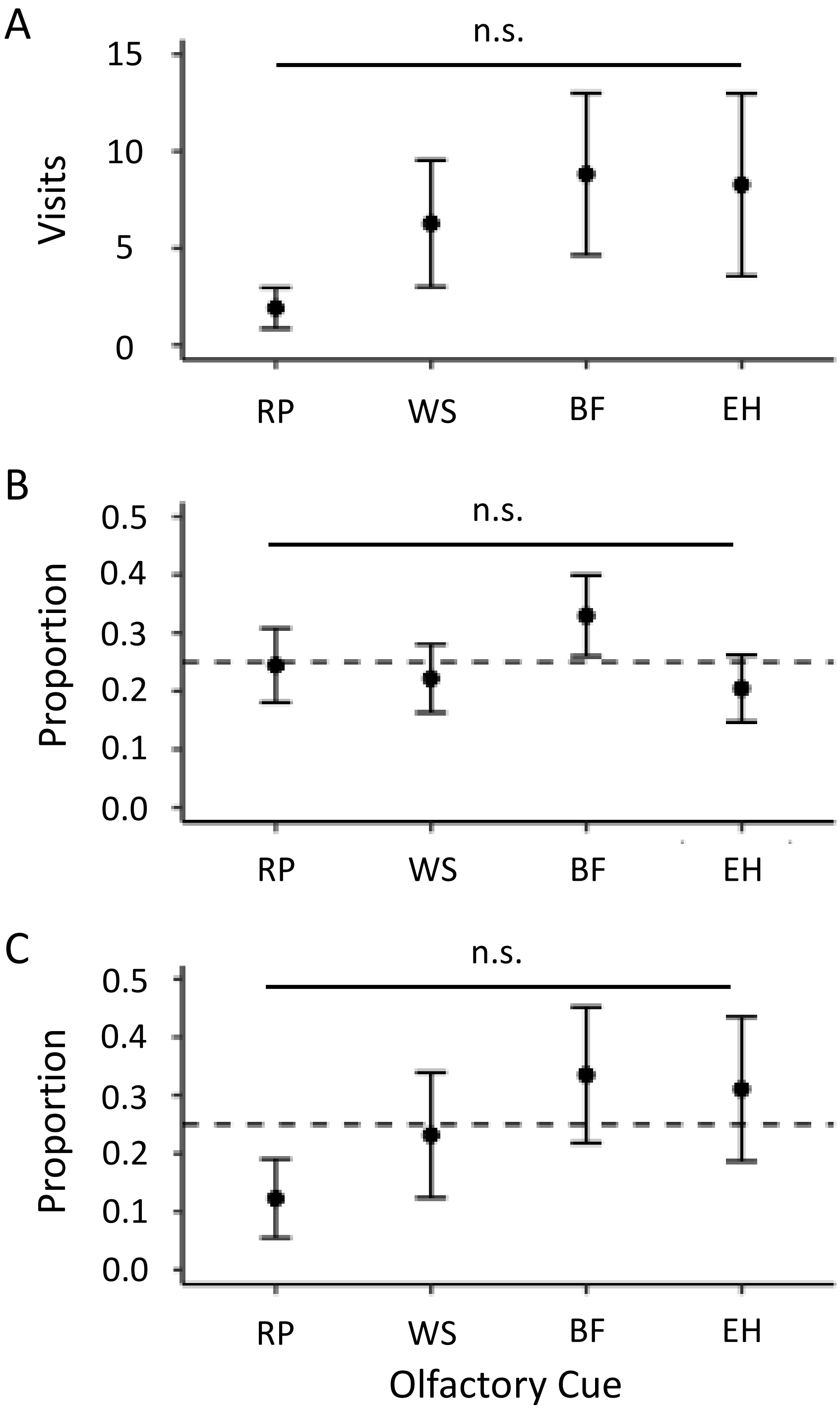


Figure 2.4 A) number of visits, B) proportion of time spent and C) proportion of caches deposited by birds in each of the four scented caching boards. The dashed line indicates chance, 0.25. Olfactory cues are identified by two-letter abbreviations:

RP, Red Pine; WS, White Spruce; BF, Balsam fir; EH, Eastern Hemlock. Alpha for all tests was set at 0.05, ‘n.s.’ indicates non-significant differences.

2.4.3 Discussion

I found no evidence to suggest that Canada Jays use olfactory cues alone to discriminate between potential caching sites. It is possible that olfaction still plays a role in the discrimination process but in the absence of additional cues, olfactory cues are not sufficient to elicit a behavioural response. A second apparent difference between the preferred conifer species in Experiment One was the structural properties of the trees.

2.5 Experiment 3 Three: Structural Identification of Cache Sites

In this experiment I assessed birds’ abilities to identify, and subsequently exploit cache sites based on structural cues, independent of any potential species specific information. There were no olfactory cues presented, and the only cues available were visual.

2.5.1 Methods

2.5.1.1 Observation room

Stimuli for Experiment Three were custom made artificial trees. Trees were composed of a 0.05 x 0.05 x 2.0 m trunk and 0.02 m diameter dowel branches of varying lengths at various heights. In total, all trees had a total branch length of 1.22 m, and mean branch height of 1.37 m. Trees were constructed to have either 2, 4, 6, or 8 evenly spaced branches in order to give the trees different structural configurations. Equal numbers of branches protruded in all directions for the 4- and 8-branch trees. Branches were perpendicular to one another on the 2-branch tree. The 6-branch tree had one branch protruding in each direction, with two additional branches that were perpendicular to one another as the lowest two branches. No branch protruded in the same direction as the branch either immediately above or below it. For each testing day, a new spatial configuration of trees was used to control for spatial preferences.

2.5.1.2 Statistical Analysis

I used linear mixed effects models to analyze birds' preferences for individual artificial trees for time spent, number of visits and caches deposited.

2.5.2 Results

Birds interacted with at least one artificial tree in all trials (n = 49) and deposited at least one cache in 98% of those trials (n = 48).

Birds demonstrated no preferences in the number of times they visited a particular tree ($F_{3,144} = 1.61$, $p = 0.19$; Figure 2.5A). The marginal coefficient of determination was 0.01, while the conditional coefficient of determination was 0.48. There was a main effect of structure on time spent ($F_{3,144} = 2.89$, $p = 0.04$; Figure 2.5B), but post-hoc tests revealed no significant pairwise differences (Tukey's: all comparisons > 0.05). Random effects contributed to almost none of the variation as the marginal and conditional coefficients of determination were both 0.04. Birds did, however, demonstrate a preference for the proportion of caches they deposited in each location ($F_{3,141} = 3.86$, $p = 0.01$; Figure 2.5C). The marginal and conditional coefficients of determination were both

0.06. Individuals cached significantly more items in the eight-branch tree than any of the other trees (Tukey's: all ≤ 0.05), but had no preference between the six-, four- and two-branch trees (all > 0.05).

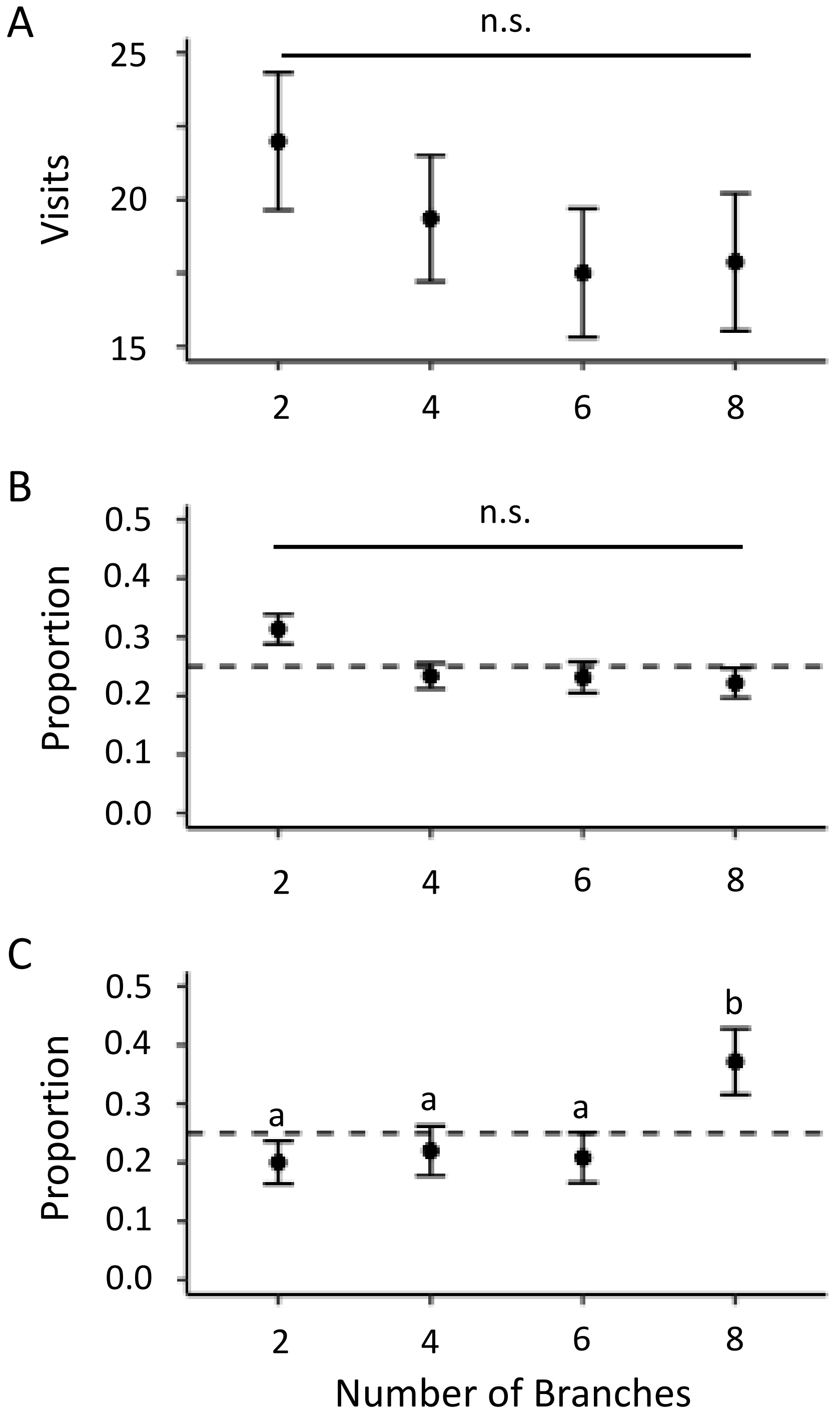


Figure 2.5 The A) number of visits, and mean proportions of B) time spent and C) caches deposited by birds in each of the four artificial trees. The dashed line indicates chance, 0.25. Structural cues are the number of branches on each tree (e.g.

2, two-branch). Lower-case letters that are not shared indicate a significant difference at $p < 0.05$, 'n.s.' indicates a non-significant difference.

2.5.3 Discussion

I found evidence that Canada Jays preferentially cached in the eight-branch tree. Because there were no differences in the time spent in each tree, I take this as evidence that Canada Jays are responding to the structural cues, and actively selecting the branchiest tree. I believe the main effect of location on time spent was driven by the increased time spent in the two-branch tree compared to the grouping of the other tree trees, but because there are no significant pairwise comparisons, I do not believe this effect is informative.

2.6 General Discussion

The aim of my study was two-fold. First, I assessed Canada Jays' ability to identify and exploit potentially beneficial cache locations, specifically spruce species. Second, I aimed to evaluate two potential cues that individuals could be using to carry discriminate among tree species. I found that Canada Jays quickly identify White Spruce and Red Pine, and preferentially cache in these species compared to deciduous trees, with a stronger preference for spruce trees. Further, I found evidence to suggest that Canada Jays use structural features of trees when making caching decisions, however, these same cues do not seem to play a role in Canada Jays' ability to initially identify conifer trees.

Conifer species, specifically spruce trees, have been proposed to preserve perishable food caches better than do other tree species (Strickland et al., 2011; Sechley et al., 2015). While the forest composition of territories jays inhabit has long been assumed to be related to food-caching preferences, my results provide a key empirical link to support that Canada Jays do indeed prefer to cache in tree species most suitable for long-term cache preservation. The active exploitation of conifers for caching helps explain the link between conifer density and Canada Jay territory occupancy described by Strickland et al. (2011). That is, territories with a higher proportion of spruce provide higher quality caching locations for long-term food storage and if individuals are exploiting these locations, then spruce-dominated territories are more likely to be occupied than other habitat types.

Additionally, I have shown that Canada Jays process and use structural cues when assessing potential cache locations. There are a variety of potential explanations for this preference. Perhaps the most obvious is that the trees with the most branches reflect most closely the physical characteristics of many conifer species, including spruce. The series of branches extending out from the trunk allows Canada Jays to move through the artificial tree most similarly to how individuals move through conifers. Additionally, it is possible that because there are more intersections with the trunk, there were more caching sites available. Birds cached along the entire length (including on the end) of branches, and although not explicitly measured, anecdotally the intersection of the branch and the trunk was a common caching location.

It is also possible that birds are selecting for these branchier physical features due to some benefit afforded to their caches when cached in such locations. For example, increased branchiness could provide more shade, similar to related species selecting for increased canopy cover (Neuschulz et al., 2015) Also, this shade could aid in decreasing temperatures around the cache, an essential component of cache preservation (reviewed in Sutton et al., 2016). It is also possible that caching in sites with increased branchiness serves to reduce cache-pilfering. Canada Jays' caches are most at risk from acute pilferage at the time of caching (Burnell & Tomback, 1985; Rutter, 1972), and caching amongst an abundance of branches may help to disguise the location of caches (broadly reviewed in Dally et al., 2006). Regardless of the benefits, it seems unlikely that Canada Jays are evaluating only structural cues to assess caching locations. Realistically, Canada Jays likely use some combination of cues, however, I have demonstrated that in absence of other cues, Canada Jays prefer cache locations that are structurally branchier.

Importantly, Canada Jays only used this structural information to inform their caching preferences. In Experiment Three, the effects seen in Experiment One regarding rapid identification and a preference for spending time in conifer trees, disappeared. I suspect this is because while the structural characteristics of the tree appear important for caching, they are less important or useful for discriminating tree species. Interestingly, olfactory cues had no impact on individuals' ability to discriminate potential locations. As noted above, Canada Jays are typically found in areas of dense conifer growth (Strickland & Ouellet, 2020). This suggests that Canada Jays may be reliant on habitat imprinting to identify particular species. Habitat imprinting (summarized in Immelmann, 1975), the preference for a habitat as an adult that was experienced early in life, could explain both birds' ability to identify conifer trees and their tendency to spend more time among them when all cues were available. If habitat imprinting is the mechanism of this behaviour, I suggest that habitat imprinting, at least in Canada Jays is primarily visual. In both Experiments Two and Three, when birds did not identify conifer trees, and had no preference for location, all the typical visual information was removed, leaving only olfactory (Exp Two) or structural (Exp Three) cues.

In general, food caching behaviour allows animals to cope with periods of resource scarcity. This behaviour, however, is only sustainable if species manage to avoid cache degradation. Caching species have developed many tactics to aid in cache-preservation, but active cache site exploitation has only been documented in a few instances (Fleck & Woolfenden, 1997; Kulahci & Bowman, 2011, Neuschulz et al., 2015, Fuirst et al., 2020). In these cases, ground-caching individuals attempted to mitigate the effects of soil moisture by caching items in drier locations. Canada Jays seemingly employ a similar strategy, but it is unlikely that these jays are attempting to manipulate cache microclimate moisture. More likely, Canada Jays are attempting to capitalize on and exploit the large percentage of volatiles in conifer resins (Langenheim, 2003; Strickland et al., 2011). Assuming caches made on spruce trees become covered in these antimicrobial and unpalatable resins, these stores would be less susceptible to degradation and more readily available for retrieval when required. This could become increasingly important as the climate in the boreal forest continues to change, and average temperatures continue to rise (Sutton et al., 2016).

Successful food caching is essential to long-term Canada Jay survival. Canada Jays rely on their caches for provisioning their offspring and are food limited during the breeding season (Derbyshire et al., 2015). Unexpected or increased degradation of caches can lead to population wide effects (Sutton et al., 2019, 2020), could have devastating long-term effects on populations of food-caching birds. Examples of such effects exist in other food-caching corvids and mammals, as well. For example, Clark's Nutcrackers (*Nucifraga columbiana*) have failed to breed on a population-wide scale when the pine-seed crop fails (Schaming, 2015), and wolverines (*Gulo gulo*) rely on cached food for successful early season breeding (Inman et al., 2012).

Canada Jays have a propensity to disperse caches evenly, or at least to avoid clustering caches by avoiding previously used locations (Waite and Reeve, 1994). While even distribution of caches may be beneficial where cache site quality is relatively even across the available home range, my results suggest when potential high-quality cache sites are limited, jays will cluster their caches in beneficial locations such as conifers, rather than cache in unfavorable locations such as deciduous trees.

Food-caching birds remember various details about their caches including location, contents, and even the relative time when the cache was made (Sherry, 1984; Clayton & Dickinson, 1998; and reviewed in Sherry, 2017). My results suggest food-caching species can actively evaluate and process information about cache sites prior to caching, in addition to retaining information about caches that have already been made. They also support the idea that Canada Jay breeding success, abundance, and distribution is closely associated with the availability of high-quality habitat, specifically a high density of spruce, because these trees may best preserve caches (Strickland et al., 2011; Sechley et al., 2015).

2.7 References

Anderson, S.H., & Shugart Jr, H.H. (1974). Habitat selection of breeding birds in an east Tennessee deciduous forest. *Ecology*, *55*, 828-837.

Bates, D., Maechler, M., Bolker, B., Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Burnell, K.L., & Tomback, D.F. (1985). Steller's Jays steal Gray Jay caches: field and laboratory observations. *The Auk*, 417-419.

Chesemore, D.L. (1975). Ecology of the Arctic Fox (*Alopex lagopus*) in North America - a review. In M.W. Fox (Ed.), *The Wild Canids: Their systematics, behavioral ecology and evolution.* (pp. 143-146). Van Nostrand Rheinhold, New York City, New York, USA.

Clayton, N.S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature*, *395*, 272.

Dally, J.M., Clayton, N.S., & Emery, N.J. (2006). The behaviour and evolution of cache protection and pilferage. *Animal Behaviour*, *72*(1), 13-23.

Fleck, D.C., & Woolfenden, G.E. (1997). Can acorn tannin predict scrub-jay caching behavior?. *Journal of Chemical Ecology*, *23*, 793-806.

Fuirst, M., Greer, J., & Bowman, R. (2020). Ontogeny of food-caching site preferences in young Florida Scrub-Jays: evidence of learning or changing social status? *Journal of Field Ornithology*, *91*(3), 241-253.

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal: Journal of Mathematical Methods in Biosciences*, *50*(3), 346-363.

Immelmann, K. (1975). Ecological significance of imprinting and early learning. *Annual Review of Ecology and Systematics*, *6*(1), 15-37.

Inman, R.M., Magoun, A.J., Persson, J., & Mattisson, J. (2012). The wolverine's niche: linking reproductive chronology, caching, competition, and climate. *Journal of Mammalogy*, *93*(3), 634-644.

Kirsch, E.M., & Wellik, M.J. (2017). Tree species preferences of foraging songbirds during spring migration in floodplain forests of the Upper Mississippi River. *The American Midland Naturalist*, *177*, 226-250.

Kulahci, I.G., & Bowman, R. (2011). Recaching decisions of Florida Scrub-jays are sensitive to ecological conditions. *Ethology, 117*, 700-707.

Lahti, K., Koivula, K., Rytkönen, S., Mustonen, T., Welling, P., Pravosudov, V.V., & Orell, M. (1998). Social influences on food caching in willow tits: a field experiment. *Behavioural Ecology*, *9,* 122-129.

Langenheim, J.H. (2003). *Plant resins: chemistry, evolution, ecology, and ethnobotany*. Timber Press, Portland, Oregon, USA.

McCord, C.M., & Cardoza, J.E. (1982). Bobcat and lynx. In G.A. Feldhamer, B.C. Thompson, J.A. Chapman (Eds.)*, Wild mammals of North America: Biology, management, economics. (pp. 728-766).* Johns Hopkins University Press, Baltimore, MD, USA.

Morgan, D.T., Green, M.C., Morrison, M.L., & Simpson, T.R. (2018). Tree Species Use and Seasonal Response to Food Availability of Black-Capped Vireo. *Southeastern Naturalist*, *17,* 560-583.

Narango, D.L., Tallamy, D.W., & Marra, P.P. (2017). Native plants improve breeding and foraging habitat for an insectivorous bird. *Biological Conservation*, *213*, 42-50.

Narango, D.L., Tallamy, D.W., & Marra, P.P. (2018). Nonnative plants reduce population growth of an insectivorous bird. *Proceedings of the National Academy of Sciences USA*, *115,* 11549-11554.

Neuschulz, E.L., Mueller, T., Bollmann, K., Gugerli, F., & Böhning-Gaese, K. (2015). Seed perishability determines the caching behaviour of a food-hoarding bird. *Journal of Animal Ecology*, *84,* 71-78.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D, & R Core Team (2018). _nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-137, URL: https://CRAN.R-project.org/package=nlme.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

Rutter, R.J. (1972). The Gray Jay: A bird for all seasons. *Nature Canada*, *1*(4), 28-32.

Schaming, T.D. (2015). Population-wide failure to breed in the Clark's Nutcracker (*Nucifraga columbiana*). *PLoS One, 10,* e0123917.

Sechley, T.H., Strickland, D., & Norris, D.R. (2014). Causes and consequences of pre-laying weight gain in a food-caching bird that breeds in late winter. *Journal of Avian Biology*, *45*, 85-93.

Sechley, T.H., Strickland, D., & Norris, D.R. (2015). Linking the availability of cached food to climate change: An experimental test of the hoard-rot hypothesis. *Canadian Journal of Zoology, 93, 411-419.*

Sherry, D.F. (1984). Food storage by Black-capped Chickadees: Memory for the location and contents of caches. *Animal Behaviour*, *32*, 451-464.

Sherry, D. F. (1985). Food storage by birds and mammals. In S. Rosenblatt, C. Beer, M-C. Busnel, & P.J.B. Slater (Eds.), *Advances in the Study of Behavior* (pp. 153-188). Academic Press.

Sherry, D.F. (2017). Food storing and memory. In C. Cate & S.D. Healy (Eds.), *Avian Cognition* (pp. 52-74). Cambridge University Press, Cambridge, UK.

Smith, C.C. & Reichman, O.J. (1984). The evolution of food caching by birds and mammals. *Annual Review of Ecology and Systematics*, *15*(1), 329-351.

Strickland, D. & Ouellet, H.R. (2020). Canada Jay (*Perisoreus canadensis*), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.

Strickland, D., Kielstra, B., & Norris, D.R. (2011). Experimental evidence for a novel mechanism driving variation in habitat quality in a food-caching bird. *Oecologia*, *167*, 943-950.

Sutton, A.O., Strickland, D., Freeman, N.E., Newman, A.E., & Norris, D.R. (2019). Autumn freeze-thaw events carry over to depress late-winter reproductive performance in Canada Jays. *Royal Society Open Science*, *6*(4), 181754.

Sutton, A.O., Strickland, D., Freeman, N.E., & Norris, D.R. (2021). Climate-driven carry-over effects negatively influence population growth rate in a food-caching boreal passerine. *Global Change Biology*, *27*(5), 983-992.

Sutton, A.O., Strickland, D., & Norris, D.R. (2016). Food storage in a changing world: implications of climate change for food-caching species. *Climate Change Responses*, *3*(1), 1-25.

Squires, K.A., & Bunnell, F.L. (2018). Early breeders choose differently – Refining measures of habitat quality for the Yellow-bellied Sapsucker (*Sphyrapicus varius*), a keystone species in the mixedwood boreal forest. *PLoS One*, *13*, e0203683.

Vander Wall, S.B. (1990). *Food hoarding in animals*. University of Chicago Press, Chicago, USA.

Waite, T.A., & Reeve, J.D. (1994). Cache dispersion by Grey Jays sequentially exploiting adjacent sources. *Animal Behaviour*, *47*(5), 1232-1234.

Wickham, H., François, R., Henry, L., & Müller, K. (2018). dplyr: A Grammar of Data Manipulation. R package version 0.7.6. URL: https://CRAN.R-project.org/package=dplyr

Wood, E.M., Pidgeon, A.M., Liu, F., & Mladenoff, D.J. (2012). Birds see the trees inside the forest: the potential impacts of changes in forest composition on songbirds during spring migration. *Forest Ecology and Management*, 280, 176-186.

Chapter 3

3. Canada Jays (*Perisoreus canadensis*) employ multiple context-dependent cache protection strategies

3.1 Introduction

Food caching, the storing of food for subsequent retrieval and consumption, is a behavioural strategy employed by a wide variety of species. While many taxonomic groups include food caching species, most caching species are birds and mammals (Smith & Reichman, 1984). Food caching is employed to alleviate predictable, future food-scarce conditions caused by environmental variation (Smith & Reichman, 1984). Food-scarce conditions often coincide with winter, making caching species (particularly those at high latitudes) dependent on stored food for extended periods.

Though caching behaviour varies greatly between species (e.g. cache dispersal, time to retrieval), some commonalities do exist. In particular, regardless of caching behaviour, caches are exposed to a variety of potential threats. Environmental threats such as exposure to weather (Sutton et al., 2016), environmental variables (e.g. moisture) or climatic conditions (Sutton et al., 2019), may be unavoidable but others, such as threats from cache-robbers, can be more actively mitigated.

Cache-robbers, or cache-pilferers, are conspecific or heterospecific individuals that retrieve and consume the caches of another individual. This can reduce the original cacher's available food reserve by as much as 30% (reviewed in Vander Wall & Jenkins, 2003). Cache robbers may use external cues (e.g. olfaction: Buitron & Nuechterlein, 1985), or encounter stored food by chance (e.g. Kamil & Balda, 1985). While larder hoarding species that make few large caches have the opportunity to defend these caches against potential robbers (e.g. Clarke & Kramer, 1994), scatter-hoarding species that cache each item in a separate location typically do not (reviewed in Dally et al., 2006). Nonetheless, scatter hoarding species must employ some measures to deter cache-robbers, to ensure that their caches are available at retrieval.

Researchers have attempted to understand and categorize the strategies used by scatter hoarding species to minimize cache robbery (reviewed in Dally et al., 2006). These include *out-of-sight*, hiding food out of sight of potential cache-robbers (e.g. Dally et al., 2005), *hard-to-see,* disguising or camouflaging cached items (e.g. Kelley & Clayton, 2017), *spacing*, distributing items widely or ‘optimally’, (e.g. Sherry et al., 1982; Waite & Reeve, 1995), and *re-caching*, re-caching the same food item repeatedly to prevent its location being known (e.g. Emery & Clayton, 2001; Clary & Kelly, 2001). More broad strategies include *up-regulation*, increasing the overall number of caches (Bossema, 1979), *down-regulation*, decreasing the overall number of caches (Stone & Baker, 1989; Clary & Kelly, 2011) or *cessation*, (Burnell & Tomback, 1985) of caching behaviour.

Canada Jays (*Perisoreus canadensis*) are year-round residents of the Canadian boreal forest and parts of the Western United States. They are long-term scatter-hoarders that rely on their cached food stores to both survive winter and to provision their offspring (Derbyshire et al., 2019; Strickland & Ouellet, 2020), though the extent to which they provision their offspring remains unclear. The importance of food caching to Canada Jays makes the consequences of cache robbery particularly acute. Steller's Jays (*Cyanocitta stelleri*), and Blue Jays (*Cyanocitta cristata*) pose a particular threat to the caches of Canada Jays (Burnell & Tomback, 1985; Rutter, 1972). Previous research on caching in the presence of potential cache-robbers yielded mixed results: free-living Canada Jays continued to cache with cache-robbers in the area but captive individuals did not (Burnell & Tomback, 1985). These conclusions, however, were based on small sample sizes. Other species of jays also show context dependent caching in the presence of potential cache robbers (Bossema, 1979; Goodwin, 1956; Emery & Clayton, 2001; Emery et al, 2005, Vernouillet et al., 2021).

My goal was to characterize more completely the strategies used by Canada Jays to mitigate the risk of cache-robbing. Specifically, I evaluated 1) broad scale strategies affecting overall caching frequency, and 2) secondary strategies that could further mitigate risk of cache loss. I recorded Canada Jay caching behaviour in captivity in the presence versus absence of a potential cache-robber (a mounted model Blue Jay, hereafter 'model jay'), in an environment that allowed caching in sight of versus out of sight of the model robber. I hypothesised that Canada Jays would employ a combination of cache protection strategies to mitigate the risk of cache-robbery in the presence of a potential cache-robber.

3.2 Methods

3.2.1 Subjects

Study subjects were seven adult Canada Jays, caught using Potter traps near Sudbury, Ontario, Canada (46.3946, -80.7982) in December 2018 and 2019 and housed at the Advanced Facility for Avian Research in London, Ontario, Canada. Some birds had participated in previous experiments, and all birds had previous experiences caching in a laboratory setting. Prior to the experiment, birds were individually housed in large, covered, outdoor, free flight aviaries (3.5 x 3.0 x 2.5 m). For the duration of the experiment (5 Oct – 8 Nov, 2020) birds were housed indoors in individual home cages (0.75 x 0.4 x 0.4 m) and were held on a 10:14 h light:dark cycle (light onset 0730 hours). Birds were physically but not visually or acoustically isolated during this time.

Except as described below, birds were provided with *ad libitum* food and water, and birds were free to cache in their indoor home cages or outdoor aviary. Food was a mixture of Mazuri Exotic Gamebird Starter (PMI Nutrition International, Brentwood, MO, U.S.A.), Mazuri Parrot Pellets (PMI Nutrition International), shell-less peanuts and sunflower chips, and was supplemented with a HARI PRiME vitamin, mineral and amino acid supplement (Rolf C. Hagen Incorporated, Baie d'Urfé, QC, Canada).

3.2.2 Ethical Note

All birds were captured, handled and tested in accordance with the guidelines set out by the Canadian Council on Animal Care. Canada Jays were collected and housed under Ontario Ministry of Natural Resources Wildlife Scientific Collector's Authorization 1091668. This research was conducted under protocol number 2019-065 approved by the Western University Animal Care Committee.

3.2.3 Testing Apparatus

I used a three-part observation suite (Figure 3.1) to observe caching behaviour in a free flight room (2.6 x 2.6 x 2.7 m). Birds were allowed to enter though doors controlled by researchers in an adjacent room, who observed birds through a one-way mirror. During all trials the observation room contained two White Spruce (*Picea glauca*) trees, a food and water table, and a stand (0.6 x 0.6 x 1.6 m) on which to present the model jay. Depending on the caching context, a black screen (1.7 x 2.5 m) and a recorded Blue Jay call were also present. The call always accompanied the model jay, played at semi-random intervals (13 calls/minute, smallest interval 1s, largest 6s) and was audible in all parts of the room. Shredded cheese was provided on the food table for Canada Jays to cache.

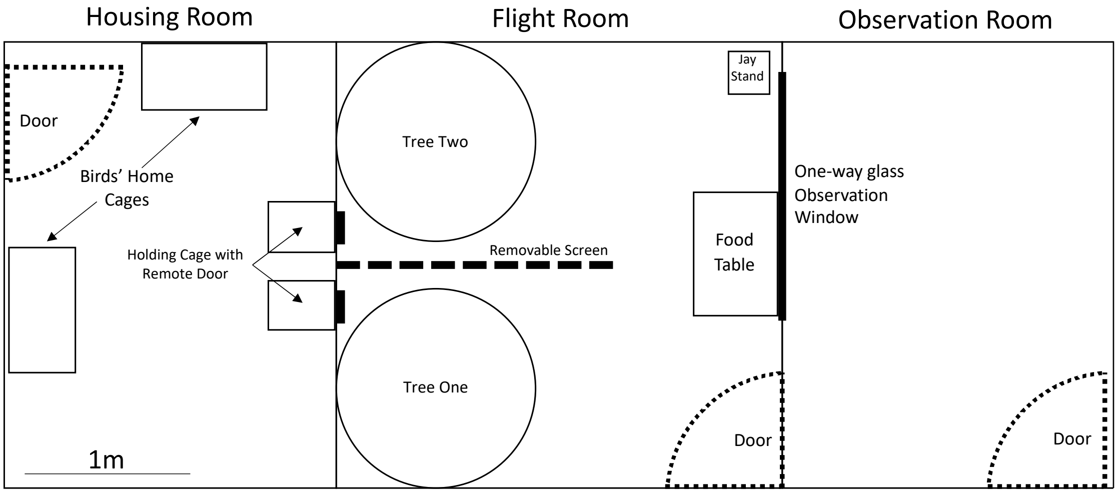


Figure 3.1 The captive testing set-up. Canada Jays were housed in individual home cages in the housing room and were transferred daily to holding cages. Birds' access to the flight room via trap doors was controlled from the observation room. Observers scored behaviour through a one-way glass observation window.

3.2.4 Caching Contexts

Birds cached in each of four distinct caching contexts; 1. *Control* (no screen, no model jay), 2. *Model-Unobstructed* (no screen, model jay), 3. *Model-Obstructed* (screen, model jay), and 4. *Screen-Control*; (screen, no model jay). These caching contexts were created by adding or removing the black screen and model jay from the testing room. When the screen was present, it was positioned so that the model jay was not visible from any part of the tree behind the screen.

3.2.5 Testing Procedure

Testing occurred over a five-week period, with each week consisting of five consecutive testing days, and two consecutive rest days. All birds were tested sequentially on each testing day, with no more than one bird in the free flight room at a time. This resulted in 5 trials per bird, per context. For all rest days, birds had access to *ad libitum* food and water, and were not removed from their home cages.

The first week was used for habituation and training. On each of the five testing days, birds were transferred from their home cages to small holding cages (0.4 x 0.3 x 0.3 m), and immediately entered the free flight room one at a time through remote doors connected to their holding cages. For all habituation flights both trees, the food and water tables and the model jay stand were present in the room. The model jay was not present. Birds were free to explore and interact with all items and trees. No food was available on the table, but the food dish was presented empty. Water was freely available throughout all sessions. At the conclusion of 20 minutes, the lights were turned off and the remote doors were opened. An observer entered the free flight room, and coaxed birds to return to their holding cages using a mesh net. Observers stopped entering the room once birds returned on their own. These sessions were not scored.

For all subsequent weeks, birds were exposed to one of the four caching contexts. All birds experienced the contexts in the following order: *Control, Model-Unobstructed, Model-Obstructed, Screen-Control,* and all contexts were consistent for the full testing week (5 testing days and two rest days). Birds were transferred to their holding cages one hour after light onset (0830) and were food deprived until their testing began. Birds were provided access to water during food deprivation. Birds entered the free flight room, one at a time, beginning at 0930 (minimum 1h food deprivation). Birds were tested in a different order each day, such that no bird was tested in the same sequential order twice in the same week. After the first four birds were tested, these birds were returned to their home cages to reduce unnecessary food deprivation. Each trial lasted 15 minutes.

Birds accessed the free flight room through remote-controlled doors connected directly to their holding cages, as they did during the habituation sessions. Birds were free to explore the room and interact with any of the objects in the room. An observer scored birds' position in the room, which included all visits to trees, food table, screen, mounted jay, and all caching events. At the conclusion of the trial, the lights were turned off, the remote door opened, and birds returned to their holding cages unassisted.

3.2.6 Behavioural Data

Three locations in the flight cage were defined: Tree One (out of view of the model in the Model-Obstructed context), Tree Two (in view of the model), and the model jay with its stand. A visit was defined as any occasion the bird landed in a location after having previously been in another location. Instances in which a bird was in one location, left, and returned without landing in a different location were not scored as a different visit. For each trial, I scored *visits* (number of visits to each location in the trial); *total duration* (total time the individual spent in each of the three locations, time spent at the food table or elsewhere in the room was excluded); *mean duration* (mean duration of all visits the bird made to a location in a trial). I also noted *total caches* as the total number of caches made by a bird in a trial. A caching event was defined as any event where a Canada Jay deposited food in bolus form, a manipulated, saliva covered piece of food, and subsequently moved away. Leaving cheese on branches in its original shredded form, leaving cheese on the table or the ground, or depositing then immediately eating a bolus without first leaving and returning, were not scored as caching events. For each tree I also calculated *caching preference* as the number of caches made in the tree as a proportion of the total caches made in both trees combined.

3.2.7 Statistical Analysis

To evaluate the effect of context I used a series of linear mixed effects model (LMM) using the ‘nlme’ package (Pinheiro et al., 2018) in R Studio v1.1.456 (R Core Team, 2018). For overall caching propensity, the initial model included *total caches* as the dependent variable and included only caching context as the independent variable. The models used to assess *caching preference*, *mean duration*, *total duration* and *visits* all initially included both context and location as within subject factors. Non-significant terms were removed from the models using backwards stepwise elimination (excluding the *total caches* model as it only had one variable initially). For the *caching preference* model, location included Tree One and Tree Two. For the *mean duration*, *total duration* and *visits* models, location included Tree One, Tree Two and the model jay with its stand. In all models, individual was included as a random factor contributing one score to each context. Significant main effects and interactions were further explored with Tukey’s HSD tests, using the ‘multcomp’ package (Hothorn et al, 2008), t-tests and one-way ANOVAs. All proportion data used to evaluate *caching preference* were arcsine transformed prior to analysis. Untransformed values are shown in figures for clarity.

3.3 Results

3.3.1 Caching Behaviour

Context had a significant effect on the total number of caches ($F_{3, 18} = 3.50$, $p = 0.04$; Figure 3.2A). The marginal coefficient of determination was 0.20 and the conditional coefficient of determination was 0.93. Jays made significantly fewer caches in the *Model-Unobstructed* condition than in either the *Model-Obstructed* condition (Tukey's HSD: $p = 0.04$) or the Control condition ($p = 0.02$). No other differences between contexts were significant. Notably, the *Model-Obstructed* context, with the model jay and the screen present, did not differ from either of the control conditions.

Overall, birds made a greater proportion of caches in Tree One, the tree with an obstructed view of the model, than Tree Two ($F_{1, 24} = 6.30$, $p = 0.02$), with a significant interaction between tree preference and context ($F_{3, 24} = 5.58$, $p = 0.005$; Figure 3.2B). The marginal and conditional coefficients of determination were both 0.30. Post hoc tests showed jays made a significantly greater proportion of caches in Tree One than in Tree Two in the *Model-Obstructed* context (t-test: $t_6 = 5.59$, $p = 0.001$) but in none of the other contexts.

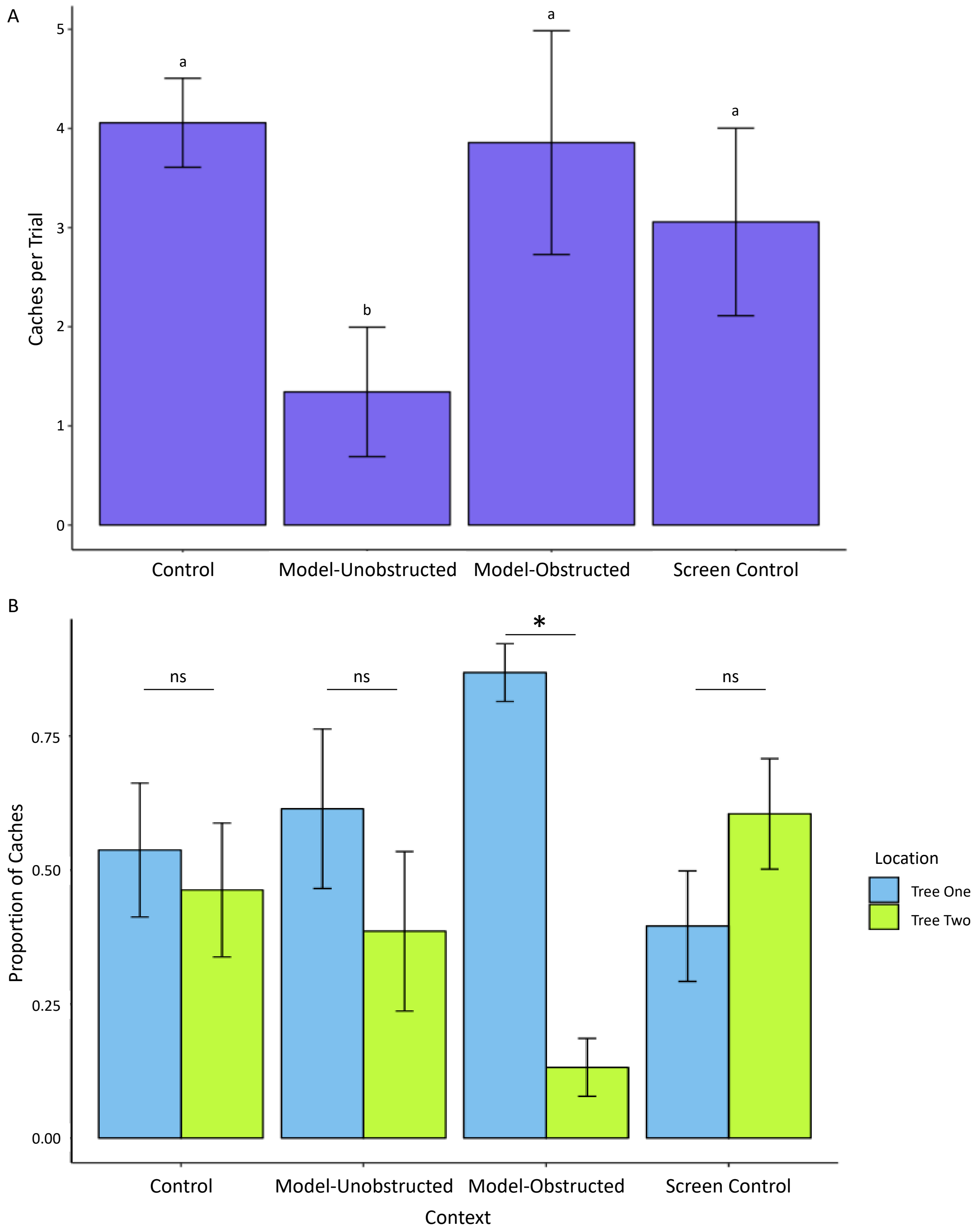


Figure 3.2 A. Caches per trial in the four experimental contexts. B. Proportion of caches made in Trees One and Two. Tree One was out of view of the model cache robber in the *Model-Obstructed* context. Bars that do not share a lowercase letter

differ significantly. The * represents a significant difference $p = 0.001$, and 'ns' represents no significant difference ($p > 0.05$). Error bars denote ± SEM in both panels.

3.3.2 Movement Behaviour

Total duration did not vary by context, but did vary with location ($F_{2, 48} = 11.90$, $p < 0.001$; Figure 3.3A). The interaction between context and location was not significant ($F_{6, 48} = 0.86$, $p = 0.53$). The marginal coefficient of determination was 0.24, and the conditional coefficient of determination was 0.36. Birds spent significantly more time in Tree One than in Tree Two (Tukey's HSD: $p = 0.03$) and more time in Tree One than at the model jay and its stand ($p < 0.001$). In no context did total duration differ between Trees One and Two (all comparisons: $p > 0.05$).

Mean duration did not differ among contexts, but did differ among locations ($F_{2, 48} = 7.15$, $p < 0.001$; Figure 3.3B). The interaction between location and context was not significant ($F_{6, 48} = 0.96$, $p = 0.46$). The marginal coefficient of determination was 0.18, and the conditional coefficient of determination was 0.41. For both trees, the mean duration of visits was longer than the mean duration of visits to the model jay and stand (Tree One $p = 0.02$; Tree Two $p < 0.001$). The mean duration of visits did not differ between trees (Tukey's HSD: $p = 0.96$)

Visits did not differ among contexts, but did differ among locations ($F_{2, 48} = 11.16$, $p < 0.001$; Figure 3.3C). There was no interaction between context and location ($F_{6, 48} = 1.29$, $p = 0.28$). The marginal coefficient of determination was 0.22, and the conditional coefficient of determination was 0.49. Birds visited Tree One significantly more than either Tree Two (Tukey's HSD: $p < 0.001$) or the model jay ($p = 0.002$). Visits to Tree Two and the model jay did not differ ($p = 0.94$). In the *Model-Obstructed* context, birds visited Tree One significantly more than Tree Two (Tukey's HSD: $p = 0.02$). In all other contexts, visits to the two trees did not differ (all comparisons, $p > 0.05$).

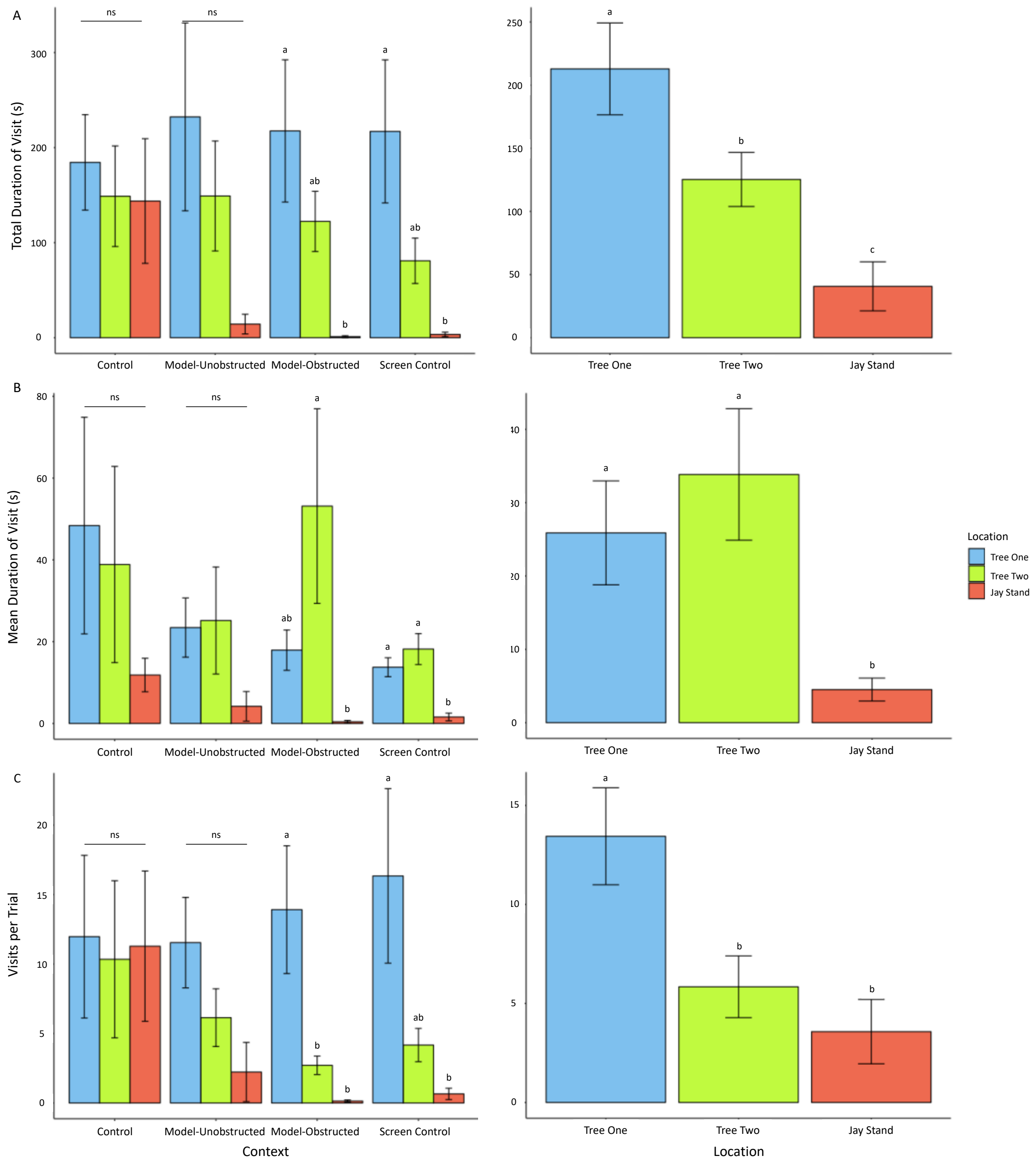


Figure 3.3 Movement behaviour of Canada Jays by context and location (left column) and pooled across context (right column). A. Total duration, B. Mean duration, C. Visits. Bars that do not share a lowercase letter differ significantly, and 'ns' represents no significant differences. Error bars denote ± SEM in all panels.

3.4 Discussion

The objective of this research was two-fold, 1) to assess the broad scale strategies affecting overall caching frequency used by Canada Jays, and 2) to assess the use of secondary strategies potentially employed by Canada Jays within the confines of these broad scale strategies. I found evidence for both a broad scale strategy, *cache-depression*, and for multiple secondary strategies, the *out-of-sight* and *spacing* defence strategies. Additionally, I found that Canada Jays may use their location in the room to reduce cache robbery.

Canada Jays down-regulated but did not cease caching when all potential cache sites were in view of the model cache-robber in the *Model-Unobstructed* context. In this context and the *Control* and *Screen-Control* contexts, the proportion of caches placed in Trees One and Two did not differ significantly, suggesting they used a *spacing* strategy to protect their caches. Such cache dispersal has been reported in Canada Jays in the wild (Waite and Reeve, 1992; 1994; 1995), indicating that captivity did not influence the jays' strategy of cache defence by spacing.

When jays had the opportunity to cache out of view of the model cache-robber in the *Model-Obstructed* context, the number of caches made did not differ significantly from the *Control* and *Screen-Control* contexts. However, jays placed over 80% of their caches in the tree that was out of view of the model cache-robber, consistent with the *out-of-sight* cache defence strategy. This preference for the tree out of view of the model cache-robber did not occur in any other context and suggests that this is an active behavioural choice.

While it is possible that because all birds experienced the contexts in the same order, context order had an effect on caching behaviour, this seems unlikely. Birds demonstrated the same overall caching levels and lack of tree preferences in the first context, *Control*, as they did in the final context, *Screen-Control*. It is also unlikely that the birds' return to original caching levels in the *Model-Obstructed* context was the result of habituation to the model. While habituation may explain the increased caching in isolation, it fails to explain the strong caching preference birds exhibited in this context.

Although jays demonstrated a caching preference in the *Model-Obstructed* context, they did not spend significantly more time in the tree out of view of the model. On the contrary, the mean duration of visits to the tree that was in view of the model were actually longer than the mean duration of visits to the tree that was out of view (50s vs. 20s; Figure 3.3B,), though not significantly so. This may indicate a preference to minimize time spent in the location where caches are made in the *Model-Obstructed* context.

The ability to flexibly employ context-dependant cache defence strategies suggests that Canada Jays are well equipped to minimize cache loss due to robbery, particularly that resulting from being observed by potential cache-robbers. Canada Jays' tendency to spend more time in view of the model cache-robber suggests that the birds were not bothered by the robber's general presence, but instead used visual information (presence of a potential cache robber) to inform their caching decisions (use of the *out-of-sight* defence in the robber-screen context) and also prioritized it when making caching decisions. By contrast, research on other corvids suggests that just the presence of a potential threat is enough to cause changes in caching behaviour (Clary & Kelly, 2011, Vernouillet et al., 2021). This is possibly due to the acute nature of cache robbery risk that Canada Jays experience from Blue Jays (Rutter, 1972) and Steller's Jays (Burnell & Tomback, 1985). Both species have been documented stealing Canada Jay caches soon after deposition, and actively following Canada Jays in order to steal caches (Burnell & Tomback, 1985; Rutter, 1972).

Canada Jays also appear to have evolved a behavioural pattern of cache dispersal that protects against cache loss due to random encounter or external cues. The wide dispersal of Canada Jay caches, both in the wild and demonstrated by the use of *spacing* in the laboratory, decreases the likelihood that the location of one cache by a cache-robber increases the chance that subsequent caches will also be discovered. This pattern appears to be consistent both in the laboratory, as I have shown, and in the wild when no threats are present (e.g. Waite & Reeve, 1994). Such consistency suggests that this strategy, *spacing,* is likely the most frequently employed, serving as a default to ensure a minimum level of cache protection, but that this behaviour can be superseded by an acute threat.

Reducing cache losses is essential to Canada Jays, as to any species that relies on stored food to survive food scarce periods. Because some sources of cache loss, like degradation due to environmental factors, are outside the reasonable control of caching individuals, mitigating those that are within an individual's control becomes more important. Context dependent usage of cache protection strategies, such as cache-depression, caching out-of-sight, optimally spacing caches and avoiding the locations of already deposited caches, allow Canada Jays to mitigate the overall cache losses they might otherwise suffer, and allow for a reliable food source through food scarce winters.

3.5 References

Bossema, I. (1979). Jays and oaks: an eco-ethological study of a symbiosis. *Behaviour, 70*(1-2), 1-116.

Buitron, D., & Nuechterlein, G.L. (1985). Experiments on olfactory detection of food caches by Black-billed Magpies. *The Condor, 87*(1), 92-95.

Burnell, K.L., & Tomback, D.F. (1985). Steller's Jays steal Gray Jay caches: field and laboratory observations. *The Auk, 102*(2), 417-419.

Clarke, M.F., & Kramer, D.L. (1994). The placement, recovery, and loss of scatter hoards by Eastern Chipmunks, *Tamias striatus*. *Behavioral Ecology, 5*(4), 353-361.

Clary, D., & Kelly, D.M. (2011). Cache protection strategies of a non-social food-caching corvid, Clark's Nutcracker (*Nucifraga columbiana*). *Animal Cognition, 14*(5), 735-744.

Dally, J.M., Clayton, N.S., & Emery, N.J. (2006). The behaviour and evolution of cache protection and pilferage. *Animal Behaviour*, 72(1), 13-23.

Dally, J.M., Emery, N.J., & Clayton, N.S. (2005). Cache protection strategies by Western Scrub-Jays, *Aphelocoma californica*: implications for social cognition. *Animal Behaviour*, 70(6), 1251-1263.

Derbyshire, R., Norris, D.R., Hobson, K.A., & Strickland, D. (2019). Isotopic spiking and food dye experiments provide evidence that nestling Canada Jays (*Perisoreus canadensis*) receive cached food from their parents. *Canadian Journal of Zoology, 97*(4), 368-375.

Emery, N.J., & Clayton, N.S. (2001). Effects of experience and social context on prospective caching strategies by scrub jays. *Nature, 414*(6862), 443-446.

Emery, N.J., Dally, J.M., & Clayton, N.S. (2005). The social suppression of caching in Western Scrub-Jays (*Aphelocoma californica*). *Behaviour, 142*(7), 961-977.

Goodwin, D. (1956). Further observations on the behaviour of the jay *Garrulus glandarius*. *Ibis, 98*(2), 186-219.

Hothorn T., Bretz F., and Westfall P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50(3), 346--363.

Kamil, A.C., & Balda, R.P. (1985). Cache recovery and spatial memory in Clark's Nutcrackers (*Nucifraga columbiana*). *Journal of Experimental Psychology: Animal Behavior Processes, 11*(1), 95.

Kelley, L.A., & Clayton, N.S. (2017). California Scrub-jays reduce visual cues available to potential pilferers by matching food colour to caching substrate. *Biology letters*, *13*(7), 20170242.

Pinheiro J., Bates, D., DebRoy, S., Sarkar, D., R Core Team (2018). _nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-137, <URL: https://CRAN.R-project.org/package=nlme>.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rutter, R.J. (1972). The Gray Jay: A bird for all seasons. *Nature Canada*, *1*(4), 28-32.

Sherry, D., Avery, M., & Stevens, A. (1982). The spacing of stored food by Marsh Tits. *Zeitschrift für Tierpsychologie* (*Journal of Comparative Ethology*), *58*(2), 153-162.

Smith, C.C., & Reichman, O.J. (1984). The evolution of food caching by birds and mammals. *Annual Review of Ecology and Systematics*, *15*(1), 329-351.

Stone, E.R., & Baker, M.C. (1989). The effects of conspecifics on food caching by Black-capped Chickadees. *The Condor*, *91*(4), 886-890.

Strickland, D. & Ouellet, H.R. (2020). Canada Jay (Perisoreus canadensis), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.gryjay.01

Sutton, A.O., Strickland, D., & Norris, D.R. (2016). Food storage in a changing world: implications of climate change for food-caching species. *Climate Change Response*s, *3*(1), 1-25.

Sutton, A.O., Strickland, D., Freeman, N.E., Newman, A.E., & Norris, D.R. (2019). Autumn freeze-thaw events carry over to depress late-winter reproductive performance in Canada Jays. *Royal Society Open Science*, *6*(4), 181754.

Vander Wall, S.B., & Jenkins, S.H. (2003). Reciprocal pilferage and the evolution of food-hoarding behavior. *Behavioral Ecology*, *14*(5), 656-667.

Vernouillet, A., Casidsid, H.J.M., Kelly, D.M. (2021). Conspecific presence, but not pilferage, influences Pinyon Jays' (*Gymnorhinus cyanocephalus*) caching behaviour. *Learning & Behavior*, *49*, 23-35.

Waite, T.A., & Reeve, J.D. (1992). Gray Jay scatterhoarding behavior, rate maximization, and the effect of local cache density. *Ornis Scandinavica*, *23*(2), 175-184.

Waite, T.A., & Reeve, J.D. (1994). Cache dispersion by Grey Jays sequentially exploiting adjacent sources. *Animal behaviour*, *47*(5), 1232-1234.

Waite, T.A., & Reeve, J.D. (1995). Source-use decisions by hoarding Gray Jays: effects of local cache density and food value. *Journal of Avian Biology*, *26*(1), 59-66.

Chapter 4

4. Canada Jays (*Perisoreus canadensis*) do not “plan for the future”

4.1 Introduction

Intentional future planning is a complex learned cognitive ability (reviewed in Schacter et al., 2012), historically thought to be unique to humans (Suddendorf & Corballis, 1997; Roberts, 1998). The Bischof-Köhler hypothesis (Suddendorf & Corballis, 1997) states that humans are the only species able to act in the present in anticipation of future needs, and that behaviour in other species that appears to meet this requirement is either innate or the result of the animal’s current state. Numerous studies have challenged this idea and attempted to show various aspects of future planning in animals (e.g. Clayton & Dickinson, 1998, Babb & Crystal, 2005; and reviewed in Clayton et al., 2003, Roberts, 2012).

Because they cache food in the present and consume it days to months later, and because they rely on memory to find their caches, food-caching birds, especially corvids, have been the subjects of many of these studies (e.g. Clayton & Dickinson, 1998; Clayton & Dickinson, 1999; Feeney et al., 2009; Zinkivskay et al., 2009). There have been critiques of these claims of future planning ability, however (e.g. Suddendorf & Corballis, 1997, 2007; Roberts, 1998), with one of the most common criticisms being that there are explanations for the results that do not involve future planning (e.g. Suddendorf & Corballis, 2007, 2008, 2010).

One well-known study of future planning by corvids (see Roberts, 2007; Shettleworth, 2007) assessed the ability of Western Scrub-Jays (*Aphelocoma californica*) to anticipate their future access to food and plan for it accordingly (Raby et al., 2007). Birds were found to anticipate their future needs by caching more food in the location in which food was not usually available. When food of a particular type was only available in one location, and food of a different type only available in another location, birds distributed their caches so that both food types were available in both locations. The researchers concluded that the birds anticipated their future state, and, motivated by anticipated future need for food, acted in advance to provide food for the future. These findings directly challenge the Bischof-Köhler hypothesis.

The purpose of my study was to test whether Canada Jays (*Perisoreus canadensis*) would exhibit future planning, in this case planning for predictable food restriction, using methods adapted from Raby et al.'s (2007) original study of future planning in Western Scrub-Jays. Canada Jays are year-round residents of the Nearctic boreal forest and can be found throughout Canada and parts of the northern United States. Canada Jays rely on cached food, in the form of saliva covered boluses (Dow, 1965), to survive periods of food scarcity in winter (Strickland & Ouellet, 2020) and use memory to recover their caches (Bunch & Tomback, 1986).

4.2 Methods and Materials

4.2.1 Subjects and Husbandry

Six wild-caught Canada Jays housed at the Advanced Facility for Avian Research at Western University, London, Ontario, Canada were used for this study. Individuals had been in captivity for between 8 and 18 months prior to the start of the experiment. All individuals had captive caching experience prior to the beginning of this experiment. Birds were caught under Ontario Ministry of Natural Resources Wildlife Scientific Collector's Authorization Permit 1091668. All activities, including housing and testing, were completed in accordance with all local, provincial and federal regulations and laws, and all procedures were approved and conducted under Western University Animal Care Committee permit 2019-065.

Birds were held on a 10 L:14 D h photoperiod and housed individually in free flight home cages (1.0 x 1.5 x 2.0 m) or experimental cages (0.6 x 1.8 x 0.6 m). Birds were physically, but not visually or acoustically isolated regardless of cage. Home cages and experimental cages were in separate rooms. Home cages contained perches of varying sizes, and, while in their home cages, birds had access to *ad libitum* food and water. Experimental cages were divided into three adjacent compartments; A, B and C, which could be either connected or separated using removable barriers (Figure 4.1). Each of the three compartments (0.6 x 0.6 x 0.6 m) was furnished according to its purpose. Compartments A and C had two standard 12-cube ice cube trays to provide potential caching locations, while compartment B was left empty. One tray was mounted to the side wall of the cage vertically, while the second tray was left on the ground. Food was available in the appropriate compartment (as described below), and water was available *ad libitum*.

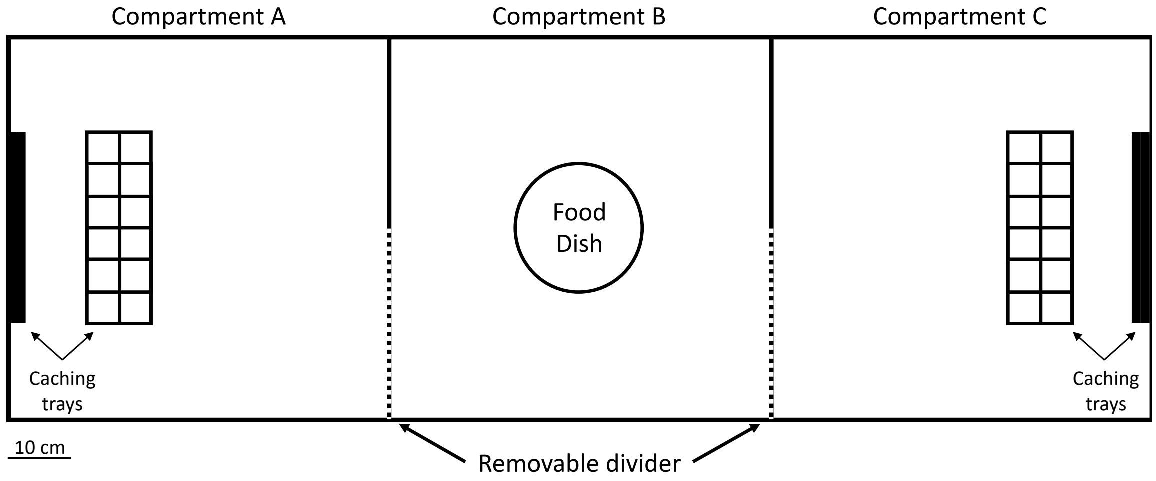


Figure 4.1 The experimental cage, to scale. Each compartment measured 0.6 x 0.6 m; compartments A and C each contained 2 caching trays, one mounted vertically to the cage wall and one placed flat on the ground. Dashed lines indicate removable dividers, while solid lines indicate non-removable barriers.

4.2.2 General Procedure

I conducted the experiments during four consecutive weeks. During the first week I conducted the *Preparing for Breakfast* experiment (Figure 4.2A), followed by the *Breakfast Choice* experiment (Figure 4.2B) in the second week. I then repeated the *Preparing for Breakfast* experiment two additional times during weeks three and four. All food introduced was novel at the time of first introduction, and no obvious preferences were observed between foods.

4.2.3 Preparing for Breakfast Procedure

Between 15:30 and 16:00 daily birds were transported from their home cages and confined to Compartment B of the experimental cage, where they were food deprived for 1.5 h. At 17:30 I provided birds with 10 g of powdered cat food (IAMS Proactive Health Adult Hairball Care, Mars Incorporated, USA) that could not be cached and removed the dividers giving birds access to explore all three compartments. Birds were allowed access to the cat food for 0.5 h, at which time (18:00) the food was removed, the lights were shut off, and the birds were re-confined to Compartment B, where they remained overnight. The following morning at 08:00, birds were confined to either Compartment A or Compartment C, and either provided with an additional 10g of cat food (Feeding Condition), or no food at all (Fasting Condition). Food availability by compartment was consistent throughout training and was counterbalanced between birds such that three birds experienced the Fasting Condition in Compartment A, and three experienced the Fasting Condition in Compartment B. Birds were confined to their designated compartments for 2.0 h, after which time individuals were transported back to their home cages. Each bird completed 6 training trials, on consecutive days. Birds alternated between the Feeding Condition and the Fasting Condition such that each bird experienced each condition on three training trials, and no bird experienced the same condition on two consecutive days.

Test trials took place on the first day following the training trials. The test trials followed the procedure for the training trials beginning at 15:30; however, at 17:30 birds were given 15g of cacheable, whole cat food in place of the powdered cat food.

Additionally, at 18:00 the birds were transported back to their home cages. Birds were not given the opportunity to recover their caches. I repeated the experiment three times, in weeks one, three and four. Procedures and conditions were identical in all three repetitions.

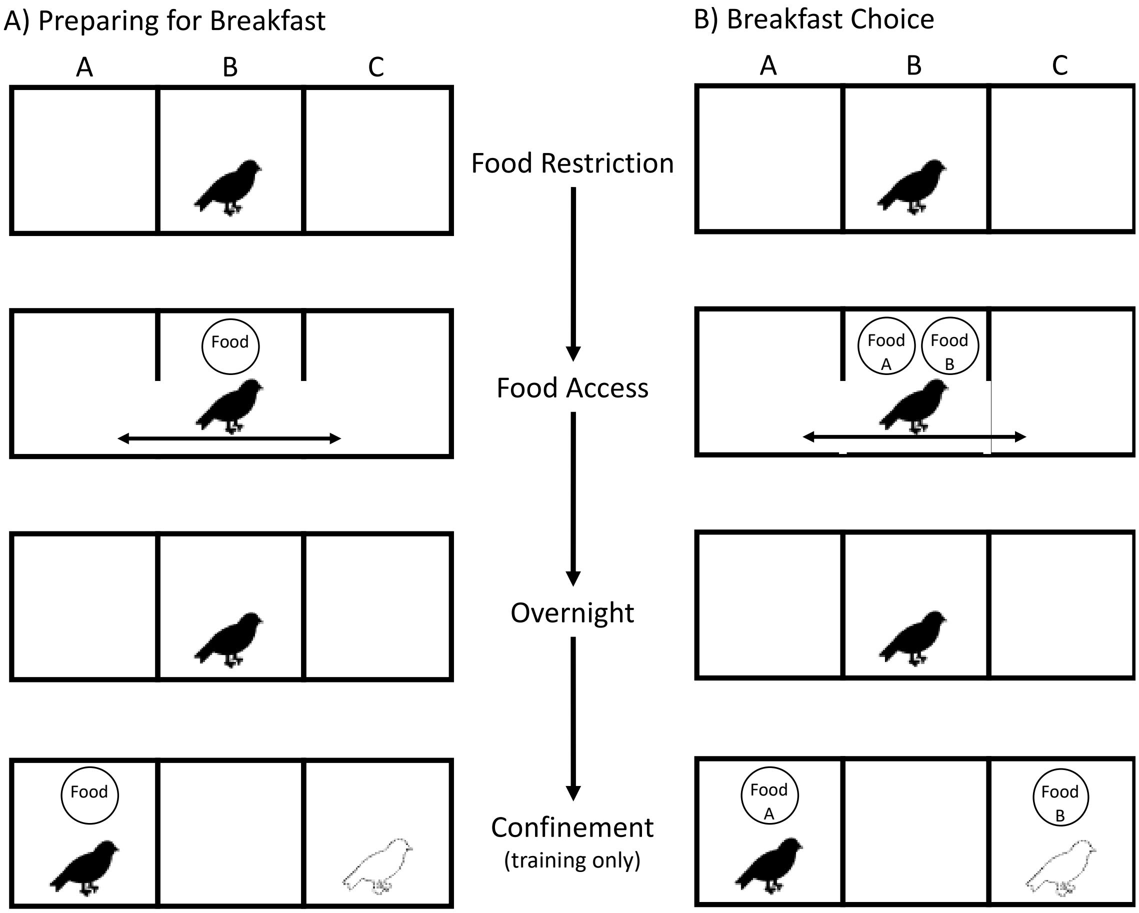


Figure 4.2 A flow chart for both the Preparing for Breakfast and Breakfast Choice experiments showing the progression of a single bird through a single trial. Black birds indicate the compartment in which the bird is confined. White, outlined birds illustrate the alternate condition. Powdered food was provided for training trials, and whole food was provided during test trials. The Confinement phase was not completed during test trials.

4.2.4 Breakfast Choice Procedure

Breakfast Choice followed the same procedure as the *Preparing for Breakfast* experiment, except that the Fasting Condition was replaced with a second Feeding Condition in which a different food item, powdered Cheerios (Cheerios, General Mills, USA), was available. On training days, birds were offered 10 g of both powdered cat food and powdered Cheerios in separate dishes placed equidistant from compartments A and C. The following morning birds were confined to either Compartment A or Compartment C and provided with either 10 g of powdered cat food, or 10 g of powdered Cheerios, depending on which compartment they were confined to. The food type offered in each compartment was again consistent throughout training, and counterbalanced between birds, such that three birds experienced cat food in Compartment A and Cheerios in Compartment B, and three birds experienced the opposite. On test day, birds were provided with 15 g each of whole cat food and whole cheerios to cache. Birds were free to cache either food type in either chamber.

4.2.5 Statistical Analysis

For the initial *Preparing for Breakfast* (week 1) experiment, I used a paired *t*-test to compare food items cached in the Food and No Food compartments. For the combined *Preparing for Breakfast* experiments (weeks 1,3,4) and for the *Breakfast Choice* experiment, I used a repeated measures ANOVA to compare the distribution of cached items. For all tests, n = 6, alpha = 0.05, and all analyses were carried out using R Studio v1.1.456 (R Core Team, 2018).

4.3 Results

4.3.1 Preparing for Breakfast

Over three iterations of the *Preparing for Breakfast* experiment, individuals cached more food items in the Feeding compartment than the Fasting compartment ($F_{1,16} = 12.18$, $p = 0.003$; Figure 2A). The total number of caches made did not vary between iterations ($F_{1,11} = 0.04$, $p = 0.85$), with mean values of 8, 7.5, and 8.5 caches per bird per iteration. Additionally, there was no interaction between compartment and iteration ($F_{1,16} = 0.19$, $p = 0.67$).

4.3.2 Breakfast Choice

Birds showed no caching preferences for food items or chambers. The total number cached of each food item did not differ significantly ($F_{1,15} = 3.07$, $p = 0.10$), nor did the total number of food items cached in each chamber ($F_{1,15} = 2.50$, $p = 0.13$). Most importantly, the jays showed no preference for which food items were cached in which chamber ($F_{1,15} = 0$, $p = 1$, Figure 4.3B). Three birds cached a total of 0 items, while the other three birds averaged 6 total caches.

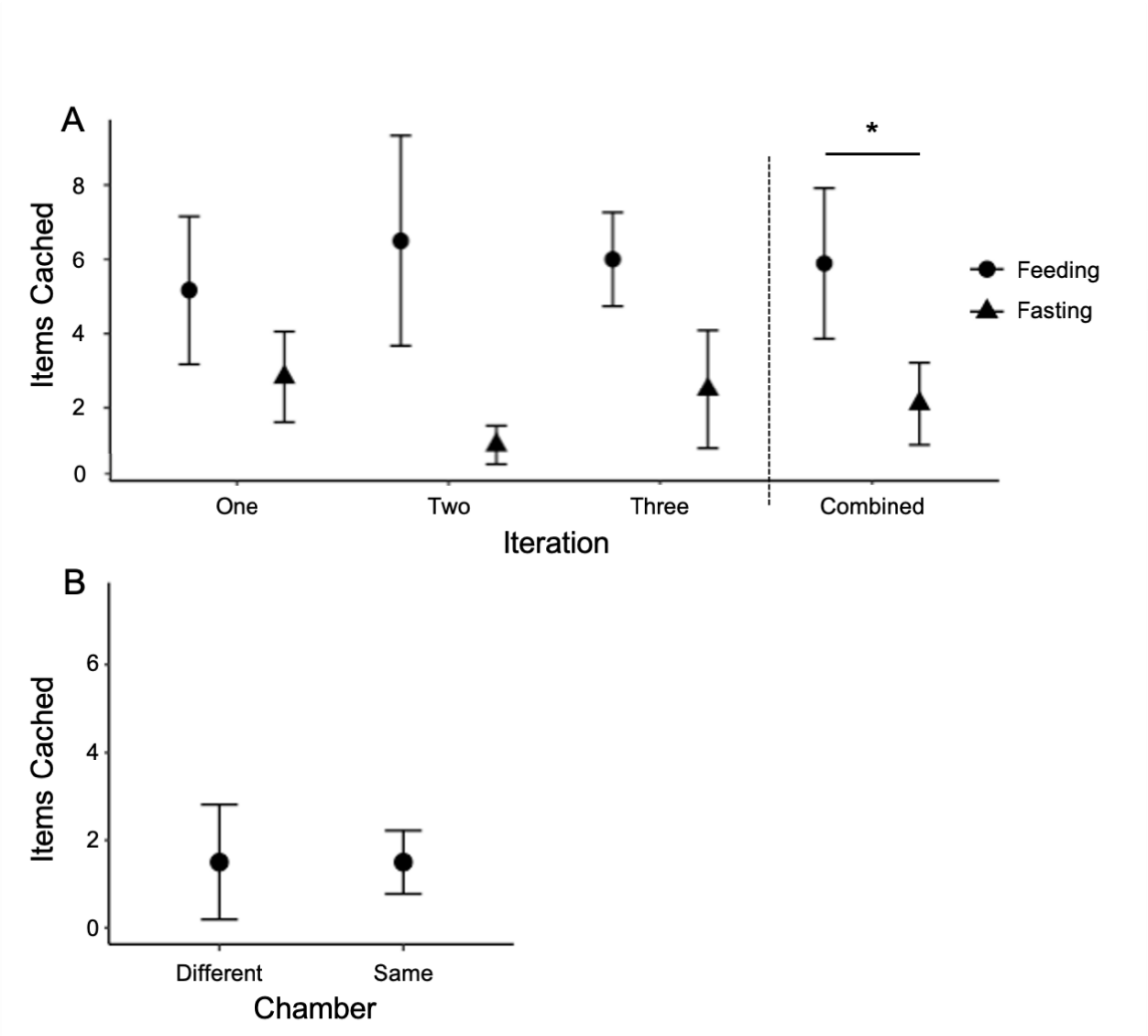


Figure 4.3 The mean number of items cached in each compartment. A) The number of cached items in the Feeding and Fasting compartments across the three iterations of the Preparing for Breakfast experiment, with values for all iterations combined at right. Asterisk indicates a significant difference, p = 0.003. B) The number of items cached in the compartment initially containing food of the Same or Different type in the Breakfast Choice experiment.

4.4 Discussion

I did not observe the behaviour described by Raby et al. (2007) and found, moreover, that, when given three iterations of the experiment, Canada Jays cached significantly more food where they had previously found food, the opposite of the result obtained with Western Scrub-Jays. These results indicate that Canada Jays do not plan for the future in the context of caching food preferentially in locations where food is otherwise not available. There are two broad reasons my results may differ from those of Raby et al (2007), 1) species differences between Canada Jays and Western Scrub-Jays, and 2) differences in experimental procedures or conditions.

The Western Scrub Jay genus *Aphelocoma* belongs to the monophyletic clade of New World jays while *Perisoreus*, the Canada Jay genus, is a Holarctic genus in a corvid group that includes the genera *Corvus* and *Garrulus* (Bonaccorso & Peterson, 2007; Huang & Ruan, 2018). Western Scrub-Jays are found in oak and oak-pine woodlands (Curry et al., 2020), and Canada Jays in boreal forest dominated by White and Black Spruce (Strickland & Ouellet, 2020). Despite these differences, similarities between the species are also plentiful. Both species are non-migratory and omnivorous. Both species recover some stored food soon after caching it but leave much of their cached food in place for months (Curry et al., 2020; Strickland & Ouellet, 2020). Both retrieve stored food by remembering the spatial locations of caches (Bunch & Tomback, 1986; Balda & Kamil, 1989; Clayton et al., 2001). It is not obvious that one species would be more predisposed to future planning than the other. The ecological cost of being denied access to cached resources would undoubtedly be high for Western Scrub-Jays, but the potential cost for Canada Jays would be as high, or higher, given their direct reliance on cached food for survival. Assuming that continuous access to cached resources is motivating the future planning observed in the Raby et al. (2007) conclusions, I would expect Canada Jays to be equally, or perhaps more, motived to ensure this access. It is of course possible that Western Scrub-Jays have evolved this ability to ‘plan for the future’ in response to some ecological constraint that Canada Jays do not encounter, or that Canada Jays have found some alternative mechanism of coping with a similar constraint. I find this unlikely, however, given Canada Jays increased reliance on cached food items for survival.

Furthermore, the hypothesis tested by Raby et al. (2007) was not explicitly that Western Scrub-Jays are adaptively specialized for future planning but instead that scrub-jays possess episodic-like memory for caching episodes and “To the extent that episodic memory and future planning depend on common processes, the caching behaviour of these birds should reflect an ability to anticipate future need states” (Raby et al., 2007, p.919). In addition, it is argued that prospection and other forms of complex cognition are traits of the corvids in general and not restricted to the New World jays (Clayton & Emery, 2004; Correia et al., 2007).

It is possible that unknown confounding factors influenced either the results of my study or the Raby et al. (2007) results. For example, it is possible that extra-apparatus cues were present in either experimental set up, or that researchers were in some way biasing individuals’ responses during experiment set up. These unintentional, and unforeseeable factors could explain my failure to replicate. I again, however, find this explanation unlikely. I was able to follow the elegantly simple design of the Raby et al. (2007) experiment closely, including the arrangement of compartments A, B, and C, the use of cacheable and non-cacheable foods, the timing of events in the procedure, and statistical treatment of the results. Raby et al. (2007) observed 8 birds in the *Preparing for Breakfast* experiment and 9 in the *Breakfast Choice* experiment; I observed 6 birds in both. Raby et al. (2007) tested scrub-jays' preference to cache in the Food and No Food compartments once; I tested Canada Jays' preference three times with no obvious differences among iterations of the experiment (Figure 4.3C).

Other experiments, with both Western Scrub-Jays and, notably, with Eurasian Jays (*Garrulus glandarius*), have suggested evidence of future planning as well (Correia et al., 2007; Cheke & Clayton, 2012), exploiting 'specific satiety', the lessened satisfaction gained from a particular food item, to discriminate current and future motivations. These studies, however, have faced similar criticisms to the Raby et al. (2007) study I examined here (Suddendorf & Corballis, 2008; Cheke & Clayton, 2012). Essentially, while the behaviours observed are convincing, the attribution of these behaviours to 'future planning' might be premature. Both studies required either pre-training, or the assumption that birds learned 'the rules' of rather complex tasks very quickly – within 1-2 trials. Additionally, it is possible that associative mechanisms could produce the same results, or that birds are not 'future planning' but instead relying on some episodic-like what-where-when memory as in the Raby et al. (2007) result. Birds could be remembering a sequence of past events, rather than planning for their imminent future – a "yesterday I needed access to Food A, so I should cache that now" strategy motivated by past events, as opposed to future ones.

I suggest that the most likely reason for my observed contrasting result is that the Canada Jays formed a simple association between the chamber with food and access to that food. Thus, when Canada Jays were allowed to freely explore the apparatus, they simply spent more time in the chamber previously containing food, and as a result they deposited more caches in that chamber. This explanation, however, leaves us with numerous questions. Because future planning is hypothesized to share common processes with episodic memory, do Canada Jays and other *Perisoreus* jays possess episodic, or episodic-like, memory? Does future planning in corvids in fact share common processes with episodic memory and episodic-like what-where-when memory (Zinkivskay et al., 2009)? How do other New World jays, and corvids in general, behave in the *Preparing for Breakfast* and *Breakfast Choice* experiment? Are there features of the scrub-jays' and Canada Jays' previous experience in the wild or in captivity that affect their behaviour in the future planning experiment?

Overall, my results suggest that Canada Jays fail to 'plan for the future' in the context of this experiment and using the criteria laid out by Raby et al. (2007). Further, I attribute Canada Jays' behaviour to a simple cognitive mechanism, raising a number of important questions that are worthy of exploration. Answering these questions will help identify the reasons for differing outcomes of an important experiment in animal cognition.

4.5 References

Babb, S.J., & Crystal, J.D. (2005). Discrimination of what, when, and where: Implications for episodic-like memory in rats. *Learning and Motivation*, *36*(2), 177-189.

Balda, R.P. & Kamil, A.C. (1989). A comparative study of cache recovery by three corvid species. *Animal Behaviour, 38*, 486-495.

Bonaccorso, E., & Peterson, A.T. (2007). A multilocus phylogeny of New World jay genera. *Molecular phylogenetics and evolution*, *42*(2), 467-476.

Bunch, K.G., & Tomback, D.F. (1986). Bolus recovery by Gray Jays: an experimental analysis. *Animal Behaviour*, *34*(3), 754-762.

Cheke, L.G., & Clayton, N.S. (2012). Eurasian Jays (*Garrulus glandarius*) overcome their current desires to anticipate two distinct future needs and plan for them appropriately. *Biology Letters*, *8*(2), 171-175.

Clayton, N.S., Bussey, T.J., & Dickinson, A. (2003). Can animals recall the past and plan for the future?. *Nature Reviews Neuroscience*, *4*(8), 685-691.

Clayton, N.S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature*, *395*(6699), 272-274.

Clayton, N.S., & Dickinson, A. (1999). Memory for the content of caches by scrub jays (*Aphelocoma coerulescens*). *Journal of Experimental Psychology: Animal Behavior Processes*, *25*(1), 82.

Clayton, N.S. & Emery, N.J. (2015). Avian models for human cognitive neuroscience: a proposal. *Neuron*, *86*, 1330-1342.

Clayton, N.S., Yu, K.S. & Dickinson, A. (2001). Scrub jays (*Aphelocoma coerulescens*) form integrated memories of the multiple features of caching episodes. *Journal of Experimental Psychology: Animal Behavior Processes, 27,* 17-29.

Correia, S.P.C., Dickinson, A. & Clayton, N.S. (2007) Western Scrub-Jays anticipate future needs independently of their current motivational state. *Current Biology*. *17*, 856–861.

Curry, R.L., Peterson, A.T, Langen, T.A, Pyle, P., & Patten, M.A. (2020). California Scrub-Jay (*Aphelocoma californica*), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.cowscj1.01

Dow, D.D. (1965). The role of saliva in food storage by the Gray Jay. *The Auk*, *82*(2), 139-154.

Emery, N.J. & Clayton, N.S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science, 306*, 1903-1907.

Feeney, M.C., Roberts, W.A., & Sherry, D.F. (2009). Memory for what, where, and when in the Black-capped Chickadee (*Poecile atricapillus*). *Animal cognition*, *12*(6), 767-777.

Huang, Z., & Ruan, R. (2018). DNA barcodes and insights into the phylogenetic relationships of Corvidae (Aves: Passeriformes). *Mitochondrial DNA Part A*, *29*(4), 529-534.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Raby, C.R., Alexis, D.M., Dickinson, A., & Clayton, N.S. (2007). Planning for the future by Western Scrub-Jays. *Nature*, *445*(7130), 919-921.

Roberts, W.A. (2002). Are animals stuck in time?. *Psychological bulletin*, *128*(3), 473.

Roberts, W.A. (2007). Mental time travel: animals anticipate the future. *Current Biology*, *17*(11), R418-R420.

Roberts, W.A. (2012). Evidence for future cognition in animals. *Learning and motivation*, *43*(4), 169-180.

Schacter, D.L., Addis, D.R., Hassabis, D., Martin, V.C., Spreng, R.N., & Szpunar, K.K. (2012). The future of memory: remembering, imagining, and the brain. *Neuron*, *76*(4), 677-694.

Shettleworth, S.J. (2007). Planning for breakfast. *Nature*, *445*(7130), 825-826.

Strickland, D. & Ouellet, H.R. (2020). Canada Jay (*Perisoreus canadensis*), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.gryjay.01

Suddendorf, T. & Corballis, M.C. (1997). Mental time travel and the evolution of the human mind. *Genetic, Social, and General Psychology Monographs*, *123*, 133-167.

Suddendorf, T., & Corballis, M.C. (2007). The evolution of foresight: What is mental time travel, and is it unique to humans?. *Behavioral and Brain Sciences*, *30*(3), 299-313.

Suddendorf, T., & Corballis, M.C. (2008). New evidence for animal foresight?. *Animal Behaviour*, *75*(5), e1-e3.

Suddendorf, T., & Corballis, M.C. (2010). Behavioural evidence for mental time travel in nonhuman animals. *Behavioural Brain Research*, *215*(2), 292-298.

Zinkivskay, A., Nazir, F., & Smulders, T.V. (2009). What–where–when memory in Magpies (*Pica pica*). *Animal Cognition*, *12*(1), 119-125.

Chapter 5

5. Canada Jays (*Perisoreus canadensis*) balance protein and energy targets simultaneously in both food consumed and cached

5.1 Introduction

Food caching is a behavioural strategy exhibited by a wide variety of taxa (Smith & Reichman, 1984; Sherry, 1985; Vander Wall, 1990; Sutton et al., 2016). While food caching takes many different forms, its function is to ensure food availability in the future (Smith & Reichman, 1984; Sherry, 1985). This outcome is particularly important when that future is a period of food scarcity, as is the case for many caching species overwintering at northern latitudes (e.g. Vander Wall & Balda, 1981; Wrazen & Wrazen, 1982). For these species, food caching is essential to survive resource-poor environmental conditions. Because periods of food scarcity are often seasonal, for example during winter or a dry season, they are accompanied by reliable environmental cues which animals use to prepare for the upcoming challenges (reviewed in Ball, 1993; Dawson et al., 2001; Gorman et al., 2001).

There is an abundance of previous research that investigates how animals use environmental cues to optimize seasonal timing. Much of this research examines reproductive timing (e.g. Elliot, 1976; McAllan & Dickman, 1986; Goldman, 1999; Schaper et al., 2012; Martin et al., 2020) and migration (e.g. Gwinner, 1990; Dawson, 2008; Tøttrup et al., 2010; Monteith et al., 2011), particularly in birds. Some migratory birds employ dietary shifting, the changing of their primary food source, as a means of optimizing fat stores that fuel migration and increasing their motivation to fly (Parrish, 1997; Marshall et al., 2016; Guglielmo et al, 2017). For example, some species shift from heavily insectivorous diets to more frugivorous diets immediately preceding fall migration to rapidly improve body condition and accumulate fat (Parrish, 1997; Smith and McWilliams, 2009). These dietary shifts are the result of diet preference, rather than food availability (Wheelwright, 1988), and birds actively modulate both their energy and macronutrient intake to maximize fat accumulation and meet protein requirements (Wheelwright, 1988; Bairlein, 1990; Bairlein, 2002; Marshall et al., 2016).

When switching from an insectivorous diet to a frugivorous diet, birds are changing from consuming a low-carbohydrate, high-protein diet to a high-carbohydrate, low-protein diet. High protein diets promote lean-mass growth leading to increased muscle mass (Bairlein, 2002). Protein is a metabolically costly precursor to use for lipogenesis, however, with approximately 31% of energy lost in the process (Millward et al., 1976). Alternatively, high carbohydrate diets are more energetically efficient precursors for fatty acid synthesis, incurring only approximately 15% energy loss (Millward et al., 1976). This efficiency may enable high carbohydrate diets to better promote fat deposition and accumulation compared to protein-rich diets (Smith & McWilliams, 2009). These macronutrient modulating behaviours are not restricted to birds. Comparable modulation of dietary macronutrient composition to overcome social or environmental challenges have been observed in many taxa, ranging from invertebrates (Cook et al., 2010) to primates (Guo et al., 2018).

Given the widespread occurrence of macronutrient modulation, it seems possible that non-migratory food-caching birds would also benefit from dietary shifting. However, far less is known about nutrient intake in non-migratory species. American robins (*Turdus migratorius*), a partial migrant, held in captivity over winter demonstrated similar shifting, consuming more fruit during the winter months than the summer (Wheelwright, 1988). Like migratory species, resident birds that face varying seasonal environments could take advantage of dietary shifting to increase season-specific performance, as many of these birds almost entirely replenish depleted fat stores on a daily basis (Blem, 1976). Resident birds at northern latitudes that experience food-scarce winters could use dietary shifting immediately preceding and throughout the winter in order to maintain energy during the food-scarce winter. This would involve a shift from high protein diets through the summer when large fat stores are not required, to high carbohydrate diets in the fall when the accumulation and maintenance of fat stores becomes essential (reviewed in Blem, 1976). If food storing species are optimizing macronutrient intake, this should also be evident in their caches, as replenishing and rebuilding fat stores is essential for survival during food scarcity (Chaplin, 1974; Blem, 1976). This would suggest that caches should contain a greater ratio of carbohydrates to proteins than foods birds are consuming in warmer weather.

Some food-caching birds, however, provision young on cached food. While maintaining fat stores is essential for adults to survive the winter, high-protein diets are essential for offspring growth and development (Johnson, 1971; Boag, 1987, Sales & Janssens, 2003). In these cases, some combination of high protein and high carbohydrate foods should be cached to ensure adequate resources for both the caching adult and the future offspring.

Canada Jays (*Perisoreus canadensis*) are a food-storing, non-migratory, year-round resident of North American boreal and sub-alpine forests (Strickland & Ouellet, 2020). They are a generalist species that caches a wide variety of food items ranging from high protein carrion to high carbohydrate berries in heavily manipulated, saliva covered boluses, and then subsequently rely on these caches to survive harsh winters (Dow, 1965; Sutton et al., 2016; Strickland & Ouellet, 2020). It has been suggested that Canada Jays provision their offspring from their cached food (Derbyshire et al., 2019), as Canada Jays breed prior to spring green-up (Strickland & Ouellet, 2020). Because Canada Jay caches are used to both survive the food-scarce winter and provision offspring, Canada Jays would benefit from modulating not only their own food intake prior to winter, but also the food they are caching. They would be expected to benefit from caching both high carbohydrate and high protein food items.

Our study had two objectives. The first was to assess the ability of a non-migratory species to modulate dietary intake. If individuals modulate their dietary intake to improve their condition prior to winter we would expect individuals to consume a high carbohydrate, low protein diet immediately preceding winter to accumulate fat. We would also expect this elevated carbohydrate intake to be maintained through the winter months to maintain and rebuild fat stores as birds face energetic and thermogenic challenges.

Our second objective was to assess the ability of a non-migratory food-caching bird to ensure adequate nutrients are cached both to survive the food-scarce winter period and to provision offspring. If birds do not cache to anticipate future requirements, their caches should reflect the food available. They should not demonstrate any preference for caching particular diets or nutrients. If individuals do cache in anticipation of future requirements, there are a few possible forms this could take. They could show a preference for either carbohydrates - evidence that they cache to anticipate their own future needs, or protein - evidence that they cache to anticipate their offspring's future needs. It is also possible that individuals could show temporal change in preference. For example, birds might cache carbohydrates early in the fall and protein later in the season.

To investigate whether Canada Jays modulate their nutrient intake and food caching, we offered birds three diets in captivity: 1) high carbohydrate diet, 2) high protein diet, and 3) an intermediate carbohydrate/protein diet. We measured nutrient intake and the nutrient composition of caches from September to January, the time of year when we expect modulation to occur.

5.2 Materials and Methods

5.2.1 Subjects

Six wild-caught Canada Jays housed at the Advanced Facility for Avian Research at Western University, London, Ontario, Canada, were used in this study. Individuals had been in captivity for 1 year prior to the start of feeding trials and had participated in previous caching experiments. Birds were caught under Ontario Ministry of Natural

Resources Wildlife Scientific Collector's Authorization 1091668, and housed and tested in accordance with all local, provincial and federal laws and Western University Animal Care Committee protocol 2019-065.

For the duration of feeding trials birds were housed in individual cages (0.75 x 0.4 x 0.4 m), and had *ad libitum* access to food and water, except as described below. The maintenance diet was a mixture of Mazuri Exotic Gamebird Starter (PMI Nutrition International, Brentwood, MO, U.S.A.), Mazuri Parrot Maintenance Pellets (PMI Nutrition International), shell-less peanuts and sunflower chips, and was supplemented with a HARI PRiME vitamin, mineral and amino acid supplement (Rolf C. Hagen Incorporated, Baie d'Urfé, QC, Canada).

One individual was removed from the study following the September feeding period because of unrelated illness and not replaced.

5.2.2 Diets and Feeding Trials

The foraging preference trials were conducted over 15 consecutive days per month in each month from September to January inclusive. The photoperiod was changed 5 days prior to the start of each month's foraging trials and reflected the local photoperiod on the first day of the upcoming month. Duration of the light phase for each month (hh:mm) was: Sept 13:10; Oct 11:44; Nov 10:18; Dec 9:15; Jan 9:04. To increase motivation to eat and to cache, birds were transferred to feeding cages and food deprived starting 1 h before the lights went off. Formulated high carbohydrate, high protein and intermediate diets were offered 1 h after lights on the following morning and left for 3 h.

These three hours constituted the daily feeding period. Following each daily feeding period, birds were returned to their home cages where the maintenance diet was available *ad libitum*.

We used three previously formulated isocaloric diets for this study (Marshall et al., 2016): a High Carbohydrate diet (HC), a High Protein diet (HP), and an Intermediate diet (I). This resulted in three possible diet pairs that could be offered to birds: HPI, IHC, and HPHC. These diets were made by altering the amount of casein (protein source), dextrose (carbohydrate source), and canola oil (fat source), while keeping the remaining ingredients consistent (for full details and ingredients see Marshall et al., 2016). Diets were coloured with food-dye to allow birds to easily discriminate them, and for us to discriminate them when cached. Three colours, red, blue and yellow, were counter-balanced across birds and colour combination of diets was consistent across the entire experiment. For example, if a bird received the blue HC diet in the first trial, then all future presentations of the HC diet for that bird were blue. No bird received two diets in the same colour, and no more than two birds received a particular diet/colour combination. To control for neophobia, birds were offered 100 g of all three diets simultaneously for 3 days prior to each 15-day set of choice trials and in all cases, birds consumed some of each diet.

During feeding periods, birds were offered 50 g of each diet in a diet pair daily and were allowed to freely cache and consume the diets for 3 h. Presentation of diet pairs was balanced and rotated sequentially across the birds, with two birds receiving each pair each day. For example, if on a given day birds 1 and 4 received HPI, birds 2 and 5 received HCI, and birds 3 and 6 received HCHP; on the following day, birds 1 and 4 received HCI, birds 2 and 5 received HCHP and birds 3 and 6 received HPI. In total, each bird received each diet pair 5 times during each 15-day feeding period.

5.2.3 Dietary Measurements

Following each daily feeding period, the amount of diet consumed, and the amount cached was determined by recovering the remaining uneaten food and all caches from the feeding cages. All values are reported as dry matter. Dry matter (DM) was determined by drying all recovered diets, along with a reference sample of each diet at 60 °C for 23 h. DM consumption was calculated as the difference between the total DM offered and the sum of the DM remaining and cached ($DM_{consumed} = DM_{offered} - (DM_{remaining} + DM_{cached})$). Proportions of each diet consumed and cached were calculated by dividing the DM of each diet by the total DM of both diets combined.

Macronutrient allocation between consumption and caches was calculated using the known diet compositions. Each day, we calculated the total energy (TE; kJ), crude protein (CP; g), and non-protein energy (NPE; kJ) consumed and cached for each bird by combining the TE, CP, and NPE, of the individual diet items that were offered. NPE is the energy derived from carbohydrates and lipids and can be treated as the proportion of the diet used for energy. While CP can be used for energy, it is primarily and critically used for growth and maintenance. To control for differences in amounts consumed and cached, all values for nutrient allocation were standardized per gram of diet either consumed or cached.

We used a geometric framework of nutrition (GFN; Simpson & Raubenheimer, 1995; Raubenheimer & Simpson, 1997) to compare the macronutrient content of food consumed and food cached, and to determine whether macronutrient targets could be identified in the jays' choices among the diets offered. This approach hypothesizes that there exist optimal combinations of macronutrient intake in a state space defined by the amount of each macronutrient consumed. The diets that are available determine whether an animal can meet these macronutrient targets by varying the amount of each diet it consumes, or caches in this case. (for details see Raubenheimer & Simpson, 1997; Raubenheimer et al., 2009; Rothman et al., 2011). We used CP and NPE as the axes of the macronutrient state space and HPI, IHC, and HPHC were the diets available to Canada Jays. We evaluated both the total amount of the diets consumed and cached, as well as the macronutrient ratios per gram of diets consumed and cached.

5.2.4 Statistical Analysis

All statistical analyses were linear mixed effects models performed using the 'nlme' package (Pinheiro et al., 2018) in R Studio v1.1.456 (R Core Team, 2018). Diet preference data were normalized using an arcsine transformation. If interactions were not significant, they were removed from the analysis. P-values less than 0.05 were considered significant and any significant results which warranted further analysis were explored with Tukey's HSD tests using the 'multcomp' package (Hothorn et al., 2008). Except where directly compared, consumption and caching data were analysed separately. In addition, except where directly compared each diet pair was analysed independently.

Month was included as a repeated measure and individual was included as a random effect in all models.

The initial model for total amount consumed or cached included diet pair and month as independent variables. To compare the total amount cached and consumed, the model included diet utilization (consumed or cached), diet pair, and month. The analysis to assess diet preferences included proportion of diet consumed or cached as the dependant variable, with diet and month included as independent variables. To assess macronutrient allocation the model included amount of crude protein as the dependent variable, with utilization and month included as independent factors.

5.3 Results

5.3.1 Total Food Consumed and Cached

Birds consumed the same total amount of food daily regardless of month ($F_{4,16} = 2.09$, $p = 0.13$) or which diet pair they were offered ($F_{2,50} = 2.44$, $p = 0.10$; Figure 5.1A). The marginal and conditional coefficients of determination were 0.15 and 0.88 respectively. They also cached the same total amount of food daily, regardless of month ($F_{4,16} = 2.08$, $p = 0.13$; Figure 5.1B). However, individuals cached more when presented with IHC diet pair than either of the other two diet pairs (Diet Pair: $F_{2,50} = 5.59$, $p = 0.006$; Tukey's HSD: HPI vs HPHC, $p = 1.0$; IHC vs HPHC, $p = 0.008$; IHC vs HPI, $p = 0.02$; Figure 5.1B). The marginal and conditional coefficients of determination were 0.10 and 0.90 respectively. In addition, birds consumed significantly more than they cached ($F_{1,127} = 51.41$, $p < 0.0001$; Figure 5.1C), regardless of diet pair ($F_{2,127} = 2.77$, $p = 0.07$) or month ($F_{4,16} = 2.39$, $p = 0.09$). The marginal coefficient of determination was 0.17 and the conditional coefficient of determination was 0.80.

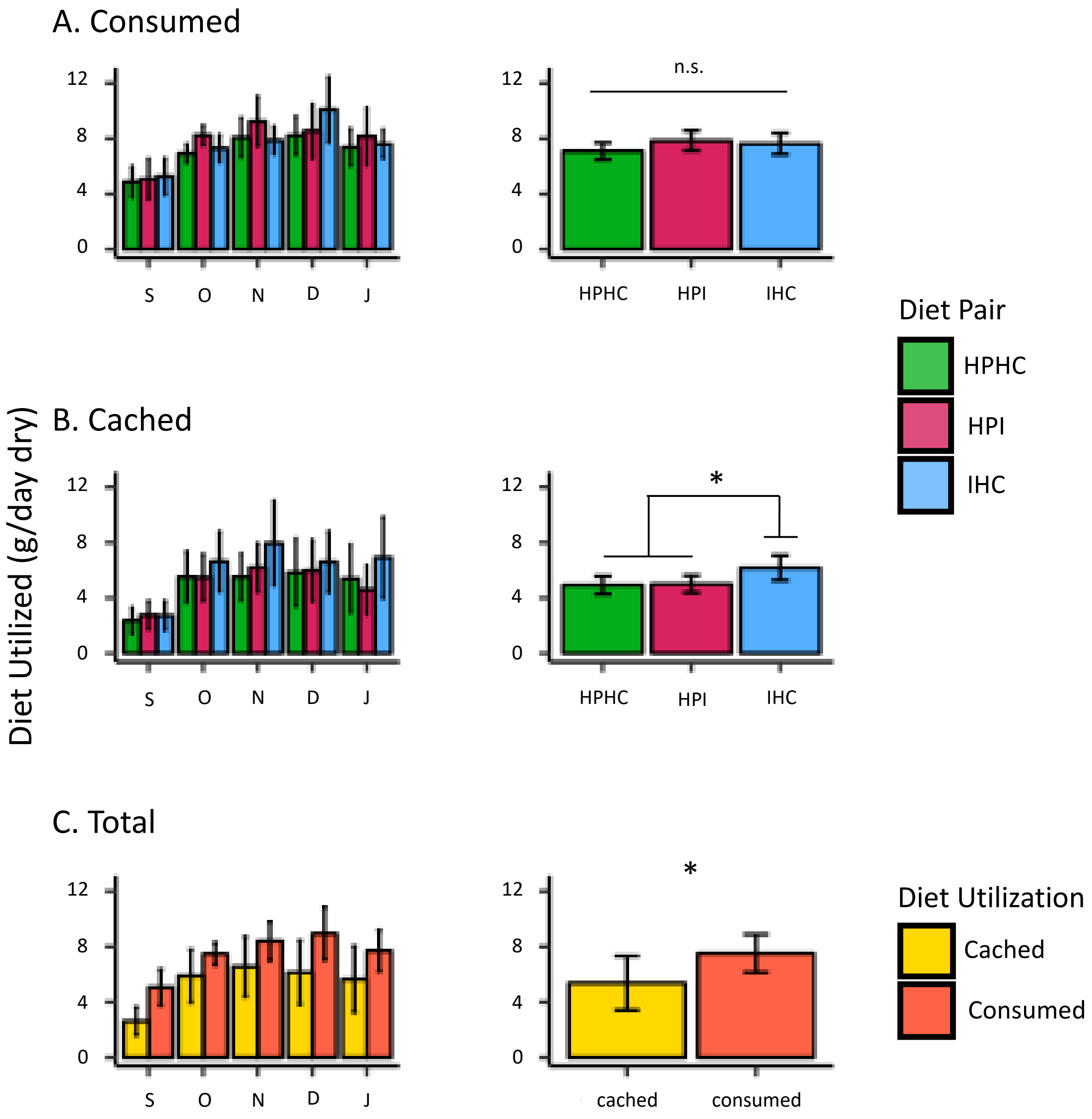


Figure 5.1 The mean (± SE) total food consumed (A) and total food cached (B) per day as a function of diet pair offered. Panel C shows the mean (± SE) total food cached and consumed per day regardless of diet pair. The graphs in the left column show monthly diet utilization, while the graphs in the right column show utilization

across the entire study. Asterisks indicate a significant difference $p < 0.05$, n.s. indicate non-significant comparisons.

5.3.2 Diet Preferences

For all three diet pairs, month had no effect on preference for which diet was consumed within the diet pair (IHC: $F_{4,16} = 0.01$, $p = 0.99$; HPI: $F_{4,16} = 0.06$, $p = 0.99$; HPHC: $F_{4,16} = 0.01$, $p = 0.97$). Individuals did, however, significantly prefer consuming the Intermediate diet both to the High Carbohydrate diet when offered IHC diet pair ($F_{1,25} = 4.57$, $p = 0.04$) and to the High Protein diet when offered HPI diet pair ($F_{1,25} = 28.84$, $p < 0.0001$; Figure 5.2A). They showed no preference between the High Carbohydrate and High Protein diets when offered HPHC ($F_{1,25} = 0.58$, $p = 0.45$).

Birds also preferred to cache the Intermediate diet over the High Protein diet when offered HPI diet pair ($F_{1,25} = 30.6$, $p < 0.0001$; Figure 5.2B), but did not prefer caching the Intermediate diet over the High Carbohydrate diet when offered the HCI diet pair ($F_{1,25} = 1.69$, $p = 0.21$). A slight but not significant, preference for caching HC over HP can be observed in Figure 5.2B when the birds were offered HPHC diet pair ($F_{1,25} = 3.02$, $p = 0.09$). Month had no effect on which diet birds preferred to cache within any of the three diet pairs (IHC: $F_{4,16} = 0.04$, $p = 0.99$; HPI: $F_{4,16} = 0.01$, $p = 0.99$; HPHC: $F_{4,16} = 0.02$, $p = 0.99$).

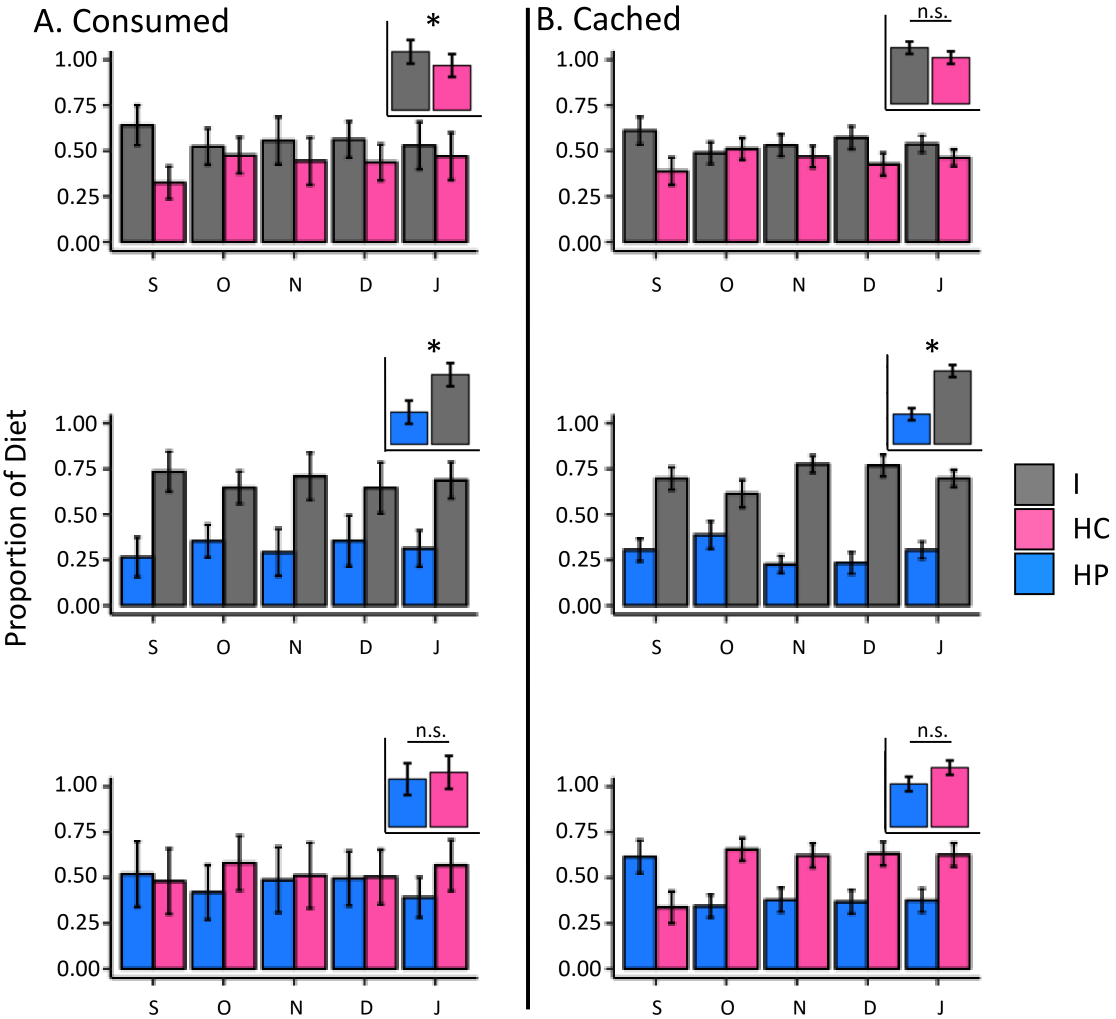


Figure 5.2 The proportion (± SE) of each diet consumed (A; left column) and cached (B; right column) for each diet pair offered. Upper row IHC, middle row HPI diet pair, lower row HPHC. The inset graphs in the upper right of each panel show mean proportions across the entire study. Asterisks indicate a significant difference $p < 0.05$, n.s. indicates non-significant comparisons.

5.3.3 Macronutrient Allocation

Because the total amount of food consumed was greater than that cached (Figure 5.1), the total macronutrients consumed were greater than those cached as well (Figure 5.3A). However, the amount of crude protein per gram cached and NPE per gram cached did not differ from the crude protein per gram consumed and NPE per gram consumed, respectively, regardless of the diet pair offered (crude protein: IHC: $F_{1,25} = 1.06$, $p = 0.31$; HPI: $F_{1,25} = 0.03$, $p = 0.85$; HPHC: $F_{1,25} = 1.13$, $p = 0.30$; NPE: IHC: $F_{1,25} = 1.07$, $p = 0.31$; HPI: $F_{1,25} = 0.03$, $p = 0.86$; HPHC: $F_{1,25} = 1.12$, $p = 0.30$; Figure 5.3B). As the diets were isocaloric, the TE per gram also did not differ between food cached and consumed, regardless of diet pair (IHC: $F_{1,25} = 1.07$, $p = 0.31$; HPI: $F_{1,25} = 0.04$, $p = 0.85$; HPHC: $F_{1,25} = 1.14$, $p = 0.30$). Month had no effect on birds' macronutrient allocation regardless of diet pair offered ($p > 0.1$ for all).

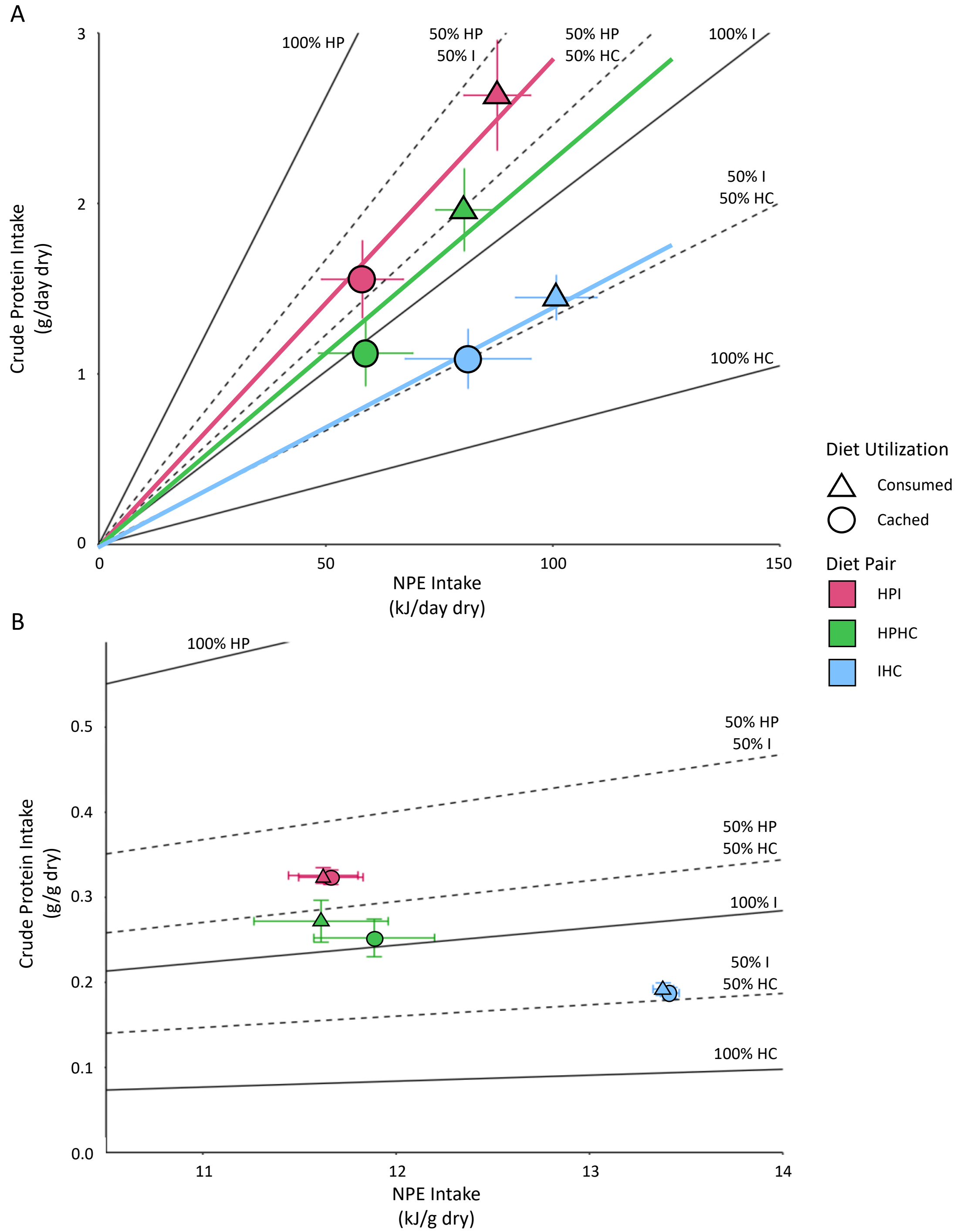


Figure 5.3 In panel A, the total (± SE) crude protein (CP) and non-protein energy (NPE) cached or consumed by Canada Jays are shown for each diet pair in a standard Geometric Framework of Nutrition plot. Solid black lines represent the possible values achieved by consuming or caching only one of the available diets in a

diet pair. Dashed lines represent the possible values achieved by consuming (or caching) equal amounts of each diet in a diet pair. Thick coloured lines represent the possible values achieved by caching and consuming the observed proportions of macronutrients. Panel B shows the same data, standardized to CP and NPE per gram of diet consumed or cached (± SE). Error bars not visible are covered by the data points. Birds cached the same relative amounts of each macronutrient as they consumed, illustrated by coloured lines in A, and the grouping of points in B.

5.4 Discussion

We evaluated the ability of Canada Jays to modulate macronutrient intake, and to secure the future availability of non-protein energy (NPE) such as carbohydrates through caching behaviour. We found strong evidence that Canada Jays consume and cache non-randomly, but no evidence that caching behaviour disproportionately increased future NPE availability. We also found no evidence that Canada Jays employed dietary shifting over the period from September to January, and that month was not significant in any of our models.

Although the birds cached and consumed different amounts of food (Figures 1 & 3A), the macronutrient profile of food cached matched that of the food consumed on a per gram basis (Figure 3B). The difference in overall food consumed and cached is likely because caching species typically eat to satiation prior to caching (Vander Wall, 1990), and so birds prioritized eating before caching in the three-hour foraging window. The similarities in macronutrient profiles, however, suggest that Canada Jays forage non-randomly to meet target amounts for each macronutrient. In Figure 3B, it appears the birds have a minimum NPE target of approximately 11.7 kJ/gram, shown by the position on the NPE axis of the intakes of birds when offered the HPI and HPHC diet pairs. This is further shown by the preference birds had for the Intermediate diet when offered HPI. This preference for the Intermediate diet increases the NPE content of the food consumed and cached and meets the minimum NPE target with less total consumption or caching than would occur with a preference for HP or equal preference for HP and I. Birds also appear to be simultaneously meeting a minimum protein target. When offered IHC birds showed a preference for consuming the Intermediate diet. Birds also cached a higher proportion of the Intermediate diet than the High Carbohydrate when offered IHC although this effect was not statistically significant. These preferences for the Intermediate diet enabled birds to achieve higher NPE and CP levels than caching the diets randomly.

The diet pair offered likely dictated which macronutrient target was actively selected. The crude protein target was likely easily met in either diet pair containing HP, and thus the NPE target had a greater effect on the total amount of food consumed or cached, as noted earlier in connection with the minimum NPE target. Similarly, the NPE target was likely easily met when offered IHC. Further evidence for simultaneous macronutrient targets is illustrated by the lack of diet preference when birds were offered HPHC. With no Intermediate diet available to acquire both carbohydrates and protein in relatively high amounts, birds needed to combine the High Carbohydrate diet to meet the NPE minimum with the High Protein diet to meet the protein target in their caching and consumption. These observations suggest that while Canada Jays do not disproportionately increase the future availability of protein or carbohydrates in caches, they are ensuring the minimum requirements will be available in caches. These results also suggest that birds work towards long term energy and protein targets, even when they are not nutrient deprived. Birds had their food limited for only 3 hours per day, but this short duration was enough to elicit behaviours allowing us to detect their nutrient goals. This suggests that birds are actively regulating macronutrients on a fine scale, perhaps daily or even hourly.

A minimum NPE level for caches allows Canada Jays to accumulate fat more easily and efficiently (Smith & McWilliams, 2009, Marshall et al., 2016), which is an essential aspect of winter survival (Chaplin, 1974; Blem, 1976). Simultaneously ensuring the availability of protein means that muscle mass will be maintained (Bairlein, 2002), and protein will be available for offspring growth. Canada Jays consume and cache a wide variety of foods (Strickland & Ouellet, 2020), and the ability to modulate the macronutrient contents of both their current and future diets is an important prerequisite for being a diet generalist.

The mechanistic causes of these results remain unclear. Selection of diets to maintain the protein and NPE content of caches could be the result of cognitive processes by which birds anticipate and respond to their future needs. A number of corvid species have been suggested to have some prospective or future planning ability (but see Chapter 4). Western Scrub-Jays (*Aphelocoma californica*), for example, have the ability to use caches to ensure food availability the following day when trained to expect a period without food (Raby et al., 2007) and Eurasian jays (*Garrulus glandarius*) are reported to cache for multiple states of future need (Cheke & Clayton, 2012). There is, however, no evidence of more long-term anticipatory abilities in any corvid, and anticipatory caching based on experiencing and remembering previous winter conditions would not be possible for first year Canada Jays.

Alternatively, it is possible that through previous caching experience, birds have formed associations between the quality and viability of food at retrieval and the nutrient content of a cache when it is made. These associations could be made throughout the year and would lead to consistency between current consumption and caches. Similarly, birds could have formed associations from previous experience based on their physiological responses to consuming or recovering caches, even if all caches remained viable. Both these strategies would utilize a less complex cognitive process than future planning and would be potentially available to first year birds, though first year birds would still be at a disadvantage having less time for these associations to form.

A third, and possibly most likely explanation, is that the consistency between items cached and consumed is not learned. Birds could be responding to metabolic signals driving their food preferences to meet both protein and NPE targets. Such metabolic signals would assume birds required the same macronutrients to survive year-round and could have shortcomings in the winter if conditions became unusually energetically demanding, or if the birds were forced to provision their offspring from cached food to an unusual level.

We found no evidence that Canada Jays employ dietary shifting to increase fat accumulation prior to winter. Regardless of which diet combination individuals were offered, birds were able to distinguish the diets based on their macronutrient profile and preferentially consumed an intermediate diet containing both protein and carbohydrates.

Birds also consumed roughly the same total amount of food each month. There are, however, factors that may affect dietary shifting that we did not examine. Temperature could play a role in dietary shifting for resident species because temperature provides a specific and localized environmental cue. Many overwintering birds replenish fat stores daily and subsequently utilize that fat to survive the night (Blem, 1976), and it is likely that Canada Jays also exhibit this pattern of fat utilization. Canada Jays may respond to more immediate cues like temperature to modulate daily nutrient intake and respond to reliable long-term cues like photoperiod to make decisions about nutrient composition of caches.

We found no evidence that Canada Jays specifically prepare to provision their offspring from cached foods. Although every individual's caches did contain protein, the observation that birds were prioritizing carbohydrates suggests that caching an abundance of protein relative to energy is not the primary objective. While there are many potential explanations for this, the most likely is that self-survival takes priority over reproduction. If an individual does not survive the winter, the amount of food stored to provision offspring is unimportant. It is also possible that high protein food in the form of insects, spiders and carrion is available during the Canada Jay breeding season and cached food is supplementary. While evidence indicates Canada Jays do feed their offspring cached food (Derbyshire et al., 2019) it has been proposed that this serves more as a failsafe than the primary provisioning source (Strickland & Ouellet, 2020).

The goal of this study was to investigate how a non-migratory resident that overwinters at high latitudes utilizes macronutrients as winter approaches. We found that birds ensure the macronutrient composition of their caches meets their minimum targets and found that the food cached does not differ in relative macronutrient content to the food they consume.

5.5 References

Bairlein, F. (1990). Nutrition and food selection in migratory birds. In *Bird Migration* (pp. 198-213). Springer, Berlin, Heidelberg.

Bairlein, F. (2002). How to get fat: nutritional mechanisms of seasonal fat accumulation in migratory songbirds. *Naturwissenschaften*, *89*(1), 1-10.

Ball, G.F. (1993). The neural integration of environmental information by seasonally breeding birds. *American Zoologist*, *33*(2), 185-199.

Blem, C.R. (1976). Patterns of lipid storage and utilization in birds. *American Zoologist*, *16*(4), 671-684.

Boag, P.T. (1987). Effects of nestling diet on growth and adult size of Zebra Finches (*Poephila guttata*). *The Auk*, *104*(2), 155-166.

Chaplin, S. B. (1974). Daily energetics of the Black-capped Chickadee, *Parus atricapillus*, in winter. *Journal of Comparative Physiology*, *89*(4), 321-330.

Cheke, L. G., & Clayton, N. S. (2012). Eurasian Jays (Garrulus glandarius) overcome their current desires to anticipate two distinct future needs and plan for them appropriately. *Biology Letters*, *8*(2), 171-175.

Cook, S. C., Eubanks, M. D., Gold, R. E., & Behmer, S. T. (2010). Colony-level macronutrient regulation in ants: mechanisms, hoarding and associated costs. *Animal Behaviour*, *79*(2), 429-437.

Dawson, A. (2008). Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1497), 1621-1633.

Dawson, A., King, V.M., Bentley, G.E., & Ball, G.F. (2001). Photoperiodic control of seasonality in birds. *Journal of Biological Rhythms*, *16*(4), 365-380.

Derbyshire, R., Norris, D. R., Hobson, K. A., & Strickland, D. (2019). Isotopic spiking and food dye experiments provide evidence that nestling Canada Jays (Perisoreus canadensis) receive cached food from their parents. *Canadian Journal of Zoology*, *97*(4), 368-375.

Dow, D.D. (1965). The role of saliva in food storage by the Gray Jay. *The Auk*, *82*(2), 139-154.

Elliott, J.A. (1976). Circadian rhythms and photoperiodic time measurement in mammals. *Federation Proceedings*, *35*, 2339-2346

Goldman, B.D. (1999). The circadian timing system and reproduction in mammals. *Steroids*, *64*(9), 679-685.

Gorman, M.R., Goldman, B.D., & Zucker, I. (2001). Mammalian photoperiodism. In *Circadian Clocks* (pp. 481-508). Springer, Boston, MA.

Guglielmo, C. G., Gerson, A. R., Price, E. R., & Hays, Q. R. (2017). The effects of dietary macronutrients on flight ability, energetics, and fuel metabolism of Yellow-rumped Warblers *Setophaga coronata*. *Journal of Avian Biology*, *48*(1), 133-148.

Guo, S. T., Hou, R., Garber, P. A., Raubenheimer, D., Righini, N., Ji, W. H., Jay, O., He, S.J., Wu, F., Li, F.F. & Li, B. G. (2018). Nutrient-specific compensation for seasonal cold stress in a free-ranging temperate colobine monkey. *Functional Ecology*, *32*(9), 2170-2180.

Gwinner, E. (1990). Circannual rhythms in bird migration: control of temporal patterns and interactions with photoperiod. In *Bird Migration* (pp. 257-268). Springer, Berlin, Heidelberg.

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, *50*(3), 346--363.

Johnson, N.F. (1971). Effects of levels of dietary protein on wood duck growth. *The Journal of Wildlife Management*, 798-802.

Marshall, T.J., Dick, M.F., & Guglielmo, C.G. (2016). Seasonal dietary shifting in Yellow-rumped Warblers is unrelated to macronutrient targets. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *192*, 57-63.

Martin, R.J., Kruger, M.C., MacDougall-Shackleton, S.A., & Sherry, D.F. (2020). Black-capped Chickadees (*Poecile atricapillus*) use temperature as a cue for reproductive timing. *General and Comparative Endocrinology*, *287*, 113348.

McAllan, B.M., & Dickman, C.R. (1986). The role of photoperiod in the timing of reproduction in the dasyurid marsupial *Antechinus stuartii*. *Oecologia*, *68*(2), 259-264.

Millward, D. J., Garlick, P. J., & Reeds, P. J. (1976). The energy cost of growth. *Proceedings of the Nutrition Society*, *35*(3), 339-349.

Monteith, K.L., Bleich, V.C., Stephenson, T.R., Pierce, B.M., Conner, M.M., Klaver, R.W., & Bowyer, R.T. (2011). Timing of seasonal migration in Mule Deer: effects of climate, plant phenology, and life-history characteristics. *Ecosphere*, *2*(4), 1-34.

Parrish, J.D. (1997). Patterns of frugivory and energetic condition in Nearctic landbirds during autumn migration. *The Condor*, *99*(3), 681-697.

Pinheiro J, Bates D, DebRoy S, Sarkar D, & R Core Team (2018). _nlme:Linear and Nonlinear Mixed Effects Models_. R package version 3.1-137, <URL: https://CRAN.R-project.org/package=nlme>

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Raby, C. R., Alexis, D. M., Dickinson, A., & Clayton, N. S. (2007). Planning for the future by Western Scrub-Jays. *Nature*, *445*(7130), 919-921.

Raubenheimer, D. & Simpson, S.J. (1997). Integrative models of nutrient balancing: application to insects and vertebrates. *Nutrition Research Reviews*, 10, 151-179.

Raubenheimer, D., Simpson, S.J. & Mayntz, D. (2009). Nutrition, ecology and nutritional ecology: toward an integrated framework. *Functional Ecology*, 23, 4-16.

Rothman, J.M., Raubenheimer, D. & Chapman, C.A. 2011. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. *Biology Letters*, 7, 847-849.

Sales, J., & Janssens, G. P. J. (2003). Nutrition of the Domestic Pigeon (*Columba livia domestica*). *World's poultry science journal*, *59*(2), 221-232.

Schaper, S. V., Dawson, A., Sharp, P. J., Gienapp, P., Caro, S. P., & Visser, M. E. (2012). Increasing temperature, not mean temperature, is a cue for avian timing of reproduction. *The American Naturalist*, *179*(2), E55-E69.

Sherry, D. F. (1985). Food storage by birds and mammals. *Advances in the Study of Behavior*, *15*(5), 153-188.

Simpson, S.J., & Raubenheimer, D. (1995). The geometric analysis of feeding and nutrition: a user's guide. *Journal of Insect Physiology*, 41(7), 545-553.

Smith, S. B., & McWilliams, S. R. (2009). Dietary macronutrients affect lipid metabolites and body composition of a migratory passerine, the White-throated Sparrow (*Zonotrichia albicollis*). *Physiological and Biochemical Zoology*, *82*(3), 258-269.

Smith, C. C., & Reichman, O. J. (1984). The evolution of food caching by birds and mammals. *Annual Review of Ecology and Systematics*, *15*(1), 329-351.

Strickland, D. & Ouellet, H.R. (2020). Canada Jay (*Perisoreus canadensis*), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.gryjay.01

Sutton, A. O., Strickland, D., & Norris, D. R. (2016). Food storage in a changing world: implications of climate change for food-caching species. *Climate Change Responses*, *3*(1), 12.

Tøttrup, A. P., Rainio, K., Coppack, T., Lehikoinen, E., Rahbek, C., & Thorup, K. (2010). Local temperature fine-tunes the timing of spring migration in birds. *Integrative and Comparative Biology*, *50*(3), 293-304.

Vander Wall, S. B. (1990). *Food hoarding in animals*. University of Chicago Press.

Vander Wall, S. B., & Balda, R. P. (1981). Ecology and evolution of food-storage behavior in conifer-seed-caching corvids. *Zeitschrift für Tierpsychologie*, *56*(3), 217-242.

Wheelwright, N. T. (1988). Seasonal changes in food preferences of American Robins in captivity. *The Auk*, *105*(2), 374-378.

Wrazen, J. A., & Wrazen, L. A. (1982). Hoarding, body mass dynamics, and torpor as components of the survival strategy of the Eastern Chipmunk. *Journal of Mammalogy, 63*(1), 63-72.

Chapter 6

6. General Discussion: Food caching decisions by Canada Jays (*Perisoreus canadensis*)

6.1 Thesis Overview

The purpose of the research in this thesis was to explore the decisions made by Canada Jays (*Perisoreus canadensis*), a boreal caching species, during the resource acquisition and cache deposition phases of caching. While some aspects of caching behaviour are generally well studied, such as cache recovery (e.g. Sherry, 1984; Balda & Kamil, 1989; Clayton & Dickinson, 1998: Molina-Morales et al., 2020), gaps in our knowledge surrounding the factors influencing decisions during other phases remain prominent.

6.1.1 Summary of Results

Chapter 2 assessed the long-standing assumption that the overlap between Canada Jays' distribution and the distribution of spruce trees were the result of Canada Jays exploiting beneficial cache locations in these spruce trees. This chapter further explored potential cues, olfaction and structure, that could allow Canada Jays to make these decisions and affect the degree to which Canada Jays are able to exploit spruce caching locations. In a series of three experiments, Canada Jays were allowed to cache freely in an open flight room with a variety of stimuli serving as potential cache locations. First, Canada Jays had access to sectioned trees, providing a variety of caching locations as available in the wild (Exp 1: Species specific preference). In the subsequent experiments, Canada Jays were allowed to cache in either scented artificial caching boards (Exp 2: Evaluation of olfactory cues) or in custom built artificial trees (Exp 3: Evaluation of structural cues). I found evidence to support Canada Jay's ability to identify and exploit conifer trees, particularly spruce trees. I also found evidence that Canada Jays use the structural properties of trees to evaluate cache locations. I found no evidence that they use olfactory cues when evaluating potential cache sites.

In Chapter 3 I catalogued and categorized the cache-protection strategies employed by Canada Jays under a variety of caching contexts. Contexts were a combination of cache-robbing threats (a model blue jay) and respite from such threats (locations out of sight of the model), and Canada Jays were allowed to cache freely in two available White Spruce (*Picea glauca*) trees. I found that Canada Jays employed context dependent cache-protection strategies at multiple scales. Canada Jays employed a *spacing* strategy – equal distribution of caches across available cache-sites – when there was either no perceived risk of cache-pilferage, or the perceived risk was equal between potential cache sites. When a threat was present and there was no respite, Canada Jays down-regulated overall caching behaviour. When visual escape was presented, Canada Jays employed the *out-of-sight* strategy, caching food preferentially in the cache locations that could not be observed by the model robber.

Chapter 4 assessed Canada Jay's ability to anticipate food availability and to combat food restriction through two distinct caching experiments. In the first, Canada Jays were allowed to learn a predictable schedule of food access and food restriction.

Subsequently, individuals were allowed the opportunity to cache food in preparation for said predictable food restriction. In the second, Canada Jays were put on a similar schedule, but the food restriction was replaced with access to a second food type, such that birds had access to one type or the other, but not both. Birds learned this schedule of predictable access to distinct food types and were then allowed an opportunity to cache food in preparation for restriction to one food type. This project was, in part, a replication of a similar, high impact, study performed with Western Scrub-Jays (*Aphelocoma californica*; Raby et al., 2007). Not only did I fail to replicate previous results – scrub-jays correctly anticipated food restriction in both experiments and prepared for it through caching behaviour – but with repeated trials Canada Jays actually demonstrated the opposite of the scrub-jays' behaviour – a preference for cache sites where food was expected to be found.

Chapter 5 explored the macronutrient preferences of Canada Jays both when eating and caching. I offered birds a series of paired diets and recorded both the amounts of diets they consumed, and the amounts of diets they cached. I then compared the diets that were chosen for consumption and for caching and evaluated changes in these preferences over time. I also compared the macronutrients selected for consumption and for caching to each other, to assess how Canada Jays prioritized their macronutrient allocation. Birds did exhibit some dietary preferences when making a dichotomous choice, but I found no evidence that Canada Jays utilize dietary shifting akin to that seen in migratory birds. I also did not find any evidence suggesting that Canada Jays manipulate the contents of their caches to account for future needs. There were similarities in the macronutrients cached and consumed, however, suggesting non-random macronutrient selections and an active regulation of macronutrient ratios in both food consumed and cached.

6.2 Caching Decisions Revisited

In addition to the specific objectives set out in this thesis, the research presented also aimed to more broadly assess the decision-making behaviours of Canada Jays through a variety of foraging tasks. In each chapter of this thesis, Canada Jays made at least one foraging decision which was subsequently recorded and analyzed and can be evaluated in terms of predicted benefit. As mentioned previously, optimal foraging theory predicts that individuals will make choices that result in the greatest net benefit to their fitness (Andersson & Krebs, 1978). For example, Canada Jays disproportionally cache in spruce and other conifer trees (Chapter 2). Considering evidence that suggests these trees provide some preservative value to cached food (Strickland et al., 2011; Sechley et al., 2015), it is easy to understand why this behaviour would confer some fitness benefit to Canada Jays, and thus why Canada Jays might exhibit this behaviour.

By combining the results of Chapters 2, tree species preferences, and 3, cache-protection strategies, we get further evidence that Canada Jays are assessing their environment and making active decisions when caching. I found evidence that Canada Jays employ a *spacing* strategy almost by default (Chapter 3). That is, when all potential cache sites had the same perceived level of risk, Canada Jays distribute their caches uniformly to limit cache-pilferage. This pattern has been previously documented in field studies of Canada Jays as well (Waite & Reeve, 1994). Importantly, this observed uniform spacing distribution occurred only when available caching locations were of similar quality. When the cache sites varied in quality, Canada Jays ignored this rule and cached disproportionally in spruce and other conifer trees, even though the threat of pilferage was uniform (Chapter 3). Seemingly, Canada Jays assessed their environment and available cache locations, and decided to prioritize the benefits conferred by the preservative qualities of the spruce tree at the cost of employing their typical spacing strategy. A similar argument can be made about combining the results from Chapters 3 and 4. Canada Jays again violated their spacing strategy in order to cache disproportionate amounts of food in the chamber they previously associated with food (Chapter 4). These violations of Canada Jays' apparent default cache-protection strategy lend credence to the idea that Canada Jays are constantly performing the cost/benefit analyses that optimal foraging models assume. The benefits gained from the preservative qualities of spruce trees or the consistency of a reliable food source must outweigh the potential costs of not spacing their caches uniformly.

This research has also helped to elucidate the prioritization of information Canada Jays use when assessing their environment. In two separate experiments (Chapter 2: Experiment 3, and Chapter 3) Canada Jays prioritized visual information over alternative sources of information. In Chapter 2 Canada Jays demonstrated a preference when presented with visually distinct trees, while failing to respond to olfactory cues, while in Chapter 3 visual information was enough to increase perceived risk but auditory cues were not. This prioritization of visual information is likely tied directly to their foraging ecology. While spruce and other conifers have potentially distinct scents, these scents are likely diluted or not distinguishable in a forest making visual information essential. Similarly, Canada Jays' most direct threats to their caches come at the time of cache-deposition (Burnell & Tomback, 1985; Rutter, 1972). Birds in the area, but with no line of sight to the caching individual are likely not a threat to Canada Jay caches, and thus do not illicit any behavioural response.

Another useful context for examining the caching decisions of Canada Jays is through comparisons to both related species and to species that inhabit similar environments. Other corvids have demonstrated a variety of cache-site preferences (e.g. Kulahci & Bowman 2011; Neuschulz et al, 2015; Fuirst et al., 2020) though few preferences, if any, seem to be for a particular species. They do, however, seem to be related to cache preservation, the postulated reason for Canada Jays' spruce preference (Strickland et al., 2011; Sechley et al., 2015). Conversely, caching species such as nuthatches and chickadees, inhabit the same broad habitats as Canada Jays, however, cache-site selection in these species seems to reflect preferences for areas on chosen trees (e.g. branches, trunk) as opposed to preferences for tree species themselves (Petit et al., 1989). Interestingly, evidence in Willow tits (*Poecile montanus*) suggests a preference for conifers, particularly pine (Lahti et al., 1998), however, this preference has been previously attributed to lowering the costs of foraging for forgotten seeds (Brodin, 1994). Essentially, a 'cache where you most like to forage, increasing the chance you can relocate a cache by chance' strategy. Both these cache-site preferences are ecologically intuitive. Because the duration of caching varies so greatly, it makes sense that the long-term storing corvids are more concerned with cache degradation and cache preservation, while the shorter duration storing parids may show more concern for other factors such as cache-pilferage, or low-cost cache recovery. These logical differences in cache-site preference between related and geographically similar species add support to the idea that caching behaviour is refined and species specific. These observations suggest that caching behaviour should be examined in a wide variety of species in order to better understand and catalogue the extent of the benefits conferred to these caching species.

Understanding behaviour requires some speculation regarding the mechanisms that underpin it. For example, I presented evidence that Canada Jays use structural aspects of trees to assess caching location (Chapter 2). I speculate that this is due to some association between the structural properties chosen and those of spruce trees, however, without further study that claim remains purely speculation. Assessing the mechanisms of complex behaviours should begin with the simplest of interpretations ("Morgan's canon", Morgan, 1894). Fundamentally, complex behaviours can be the result of simple cognitive processes, and complex cognition should only be attributed under circumstances where simpler explanations are inadequate. This interpretation of Morgan's canon is, however, not always applied in practice. Some researchers have argued that this interpretation of Morgan's canon has serious issues, was not the original intent, and that it should be ignored altogether (Costall, 1993; Fitzpatrick, 2008). These objections, however, create a scenario in which researchers may attribute complex cognitive functions to behaviours that are the product of simpler processes. This sequence of events typically begins with researchers observing an unexpected, seemingly spontaneous, behaviour and attributing the behaviour to a complex cognitive process, only for the behaviour later to be shown as the result of simpler cognitive processes. For example, Betty the crow famously bent a piece of garden wire creating a novel tool, which was then used to retrieve food (Weir et al., 2002). This became a classic example of animal intelligence and has been used since as evidence of 'how smart animals are'. Even though the authors acknowledged at the time that these crows performed similar behaviours in the wild, they argued that the behaviour observed implied a causal understanding of the feeding task (Weir et al., 2002). In 2016 however, researchers demonstrated that the behaviour Betty engaged in was not novel. Instead, researchers found the behaviour was part of the species' natural behavioural repertoire and that Betty was likely engaging in a learned manipulation behaviour (Rutz et al., 2016). They argue that Betty likely did not have a casual understanding of the task, but instead employed a pre-existing behaviour in order to acquire food in a novel context. While the later study cannot rule out a casual understanding of the task, Morgan's canon would suggest that the application of a pre-existing strategy in far more likely.

Abiding by foundational principles like Morgan's canon is important when assessing behaviour because, as mentioned, assessing behaviour typically requires some speculation as to the mechanism. The explanations offered in Chapters 2-5 are the simplest explanations that could reasonably cause the results. Although flashier headlines could likely have been achieved by attributing complex cognition to Canada Jays, the data suggest, and therefore I have argued for, relatively simple cognitive processes as causes of seemingly complex behaviours.

6.3 Future Research and Next Steps

This thesis and much of the existing research on caching species is focused on the behavioural components of caching, many examples of which have been previously discussed. Because of this focus on behaviour, the mechanisms underlying these behaviours are less well explored. That is not to say that attempts at characterizing the mechanisms do not exist (e.g. Sherry, 1984; Bunch & Tomback, 1986; Clayton & Dickinson, 1998), however, better understanding these mechanisms is a place where future research is warranted. For example, I provided evidence that Canada Jays use context dependent cache protection strategies, and evidence that visual information is important in making these assessments (Chapter 3). However, in other corvid species it has been suggested that visual inputs are not the only important source of information used to assess potential cache-pilfering threats. In Clark's Nutcrackers (*Nucifraga columbiana*), for example, birds have been shown to still perceive an elevated risk to caches even when potential pilferers are out of site (Clary & Kelly, 2011). These perceived risks are potentially due to acoustic or olfactory cues. While some explanations for these differences exist – Canada Jays and Clark's Nutcrackers differ in their general foraging ecology and what constitutes a risk to caches – further exploration of these mechanisms, in additional species, would allow researchers to more completely categorize these essential behaviours.

The replication of high impact studies should also be a priority for future research. Chapter 4 in this thesis represented a replication of a high impact study that found evidence of complex cognitive function in a corvid (Raby et al., 2007). I failed to replicate these results, suggesting that the generalizability of the initial findings may not be as great as originally argued. Alternatively, it is possible that unknown or unaccounted for variables influenced my replication attempt. The only way to ascertain the correct interpretation is to collect more data. Further replications, especially of high impact studies, should be given attention and not disregarded due to a lack of novelty.

6.4 Implications for Conservation

Canada Jays are listed by the International Union for Conservation of Nature (IUCN) as a species of *least-concern* (Birdlife International, 2018). Despite this assessment, population decline in Canada Jays is well documented (Waite & Strickland, 2006; Birdlife International, 2018; Strickland & Ouellet, 2020). Evidence also exists to suggest that climate change poses a particular strong risk to Canada Jays due to the nature of their caching behaviour (Sutton et al., 2016). In addition to Canada Jays, other boreal caching species face similar risks. At the extreme, climatic changes have created *no-analog communities* – past communities unlike anything found today – and it is predicted that as global climate change continues, some of the earth's current communities could become no-analog communities in the future (Williams & Jackson, 2007). Evidence for these large-scale changes is plentiful, and climate change is altering plant and animal community composition in forests (Dieleman et al., 2015; Ralston et al., 2019; Lyons et al., 2020), driving range shifts (Ralston & Kirchman, 2013; Elmhagen et al., 2015; Kirchma & Van Keuren, 2017), altering reproductive timing (Visser et al., 2006; Martin et al., 2020) and generally disrupting centuries long ecological equilibria. These disruptions could potentially alter the availability of resources for higher level consumers to the point where consumers, such as Canada Jays, cannot sustain themselves. Better understanding caching behaviour can help in identifying the extent of the risk animals might be facing. Canada Jays demonstrated a variety of behaviours that could aid in mitigating the effects of climate change. Their close relationship with spruce trees is important in cache-preservation, and the data in Chapter 2 show convincingly that this relationship is the result of active exploitation. Additionally, in Chapter 3 Canada Jays showed flexible cache protection strategies that might aid them in hoarding resources, if those resources become more restricted.

Alternatively, Canada Jays' behaviours in Chapters 2 and 3 are only as useful as the climate potentially allows them to be. Canada Jays rely on long, deep freeze events to preserve their caches for extended durations, and multiple freeze-thaw events can depress reproductive success (Sutton et al., 2019). Without these deep freezes, Canada Jays' behaviours might not be adequate in combating current or future environmental challenges. This appears to be the case, at least to date, as Canada Jay populations along the southern edge of the range appear to be disappearing or moving north (Waite & Strickland, 2006; Strickland & Ouellet, 2020).

Understanding Canada Jay caching behaviour may also be transferable to the conservation of other caching species. While exploring other species for behaviours that resemble the cache degradation combating behaviours of Canada Jays is a start, it is important to remember that these behaviours may not be required. The Black-capped Chickadee, for example, inhabits much of the same habitat as the Canada Jay and is also listed as an IUCN species of *least-concern*. The Black-capped Chickadee population is increasing (Birdlife International, 2017), however, and has shown behavioural resistance to climate factors (Martin & Sherry, 2019).

6.4.1 Cultural Significance

It is also worth noting the importance of conservation due to the cultural significance the Canada Jay holds. The Canada Jay is commonly known as the whiskey jack, an anglicized pronunciation of the Cree-Ojibway name for a mythical prankster and teacher, *wisikejack* (Mas, 2016). Wisikejack has analogous characters in many indigenous communities. For example, to the Anishinaabe, she is *Gwiingwiishi*. The stories teach that bravery, resilience and commitments to one another are the ways to find growth (Sinclair, 2016). Additionally, many Canadians have latched on to the Canada Jay after it was named Canadian Geographic's choice for national bird following a public survey (Lagerquist & Dunham, 2016). Though this request has not been acted on by the federal government, the adoration of the Canada Jay by Canadians increases the need for conservation efforts to be successful and well informed.

6.5 Conclusions

E. O. Wilson said, "Nature holds the key to our aesthetic, intellectual, cognitive and even spiritual satisfaction" (McCrum, 2017). I believe that is, in part, evidenced by the way that animal behaviour and decision making has captivated researchers for more than 100 years (Romanes, 1883). As better and more refined methodologies are developed and these long-standing mysteries become clearer, the fascination still remains. The study of animal behaviour, cognition and decision making remains an active and rapidly advancing field at the intersection of biology and psychology. Caching behaviour specifically has long been under investigation by researchers, and various aspects of caching behaviour have been explored and explained over time. In this thesis, I presented data to build on this existing exploration of caching behaviour. I have provided evidence that Canada Jays, a boreal caching species dependent on cache resources for survival, are engaged in decision making during both resource acquisition and cache deposition. I suggest that a multitude of factors can influence these decisions and that behaviours resulting from these decisions can aid in cache preservation, risk avoidance and surviving climate change. I also suggest that future research better explore the fitness impacts of caching decisions and the mechanisms that underpin them. Importantly, appropriate thought should be given to the study of these mechanisms before attributing these apparently complex behaviours to complex cognitive processes.

In all, this research has advanced our understanding of Canada Jay caching behaviour, and in doing so, advanced our understanding of caching behaviour in general. I have provided avenues and ideas for future research, both at the behavioural and the mechanistic scale. For example, while I have provided some evidence of a causal link between Canada Jay range and spruce species overlap, further research into the true benefits of caching in conifers is required. Additionally, the mechanisms underlying the observed macronutrient preferences deserves the full attention of the scientific community in order to better understand how these birds are responding to their energetically demanding environments. Regardless of what next steps are taken, they should be taken with the intent to better understand important behaviours and their mechanisms, and with the goal of preserving Canada Jays and other boreal caching species for centuries to come.

6.6 References

Andersson, M., & Krebs, J.R. (1978). On the evolution of hoarding behaviour. *Animal Behaviour*, *26*, 707-711.

Balda, R.P., & Kamil, A.C. (1989). A comparative study of cache recovery by three corvid species. *Animal Behaviour*, *38*(3), 486-495.

BirdLife International. 2017. *Poecile atricapillus* (amended version of 2016 assessment). *The IUCN Red List of Threatened Species* 2017: e.T22711716A118687681. https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T22711716A118687681.en. Downloaded on 18 January 2021.

BirdLife International. 2018. *Perisoreus canadensis*. *The IUCN Red List of Threatened Species* 2018:e.T22705783A130380194.https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22705783A130380194.en. Downloaded on 18 January 2021.

Brodin, A. (1994). Separation of caches between individual Willow Tits hoarding under natural conditions. *Animal Behaviour*, *47*(5), 1031-1035.

Bunch, K.G., & Tomback, D.F. (1986). Bolus recovery by Gray Jays: an experimental analysis. *Animal Behaviour*, *34*(3), 754-762.

Burnell, K.L., & Tomback, D.F. (1985). Steller's Jays steal Gray Jay caches: field and laboratory observations. *The Auk*, *102*(2), 417-419.

Clary, D., & Kelly, D.M. (2011). Cache protection strategies of a non-social food-caching corvid, Clark's Nutcracker (*Nucifraga columbiana*). *Animal Cognition*, *14*(5), 735-744.

Clayton, N.S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature, 395*(6699), 272-274.

Costall, A. (1993). How Lloyd Morgan's canon backfired. *Journal of the History of the Behavioral Sciences, 29*(2), 113-122.

Dieleman, C.M., Branfireun, B.A., McLaughlin, J.W., & Lindo, Z. (2015). Climate change drives a shift in peatland ecosystem plant community: implications for ecosystem function and stability. *Global Change Biology*, *21*(1), 388-395.

Elmhagen, B., Kindberg, J., Hellström, P., & Angerbjörn, A. (2015). A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. *Ambio, 44*(1), 39-50.

Fitzpatrick, S. (2008). Doing away with Morgan's Canon. *Mind & Language*, *23*(2), 224-246.

Fuirst, M., Greer, J., & Bowman, R. (2020). Ontogeny of food-caching site preferences in young Florida Scrub-Jays: evidence of learning or changing social status?. *Journal of Field Ornithology*, *91*(3), 241-253.

Kulahci, I.G., & Bowman, R. (2011). Recaching decisions of Florida Scrub-Jays are sensitive to ecological conditions. *Ethology*, *117*, 700-707.

Lagerquist, J., & Dunham, J. (2016, November 17). Step aside, loon: Geographic society plucks Gray Jay as Canada's national bird. Retrieved January 19, 2021, from https://www.ctvnews.ca/canada/step-aside-loon-geographic-society-plucks-gray-jay-as-canada-s-national-bird-1.3163306

Lahti, K., Koivula, K., Rytkönen, S., Mustonen, T., Welling, P., Pravosudov, V.V., & Orell, M. (1998). Social influences on food caching in Willow Tits: a field experiment. *Behavioral Ecology*, *9*(2), 122-129.

Lyons, C. L., Branfireun, B.A., McLaughlin, J., & Lindo, Z. (2020). Simulated climate warming increases plant community heterogeneity in two types of boreal peatlands in north–central Canada. *Journal of Vegetation Science*, *31*(5), 908-919.

Martin, R.J., & Sherry, D.F. (2019). Overwinter temperature has no effect on problem solving abilities or responses to novelty in Black-capped Chickadees (*Poecile atricapillus*). *Behavioural processes*, *162*, 72-78.

Martin, R.J., Kruger, M.C., MacDougall-Shackleton, S.A., & Sherry, D.F. (2020). Black-capped Chickadees (*Poecile atricapillus*) use temperature as a cue for reproductive timing. *General and Comparative Endocrinology*, *287*, 113348.

Mas, S. (2016, December 27). Canadians divided over Grey Jay as national bird, new poll suggests. Retrieved January 19, 2021, from https://ottawacitizen.com/news/local-news/canadians-divided-over-grey-jay-as-national-bird-new-poll-suggests

McCrum, R. (2017, October 08). The Origins of Creativity review – stick to the ants, professor. Retrieved January 19, 2021, from https://www.theguardian.com/science/2017/oct/08/eo-wilson-the-origins-of-creativity-review-rambling-survey-enlightenment

Molina-Morales, M., Castro, J., Albaladejo, G., & Parejo, D. (2020). Precise cache detection by olfaction in a scatter-hoarder bird. *Animal Behaviour*, *167*, 185-191.

Morgan, C.L. (1894). *An Introduction to Comparative Psychology*. Walter Scott.

Neuschulz, E.L., Mueller, T., Bollmann, K., Gugerli, F., & Böhning-Gaese, K. (2015). Seed perishability determines the caching behaviour of a food-hoarding bird. *Journal of Animal Ecology*, *84*, 71-78.

Petit, D.R., Petit, L.J., & Petit, K.E. (1989). Winter caching ecology of deciduous woodland birds and adaptations for protection of stored food. *The Condor*, *91*(4), 766-776.

Raby, C.R., Alexis, D.M., Dickinson, A., & Clayton, N.S. (2007). Planning for the future by Western Scrub-Jays. *Nature*, *445*(7130), 919-921.

Ralston, J., & Kirchman, J.J. (2013). Predicted range shifts in North American boreal forest birds and the effect of climate change on genetic diversity in Blackpoll Warblers (*Setophaga striata*). *Conservation Genetics*, *14*(2), 543-555.

Ralston, J., FitzGerald, A.M., Scanga, S.E., & Kirchman, J.J. (2019). Observations of habitat associations in boreal forest birds and the geographic variation in bird community composition. *The Wilson Journal of Ornithology*, *131*(1), 12-23.

Romanes, G.J. (1883). *Animal intelligence*. D. Appleton.

Rutter, R.J. (1972). The Gray Jay: A bird for all seasons. *Nature Canada*, 1(4), 28-32.

Rutz, C., Sugasawa, S., Van der Wal, J.E., Klump, B.C., & St Clair, J.J. (2016). Tool bending in New Caledonian Crows. *Royal Society open science, 3*(8), 160439.

Sechley, T.H., Strickland, D., & Norris, D.R. (2015). Linking the availability of cached food to climate change: An experimental test of the hoard-rot hypothesis. *Canadian Journal of Zoology, 93, 411-419.*

Sherry, D. (1984). Food storage by Black-capped Chickadees: Memory for the location and contents of caches. *Animal Behaviour*, *32*(2), 451-464.

Sinclair, N. (2016, November 17). Anishinaabe stories about the mischievous, wise Gray Jay. Retrieved January 19, 2021, from https://www.canadiangeographic.ca/article/anishinaabe-stories-about-mischievous-wise-gray-jay

Strickland, D. & Ouellet, H.R. (2020). Canada Jay (*Perisoreus canadensis*), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.

Strickland, D., Kielstra, B., & Norris, D.R. (2011). Experimental evidence for a novel mechanism driving variation in habitat quality in a food-caching bird. *Oecologia*, *167*, 943-950.

Sutton, A.O., Strickland, D., Freeman, N.E., Newman, A.E., & Norris, D.R. (2019). Autumn freeze-thaw events carry over to depress late-winter reproductive performance in Canada Jays. *Royal Society Open Science*, *6*(4), 181754.

Sutton, A.O., Strickland, D., & Norris, D.R. (2016). Food storage in a changing world: implications of climate change for food-caching species. *Climate Change Responses*, *3*(1), 1-25.

Visser, M.E., Holleman, L.J., & Gienapp, P. (2006). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, *147*(1), 164-172.

Waite, T.A., & Reeve, J.D. (1994). Cache dispersion by Grey Jays sequentially exploiting adjacent sources. *Animal behaviour*, *47*(5), 1232-1234.

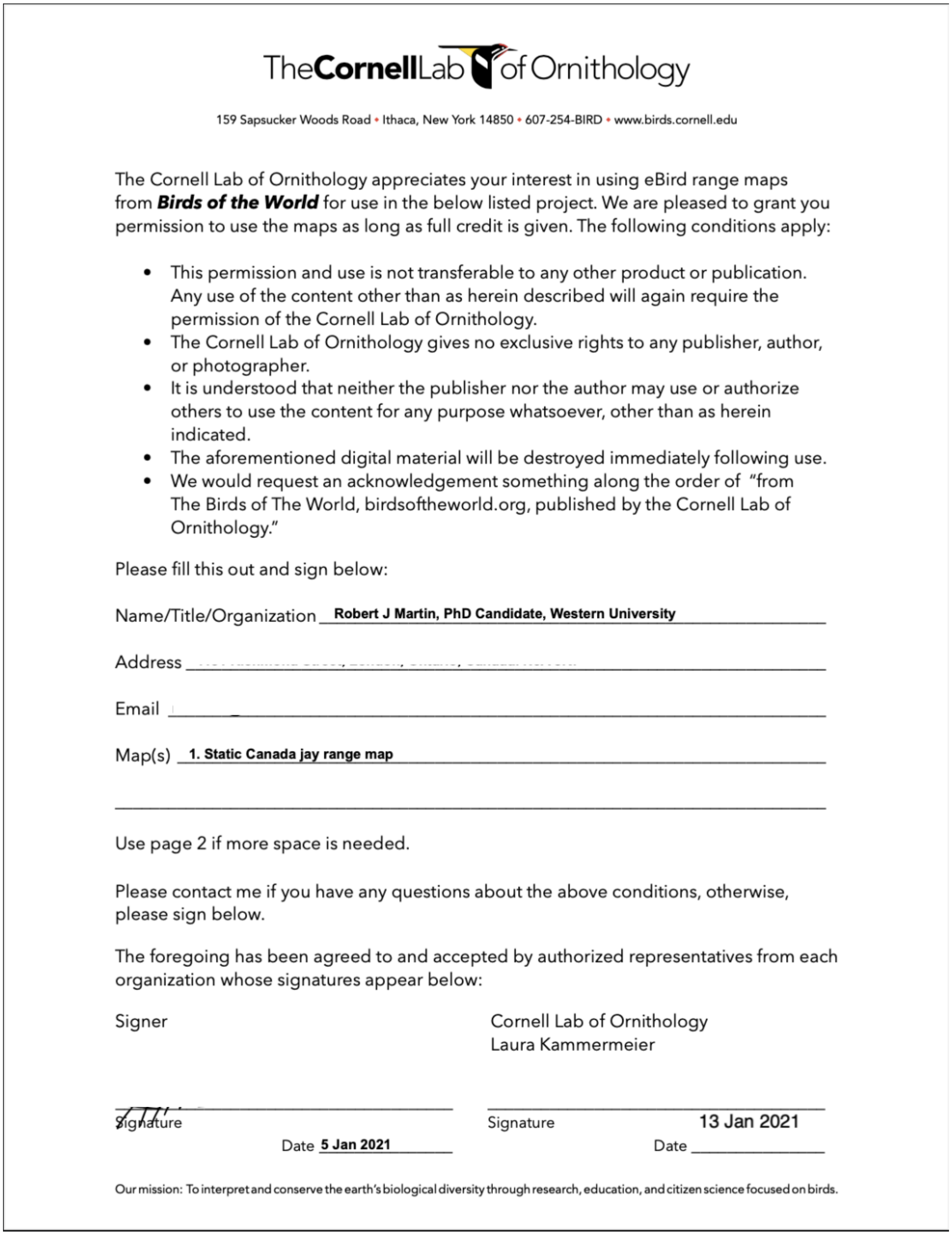
Waite, T.A., & Strickland, D. (2006). Climate change and the demographic demise of a hoarding bird living on the edge. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1603), 2809-2813.

Weir, A.A., Chappell, J., & Kacelnik, A. (2002). Shaping of hooks in New Caledonian Crows. *Science*, *297*(5583), 981-981.

Williams, J.W., & Jackson, S.T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, *5*(9), 475-482.

Appendices

Appendix I. Permission to reproduce image; Birds of the World.



TheCornellLab of Ornithology

159 Sapsucker Woods Road • Ithaca, New York 14850 • 607-254-BIRD • www.birds.cornell.edu

The Cornell Lab of Ornithology appreciates your interest in using eBird range maps from ***Birds of the World*** for use in the below listed project. We are pleased to grant you permission to use the maps as long as full credit is given. The following conditions apply:

- This permission and use is not transferable to any other product or publication. Any use of the content other than as herein described will again require the permission of the Cornell Lab of Ornithology.
- The Cornell Lab of Ornithology gives no exclusive rights to any publisher, author, or photographer.
- It is understood that neither the publisher nor the author may use or authorize others to use the content for any purpose whatsoever, other than as herein indicated.
- The aforementioned digital material will be destroyed immediately following use.
- We would request an acknowledgement something along the order of "from The Birds of The World, birdsoftheworld.org, published by the Cornell Lab of Ornithology."

Please fill this out and sign below:

Name/Title/Organization **Robert J Martin, PhD Candidate, Western University**

Address [redacted]

Email [redacted]

Map(s) **1. Static Canada jay range map**

Use page 2 if more space is needed.

Please contact me if you have any questions about the above conditions, otherwise, please sign below.

The foregoing has been agreed to and accepted by authorized representatives from each organization whose signatures appear below:

Signer

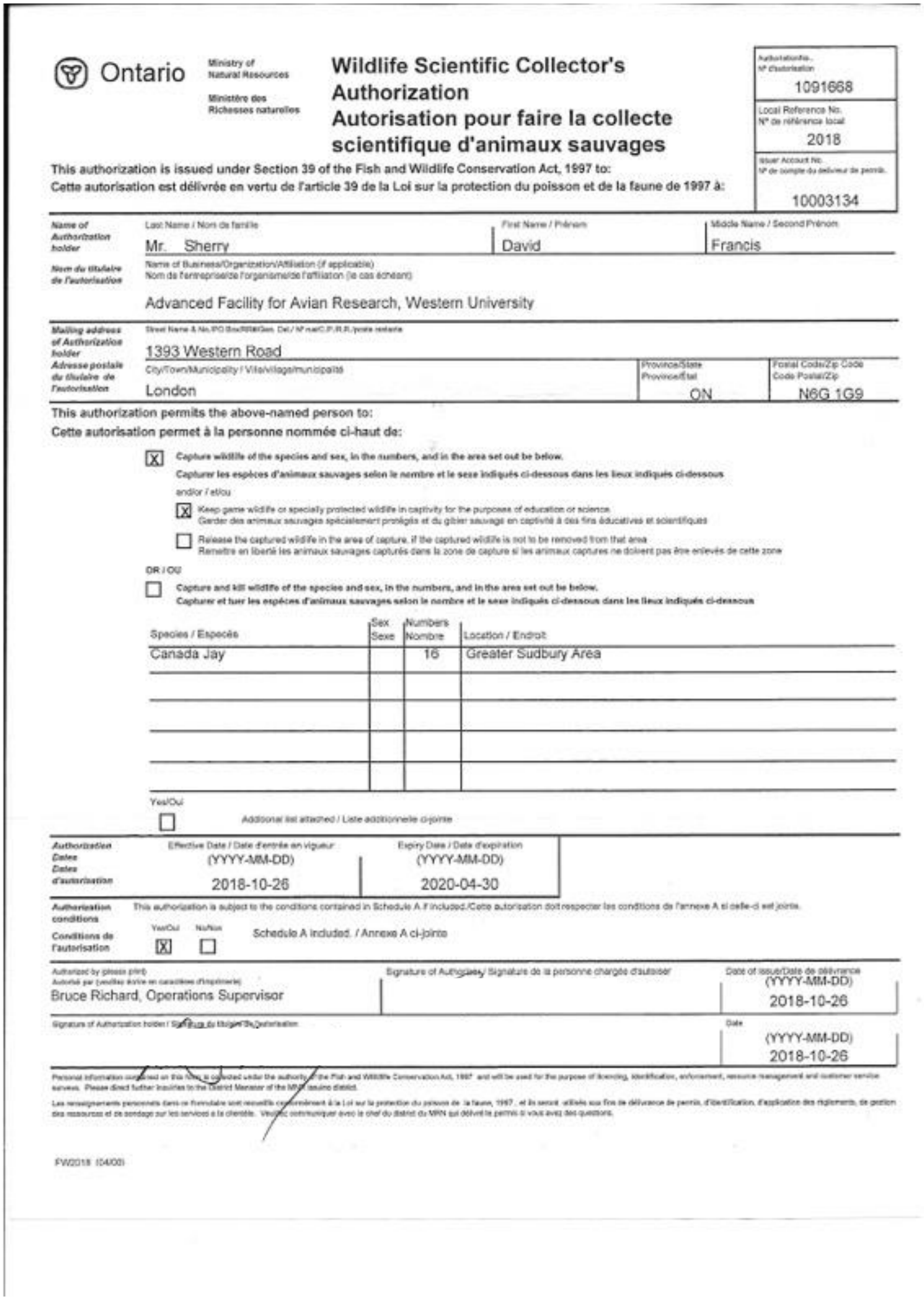
Signature
Date **5 Jan 2021**

Cornell Lab of Ornithology
Laura Kammermeier

Signature
Date 13 Jan 2021

Our mission: To interpret and conserve the earth's biological diversity through research, education, and citizen science focused on birds.

Appendix II. Ontario Ministry of Natural Resources and Forestry Permit



Ontario

Ministry of Natural Resources
Ministère des Richesses naturelles

Wildlife Scientific Collector's Authorization
Autorisation pour faire la collecte scientifique d'animaux sauvages

Authorization No. / Nº d'autorisation: 1091668
Local Reference No. / Nº de référence local: 2018
Issuer Account No. / Nº de compte du délivreur de permis: 10003134

This authorization is issued under Section 39 of the Fish and Wildlife Conservation Act, 1997 to:
Cette autorisation est délivrée en vertu de l'article 39 de la Loi sur la protection du poisson et de la faune de 1997 à:

Name of Authorization holder / **Nom du titulaire de l'autorisation**	Last Name / Nom de famille Mr. Sherry	First Name / Prénom David	Middle Name / Second Prénom Francis
	Name of Business/Organization/Affiliation (if applicable) / Nom de l'entreprise/de l'organisme/de l'affiliation (le cas échéant) Advanced Facility for Avian Research, Western University		
Mailing address of Authorization holder / **Adresse postale du titulaire de l'autorisation**	Street Name & No./PO Box/RR#/Gen. Del. / Nº rue/C.P./R.R./poste restante 1393 Western Road		
	City/Town/Municipality / Ville/village/municipalité London	Province/State / Province/État ON	Postal Code/Zip Code / Code Postal/Zip N6G 1G9

This authorization permits the above-named person to:
Cette autorisation permet à la personne nommée ci-haut de:

☒ **Capture wildlife of the species and sex, in the numbers, and in the area set out be below.**
Capturer les espèces d'animaux sauvages selon le nombre et le sexe indiqués ci-dessous dans les lieux indiqués ci-dessous

and/or / et/ou

- ☒ Keep game wildlife or specially protected wildlife in captivity for the purposes of education or science.
  Garder des animaux sauvages spécialement protégés et du gibier sauvage en captivité à des fins éducatives et scientifiques
- ☐ Release the captured wildlife in the area of capture, if the captured wildlife is not to be removed from that area
  Remettre en liberté les animaux sauvages capturés dans la zone de capture si les animaux capturés ne doivent pas être enlevés de cette zone

OR / OU

☐ **Capture and kill wildlife of the species and sex, in the numbers, and in the area set out be below.**
Capturer et tuer les espèces d'animaux sauvages selon le nombre et le sexe indiqués ci-dessous dans les lieux indiqués ci-dessous

Species / Espèces	Sex / Sexe	Numbers / Nombre	Location / Endroit
Canada Jay		16	Greater Sudbury Area

Yes/Oui
☐ Additional list attached / Liste additionnelle ci-jointe

Authorization Dates / **Dates d'autorisation**	Effective Date / Date d'entrée en vigueur (YYYY-MM-DD) 2018-10-26	Expiry Date / Date d'expiration (YYYY-MM-DD) 2020-04-30

Authorization conditions / **Conditions de l'autorisation**
This authorization is subject to the conditions contained in Schedule A if included./Cette autorisation doit respecter les conditions de l'annexe A si celle-ci est jointe.
Yes/Oui ☒ No/Non ☐ Schedule A included. / Annexe A ci-jointe

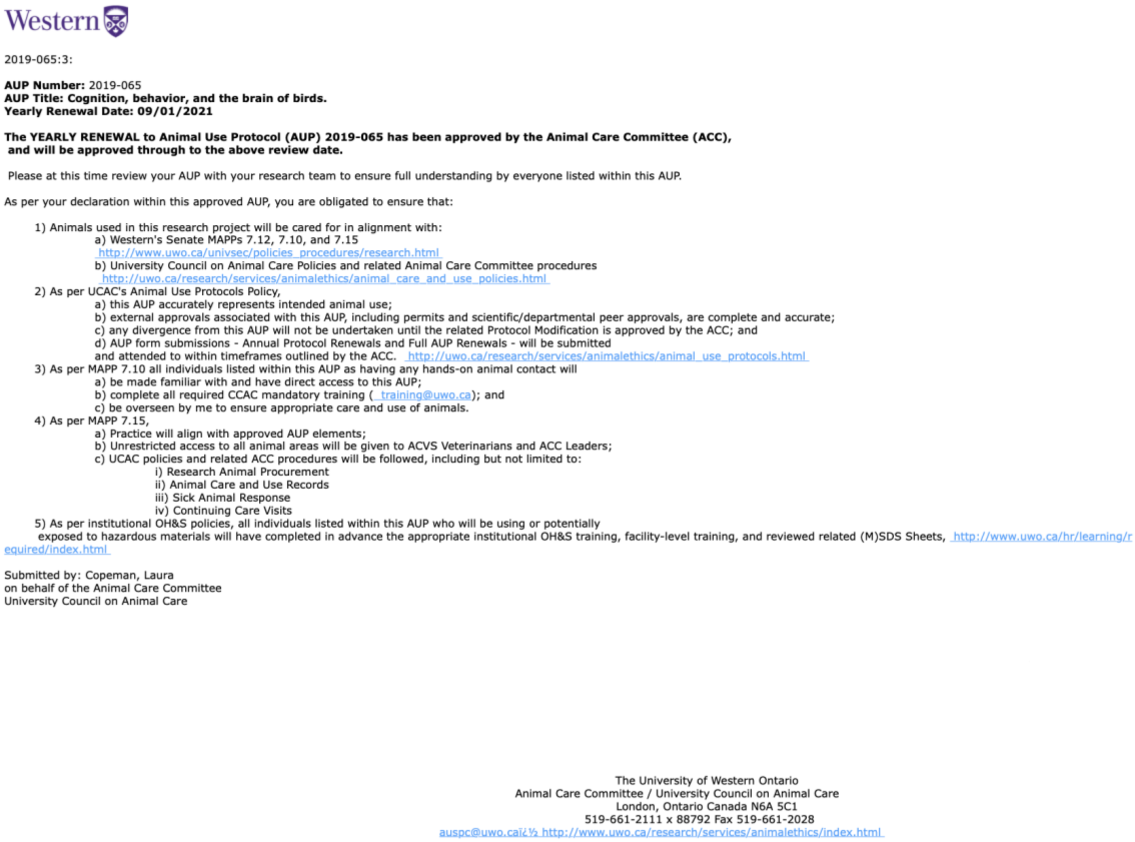
Authorized by (please print) / Autorisé par (veuillez écrire en caractères d'imprimerie) Bruce Richard, Operations Supervisor	Signature of Authorizer / Signature de la personne chargée d'autoriser	Date of issue/Date de délivrance (YYYY-MM-DD) 2018-10-26
Signature of Authorization holder / Signature du titulaire de l'autorisation		Date (YYYY-MM-DD) 2018-10-26

Personal information contained on this form is collected under the authority of the Fish and Wildlife Conservation Act, 1997 and will be used for the purpose of licensing, identification, enforcement, resource management and customer service surveys. Please direct further inquiries to the District Manager of the MNR issuing district.

Les renseignements personnels dans ce formulaire sont recueillis conformément à la Loi sur la protection du poisson et de la faune, 1997, et ils seront utilisés aux fins de délivrance de permis, d'identification, d'application des règlements, de gestion des ressources et de sondage sur les services à la clientèle. Veuillez communiquer avec le chef du district du MRN qui délivre le permis si vous avez des questions.

FW2018 (04/00)

Appendix III. UWO Animal Use Protocol Approval



Western

2019-065:3:

AUP Number: 2019-065
AUP Title: Cognition, behavior, and the brain of birds.
Yearly Renewal Date: 09/01/2021

The YEARLY RENEWAL to Animal Use Protocol (AUP) 2019-065 has been approved by the Animal Care Committee (ACC), and will be approved through to the above review date.

Please at this time review your AUP with your research team to ensure full understanding by everyone listed within this AUP.

As per your declaration within this approved AUP, you are obligated to ensure that:

1) Animals used in this research project will be cared for in alignment with:
    a) Western's Senate MAPPs 7.12, 7.10, and 7.15
    http://www.uwo.ca/univsec/policies_procedures/research.html
    b) University Council on Animal Care Policies and related Animal Care Committee procedures
    http://uwo.ca/research/services/animalethics/animal_care_and_use_policies.html
2) As per UCAC's Animal Use Protocols Policy,
    a) this AUP accurately represents intended animal use;
    b) external approvals associated with this AUP, including permits and scientific/departmental peer approvals, are complete and accurate;
    c) any divergence from this AUP will not be undertaken until the related Protocol Modification is approved by the ACC; and
    d) AUP form submissions - Annual Protocol Renewals and Full AUP Renewals - will be submitted and attended to within timeframes outlined by the ACC. http://uwo.ca/research/services/animalethics/animal_use_protocols.html
3) As per MAPP 7.10 all individuals listed within this AUP as having any hands-on animal contact will
    a) be made familiar with and have direct access to this AUP;
    b) complete all required CCAC mandatory training (training@uwo.ca); and
    c) be overseen by me to ensure appropriate care and use of animals.
4) As per MAPP 7.15,
    a) Practice will align with approved AUP elements;
    b) Unrestricted access to all animal areas will be given to ACVS Veterinarians and ACC Leaders;
    c) UCAC policies and related ACC procedures will be followed, including but not limited to:
        i) Research Animal Procurement
        ii) Animal Care and Use Records
        iii) Sick Animal Response
        iv) Continuing Care Visits
5) As per institutional OH&S policies, all individuals listed within this AUP who will be using or potentially exposed to hazardous materials will have completed in advance the appropriate institutional OH&S training, facility-level training, and reviewed related (M)SDS Sheets, http://www.uwo.ca/hr/learning/required/index.html

Submitted by: Copeman, Laura
on behalf of the Animal Care Committee
University Council on Animal Care

The University of Western Ontario
Animal Care Committee / University Council on Animal Care
London, Ontario Canada N6A 5C1
519-661-2111 x 88792 Fax 519-661-2028
auspc@uwo.caï¿½ http://www.uwo.ca/research/services/animalethics/index.html

Curriculum Vitae

Robert Jeffrey Martin

Academic History

PhD	Current	Biology	University of Western Ontario
MSc	2017	Biology	University of Western Ontario
BSc	2015	Biology	Northwestern Oklahoma State University
BSc	2015	Health and Sports Science	Northwestern Oklahoma State University

Awards and Distinctions

2021-2020	David E. Laudenbach Scholarship ($650.00)
2021-2020	Ontario Graduate Scholarship, OGS QEII ($15,000.00)
2020-2019	Ontario Graduate Scholarship, OGS QEII ($15,000.00)
2019	Travel and Accommodation Award (¥170,000) International Student Symposium for Animal Behaviour and Cognition Kyoto University, Kyoto, Japan
2019	Best Oral Presentation – 2nd Prize International Student Symposium for Animal Behaviour and Cognition Kyoto University, Kyoto, Japan
2019-2018	Ontario Graduate Scholarship, OGS QEII ($15,000.00)
2018	Western Biology Travel Grant ($120.00)
2017	Western Biology Travel Grant ($200.00)
2015	Western Science Entrance Scholarship ($2,000.00)
2015	Academic Honours; Magna Cum Laude, NWOSU, Alva, OK, USA
2015	Outstanding Senior Award, NWOSU, Alva, OK, USA
2015	Capital One Academic All-American, NWOSU, Alva, OK, USA
2015-2014	Division II Athletics Directors Association Academic Achievement Award, NWOSU, Alva, OK, USA

2015-2011	Undergraduate Academic Scholarship, NWOSU, Alva, OK, USA
2015-2011	Academic Honour Roll, NWOSU, Alva, OK, USA
2013	First Place, All Disciplines Ranger Research Day, NWOSU, Alva, OK, USA.

Invited Talks and Presentations

2018	Invited Public Lecture, Birds in a Changing World Northwestern Oklahoma State University, Alva, Oklahoma, USA
2018	Guest Lecture, Department of Biology Northwestern Oklahoma State University, Alva, Oklahoma, USA
2017	Invited Speaker, Scientific Research Society Western University, London, Ontario, Canada
2017	Guest Lecture, Department of Psychology Western University, London, Ontario, Canada
2016	Guest Lecture, Department of Psychology Brescia University College, London, Ontario, Canada

Teaching Experience

2021-2015	Teaching Assistant, Biology, Western University, London, ON, CA
2019-2017	Teaching Assistant, Enviro. Science and Sustainability, London, ON, CA

Supervision and Mentorship

2021-2020	T. Lue, Honors Thesis, Biology, Western University, London, ON, CA Advisor
2019-2018	C. Kruger, Honors Thesis, Biology, Western University, London, ON, CA Mentor (publication #2)
2019-2018	N. Jalilian, Honors Thesis, Biology, Western University, London, ON, CA Advisor
2019-2018	R. Whiley, Honors Thesis, Biology, Western University, London, ON, CA Advisor
2017-2016	T. Shoot, Honors Thesis, Biology, Western University, London, ON, CA Mentor (publication #3)

Professional and Academic Service

2021	Co-Chair, Itnl Student Symposium for Animal Behaviour and Cognition Western University, London, ON, CA
2021-2017	Graduate Student Representative, Student Services Committee (SSC) Western University, London, ON, CA
2021-2019	Graduate Education Comm., The Society of Biology Graduate Students, Western University, London, ON, CA
2019-2018	Treasurer, The Society of Biology Graduate Students, Western University, London, ON, CA
2019-2018	Organizing Committee, Biology Graduate Research Forum Western University, London, ON, CA
2018-2017	Chairperson, The Society of Biology Graduate Students Western University, London, ON, CA
2018	Media Team Chair, Ontario Ecology, Ethology and Evolution Colloquium Western University, London, ON, CA
2018	Graduate Representative, Hon. G Howard Ferguson Selection Committee Western University, London, ON, CA
2017	Chairperson, 8th Annual Biology Graduate Research Forum Western University, London, ON, CA
2017	Thesis Presentation Evaluator, BIO4999E Thesis Presentation Day Western University, London, ON, CA
2016	Oral Presentation Judge, Western Student Research Conference Western University, London, ON, CA
2016	Programming, Biology Graduate Research Forum Organizing Committee Western University, London, ON, CA
2015	Special Projects Chair, Student-Athlete Advisory Committee, NWOSU, Alva, OK, USA
2015-2013	President, Conserving Our Ranger Environment (CORE), NWOSU, Alva, OK, USA
2014	Seminar Coordinator, CORE Speaker Series, NWOSU, Alva, OK, USA
2013	Treasurer, Biology Student Organization, NWOSU, Alva, OK, USA

Outreach and Volunteer Activities

2020-2015	Assistant Coach, London Badgers 18U London District Baseball Association, London, ON, CA
2019-2015	Let’s Talk Science Visit Series, Lawrie Hawkins Public School London, ON, CA

Professional and Academic Affiliations

Present	Society for Integrative and Comparative Biology
Present	International Ornithologists’ Union
Present	Animal Behaviour Society
Present	Canadian Society for Ecology and Evolution
Present	Comparative Cognition Society

Media

2020	Biology Digest (Print), Graduate Profile Western University, London, ON, CA
2018	Western Science Speaks (Podcast), Faculty of Science Western University, London, ON, CA

Peer Reviewed Contributions

3) Edwards, S.C., Shoot, T.T., **Martin, R.J.**, Sherry, D.F., Healy, S.D. (2020). It’s not all about temperature: breeding success also affects nest design. Behavioural Ecology (31.4), 1065-1072.

2) **Martin, R.J.**, Kruger, M.C., MacDougall-Shackleton, S.A., Sherry, D.F. (2020). Black-capped Chickadees (*Poecile atricapillus*) use temperature as a cue for reproductive timing. General and Comparative Endocrinology (287), 113348.

1) **Martin, R.J.**, Sherry, D.F. (2019). Seasonal overwinter temperature has no effect on problem solving or neophobic behaviour in Black-capped Chickadees (*Poecile atricapillus*). Behavioural Processes (162), 72-78.

Submitted

Martin, R.J., Martin, G.K., Roberts, W.A., Sherry, D.F. [submitted]. Canada Jays (*Perisoreus canadensis*) fail to plan for the future. [RSBL-2021-0210]

Martin, R.J., Sherry. D.F. [submitted]. Canada Jays (*Perisoreus canadensis*) employ multiple context-dependent cache protection strategies. [ANBEH-D-21-00018]

In Preparation

Martin, R.J., Dick, M.F., Sherry. D.F. [in prep]. Canada Jays (*Perisoreus canadensis*) balance protein and energy targets simultaneously in both food consumed and cached.

Martin, R.J., Fuirst, M., Sherry, D.F. [in prep]. Canada Jays (*Perisoreus canadensis*) identify and exploit coniferous cache locations using visual cues.

Other Published Works

1) **Martin, R.J.** (2017). Winter warming affects the onset of reproduction but not cognition of the hippocampus in Black-capped Chickadees (*Poecile atricapillus*). Electronic Thesis and Dissertation Repository. 4713. [MSc Thesis]

Conference Contributions

*First author is presenting author unless indicated by asterisks (*)

22) **Martin, R.J.**, Kruger, M.C., MacDougall-Shackleton, S.A., Sherry, D.F. (2020) “Temperature as a supplementary cue in the reproductive timing of the Black-capped Chickadee (*Poecile atricapillus*)”. Society for Integrative and Comparative Biology (SICB), Austin, Texas, USA. [Talk]

21) **Martin, R.J.**, Fuirst, M, Sherry, D.F. (2019) “Cache site selection and habitat exploitation by Canada Jays (*Perisoreus canadensis*)”. International Student Symposium for Animal Behaviour and Cognition (ISSABC), Kyoto, Japan. [Talk]

20) Shoot, T.T., Edwards, S.C., **Martin, R.J.**, Healy, S.D., Sherry, D.F., & Daley, M.J. (2019) “Understanding avian incubation with a computer algorithm”. Comparative Cognition Society (CO3), Melbourne, Florida, USA. [Talk]

19) **Martin, R.J.**, Shoot, T.T., Edwards, S.C., Healy, S.D., Sherry, D.F. (2018) “The effect of ambient temperature on the growth of Zebra Finch (*Taeniopygia guttata*) offspring.” International Ornithological Congress (IOC), Vancouver, British Columbia, Canada. [Poster]

18) Edwards, S.C., Shoot, T.T., **Martin, R.J.**, Sherry, D.F., Healy, S.D. (2018) “Zebra finches build different nests at different temperatures” International Ornithological Congress (IOC), Vancouver, British Columbia, Canada. [Talk]

17) Shoot, T.T., Edwards, S.C., **Martin, R.J.**, Healy, S.D., Sherry, D.F., & Daley, M.J. (2018) “Zebra finch incubation behaviour depends on ambient temperature and experience: A hidden Markov model approach.” International Ornithological Congress (IOC), Vancouver, British Columbia, Canada. [Talk]

16) **Martin, R.J.**, Sherry, D.F. (2018) “Seasonal overwinter temperature has no effect on problem solving or neophobic behaviour in Black-capped Chickadees (*Poecile atricapillus*).” Comparative Cognition Society (CO3), Melbourne, Florida, USA. [Talk]

15) Shoot, T.T., Edwards, S.C., **Martin, R.J.**, Healy, S.D., Sherry, D.F., & Daley, M.J. (2018) “Analyzing Zebra Finch incubation with a computer algorithm” Comparative Cognition Society (CO3), Melbourne, Florida, USA. [Talk]

14) Shoot, T.T., Edwards, S.C., **Martin, R.J.**, Healy, S.D., Sherry, D.F., & Daley, M.J. (2018) “Analyzing Zebra Finch incubation with computer algorithms” Western Research Forum (WRF), London, Ontario, CA. [Poster]

13) Shoot, T.T., Edwards, S.C., **Martin, R.J.**, Healy, S.D., Sherry, D.F., & Daley, M.J. (2018) “Implication of temperature on incubation behaviour: A hidden Markov Model method” Canadian Society of Ecology and Evolution (CSEE), Guelph, Ontario, CA. [Poster]

12) Shoot, T.T., Edwards, S.C., **Martin, R.J.**, Healy, S.D., Sherry, D.F., & Daley, M.J. (2018) “Can birds flexibly adapt incubation behaviour in varying environmental conditions?” Southern Ontario Neuroscience Association (SONA), Guelph, Ontario, CA. [Poster]

11) **Martin, R.J.**, Sherry, D.F. (2017) “Cognitive responses to winter temperature variation in Black-capped Chickadees (*Poecile atricapillus*).” Animal Behaviour Society, Toronto, Ontario, Canada. [Talk]

10) Shoot, T.T., **Martin, R.J.**, Sherry, D.F. (2017) “Nest building under stress: How temperature affects nest structure in Zebra Finches” Animal Behaviour Society (ABS), Toronto, Ontario, CA. [Poster]

9) **Martin, R.J.**, Sherry, D.F. (2017) “Winter temperature experience affects cognitive responses in Black-capped Chickadees (*Poecile atricapillus*).” Canadian Society for Ecology and Evolution, University of Victoria, Victoria, British Columbia, Canada. [Talk]

8) **Martin, R.J.**, Sherry, D.F. (2017) “Effects of temperature on cognitive abilities in Black-capped Chickadees (*Poecile atricapillus*).” Comparative Cognition Society (CO3), Melbourne, Florida, USA. [Poster]

7) Shoot, T.T., **Martin, R.J.**, Sherry, D.F. (2017) “The role of temperature in Zebra Finch nest building” Comparative Cognition Society (CO3), Melbourne, Florida, USA. [Poster]

6) Edwards, S.C., Shoot, T.T., **Martin, R.J.**, Sherry, D.F. & Healy, S. D. (2017) “The nest a Zebra Finch builds depends on environmental temperature” Association for the Study of Animal Behaviour (ASAB), Liverpool, UK. [Poster]

5) Edwards, S.C., Shoot, T.T., **Martin, R.J.**, Sherry, D.F. & Healy, S.D. (2017) Cold birds put more material in their nests. European Ornithologists' Union Conference, Turku, Finland. [Poster]

4) Shoot, T.T., **Martin, R.J.**, Sherry, D.F. (2017) “The role of temperature on nest structure in Zebra Finches” Western Student Research Conference (WSRC), London, Ontario, CA. [Talk]

3) **Martin, R.J.** (2014) “Body mass in relation to song repertoire size in oscine birds.” Ranger Research Day, Northwestern Oklahoma State University, Alva, Oklahoma, USA. [Poster]

2) Ben, S., Fewins, M., Frech, B., Hoffman, D., Jones, A., **Martin, R.J.***, Ortiz, J., Quammen, S., Richmond, C., Smith, S. (2014) “Fuzzy occupancy: A modern day look at rodent gullibility.” Ranger Research Day, Northwestern Oklahoma State University, Alva, Oklahoma, USA. [Poster; Authors Alphabetized]

1) **Martin, R.J.**, Reinart, M., Conneywerdy, J. (2013) “Arsenic testing in Northwestern Oklahoma State University’s taxidermy collections and natural history museum.” Ranger Research Day, Northwestern Oklahoma State University, Alva, Oklahoma, USA. [Poster]