

Canada jays (*Perisoreus canadensis*) identify and exploit coniferous cache locations using visual cues

R. Jeff Martin^{1,2}  | Matthew Furst³ | David F. Sherry^{1,2,4}

¹Department of Biology, University of Western Ontario, London, ON, Canada

²Advanced Facility for Avian Research, University of Western Ontario, London, ON, Canada

³Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

⁴Department of Psychology, University of Western Ontario, London, ON, Canada

Correspondence

R. Jeff Martin, Department of Biology, McGill University, 845 Sherbrooke Street W, Montreal, QC H3A 0G4, Canada.
Email: rmarti88@uwo.ca

Present address

R. Jeff Martin, Department of Biology, McGill University, Montréal, QC, Canada

Funding information

This research was supported by a Natural Sciences and Engineering Research Council of Canada Discovery Grant to DFS (#105542)

Abstract

Food caching is a foraging strategy used by many vertebrates, involving the storage and subsequent recovery of food items for later consumption, when other food sources are scarce. Once cached, stored food, particularly highly perishable items, can degrade over time. 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 in the wild. We investigated eight captive Canada jays' (*Perisoreus canadensis*) ability to both identify and exploit conifer tree species. Further, we examined potential cues that birds may use to identify and select these potentially beneficial sites. We found strong evidence to suggest that birds can quickly identify conifer tree species and subsequently exploit those cache locations preferentially. Furthermore, our evidence suggests that although birds do not appear to use olfactory cues when making caching decisions, they potentially attend to structural cues. We suggest 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 amongst trees of different species and use this information to select cache-sites.

KEYWORDS

cache preservation, cache-site selection, Canada jay, corvid, food caching, *Perisoreus canadensis*

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 (Sherry, 1985; Smith & Reichman, 1984; Vander Wall, 1990). Food caching species can be broadly divided into two groups: larder- and scatter-hoarders. Within these two fundamental groups, both *short-term* and *long-term* food-cachers exist (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 periods of limited resources. These long-term caches are subjected to potentially harsh environmental conditions, putting them at a risk of degrading.

Whilst most species cache nonperishable 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 & Cardoza, 1982; Strickland & 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 amongst those most vulnerable.

Caching species should 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, particularly corvids, can actively use 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 relocate acorns to drier sites less vulnerable to degradation and germination (Fleck & Woolfenden, 1997; Furst et al., 2020; Kulahci & Bowman, 2011). Additionally, spotted nutcrackers (*Nucifraga caryocatactes*) also select cache-sites with favourable microclimatic conditions (Neuschulz et al., 2015). Whilst these studies demonstrate that food-caching species exploit certain environmental characteristics, particularly drier conditions, 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.

One observed cache-site characteristic is tree species itself. Different tree species offer different types of visual cues, structural configurations, chemical compounds and variety of caching locations to caching individuals. In noncaching birds, specific plant species – bird interactions have been demonstrated previously. Migratory birds demonstrate preferences for particular species, often exploiting the resources these plants provide for foraging (e.g. Kirsch & Wellik, 2017; Morgan et al., 2018; Wood et al., 2012) or for breeding sites (e.g. Anderson & Shugart, 1974; Squires and Bunnell, 2018). The same is true of resident species (e.g. Narango et al., 2017, 2018). New Caledonian crows (*Corvus moneduloides*) have even been shown to attend to specific parts of beneficial plants in order to identify their preferred species for tool manufacture (Klump et al., 2019). Despite these examples, evidence of active environmental exploitation in nonmigratory caching species is 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). Generally, cache-site preferences, and the mechanisms that drive such preferences, remain largely unexplored.

Canada jays (*Perisoreus canadensis*) are resident species of the boreal and subalpine forests in North America and maintain year-round territories (Strickland & Ouellet, 2020). Canada jays are a long-term food-caching species, which store perishable food items including berries, mushrooms, invertebrates and carrion in saliva covered boluses for overwinter survival and late-winter reproduction (Dow, 1965; Strickland & Ouellet, 2020; Sutton et al., 2016). These boluses, which resemble varnish covered balls when dry, are stored arboreally and likely play an important role in the long-term preservation of the stored perishable items (Dow, 1965; Strickland & Ouellet, 2020; Sutton et al., 2016). Thus, cache perishability and preservation are clearly important factors that influence the viability of cached food for future consumption, and Canada jays should engage in behaviours to promote further viability.

Canada jays also make active decisions about where to cache their food, evaluating their environment prior to caching (Martin & Sherry, 2021), and this could play a role in determining cache viability. 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 & Ouellet, 2020). These conifer tree species are known to preserve perishable food items better than deciduous trees, which also exist within Canada jay territories (Sechley et al., 2015; Strickland et al., 2011). This natural preservation, however, is only beneficial if Canada jays can identify and exploit these cache-sites when available. Whilst field experiments have shown that conifers preserve caches better than deciduous trees within the Canada jay distribution, it is not known whether the jays actively prefer to cache in conifer trees or if they opportunistically select trees for scatterhoarding. Unfortunately, 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 we experimentally tested whether Canada jays discriminate amongst tree species when caching. Additionally, we assessed two potential cues that individuals might use to make such assessments, olfaction and structure. Birds were allowed to freely cache perishable food items in a variety of experimental settings, and caching preferences were recorded. We predicted that individuals would be able to identify conifers, and preferentially cache in these trees, avoiding deciduous trees. We also expected that Canada jays would identify preferred trees based on both isolated olfactory and structural cues.

2 | GENERAL METHODS

2.1 | Subjects

Eight adult Canada jays were captured by Potter trap in Sudbury, Ontario, Canada 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 1 week before the experiment in large, outdoor, free-flight rooftop aviaries. Aviaries ranged in size from 2.5 × 3.0 m to 3.0 × 3.5 m, all were 2.5 m in height and contained numerous natural perches of various diameters. Each aviary also included shelters, and other items allowing the birds to interact with various textures, colours and patterns. One bird was removed from Experiments Two and Three due to unrelated health concerns.

One week prior to the start of each experiment, we moved the birds indoors to individual cages (0.75 × 0.4 × 0.4 m) and set the light cycle to 10:14 h light:dark cycle (light onset 0700 h). This was done to induce caching behaviour and to ensure motivation for caching upon entrance in the experimental arena. 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), 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).

2.2 | 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 (see Supplementary material for extended note).

2.3 | Behavioural observations

Observations for Experiment One occurred 12 February to 19 February 2019. Observations for Experiment Two occurred 7 March–13 March 2020. Observations for Experiment Three occurred 20 March–26 March.

We tested birds in a free-flight room (2.7 × 2.7 m; Figure 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 (slightly asymmetric; see Figure 1). Previous research with Canada jays suggests that they do not view the mirror as a pilferage threat (Martin & Sherry, 2021). 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 (see Supplementary material for examples of stimuli). In all experiments the location of a particular cache-site and its associated cues in a given trial was counter balanced across all possible locations. Additionally, a table with food and water was always present in the centre 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 (Martin & Sherry, 2021; Sechley et al., 2014).

2.4 | 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 water, but no food. Artificial trees consisted of a vertical 0.05 × 0.05 m wooden 'trunk' with 0.02 m diameter dowels protruding horizontally at varying heights. Each flight lasted 20 min, after which time the birds were returned to their holding cages.

2.5 | Behavioural testing

All testing occurred between 0930 h and 1300 h. Birds were tested in two cohorts, each consisting of either three or four birds. At 0830 h, we transferred cohort 1 from their home cages into holding cages (0.4 × 0.3 × 0.3 m) where they were deprived of food for 1–2 h. Immediately prior to testing cohort 1 (0930 h), we transferred cohort 2 to holding cages and deprived them of food (resulting in 1.5–3 h of food deprivation). We tested cohort 2 immediately following the testing of cohort 1. Water remained available *ad libitum* in the holding cages. We changed the order of testing each day such that each bird was tested in each of the possible time slots once. For Experiment One, there were eight possible slots, and for

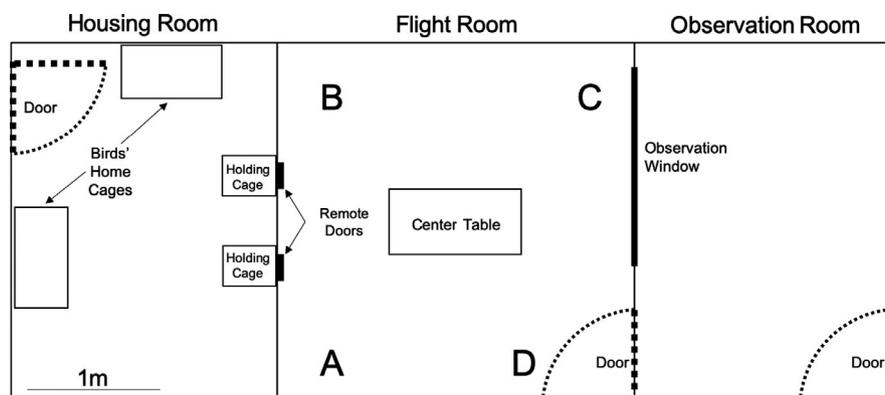


FIGURE 1 A scaled schematic of the experimental set up. Trials were run in a series of three conjoined rooms. Birds held in the Housing Room could be released into the Flight Room by an observer in the Observation Room operating the remote doors. Observers viewed trials through the one-way glass observation window. a, b, c and d mark the locations of the stimuli, and a table with water and food was present in each trial. All doors remained closed during testing

Experiments Two and Three, the slot originally occupied by the bird removed from the experiment was skipped. 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. This procedure resulted in each bird completing one trial per day, for the duration of the experiment (8 days for Exp. One, 7 days for Exp. Two & Three; see Supplementary material for detailed Table S1).

For each trial, birds accessed the testing rooms through remote doors, controlled by the observer. Whilst 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, was not scored as a cache. This occurred when birds removed large amounts of cheese from the food dish, relocated it to another flat surface and then subsequently made boluses from that cheese but did not cache it all before the trial ended, or the bird returned to caching from the food dish. Trials lasted 20 min, 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. We returned the birds to their home cages after the completion of trials for their cohort.

2.6 | Statistical analyses

Alpha was set at 0.05 threshold for all analyses, and all analyses were performed using R Studio (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 et al., 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 analysed (trials removed, Exp. One: 5; Exp. Two: 38; Exp. Three: 1).

3 | EXPERIMENT ONE: SITE IDENTIFICATION AND EXPLOITATION

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

3.1 | Methods

3.1.1 | Flight room

Stimuli for Experiment One were sections of trees with distributions that overlap with the geographic range of Canada jays in Ontario. We 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) obtained in Elginfield, Ontario (16 tree sections total). Tree sections were cut no more than 7 days prior to the beginning of the experiment and 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 trunk, 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. Spatial and section configuration was established the evening prior to testing to allow the tree sections to warm up, and the resin to flow more freely.

3.1.2 | Statistical analysis

Birds interacted with at least one tree in all trials ($n = 64$) and deposited at least one cache in 81% of trials ($n = 52$). We used linear mixed effects models to analyse time spent in each tree and cache locations. For the time spent model, the proportion of time spent in a given tree per trial was the response variable whilst for cache location model, the proportion of caches per tree in a given trial was the response variable. Trial number was nested within individual and was included as random effect.

To assess the exploitation of cache-sites, we compared the caching rate per tree using a Poisson regression. Caching rate was calculated as the number of caches made per 10 min. Tree type was included as a covariate and individual was included as a random effect. We also assessed how likely an individual was to make a cache on each visit to a particular tree. Caches per 20 visits were calculated and a second Poisson regression was performed.

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

3.2 | Results

3.2.1 | First tree interaction

Canada jays demonstrated a strong preference for which tree species they interacted with first ($F_{3,1} = 13.5, p < .0001$; Figure 2a). Jays

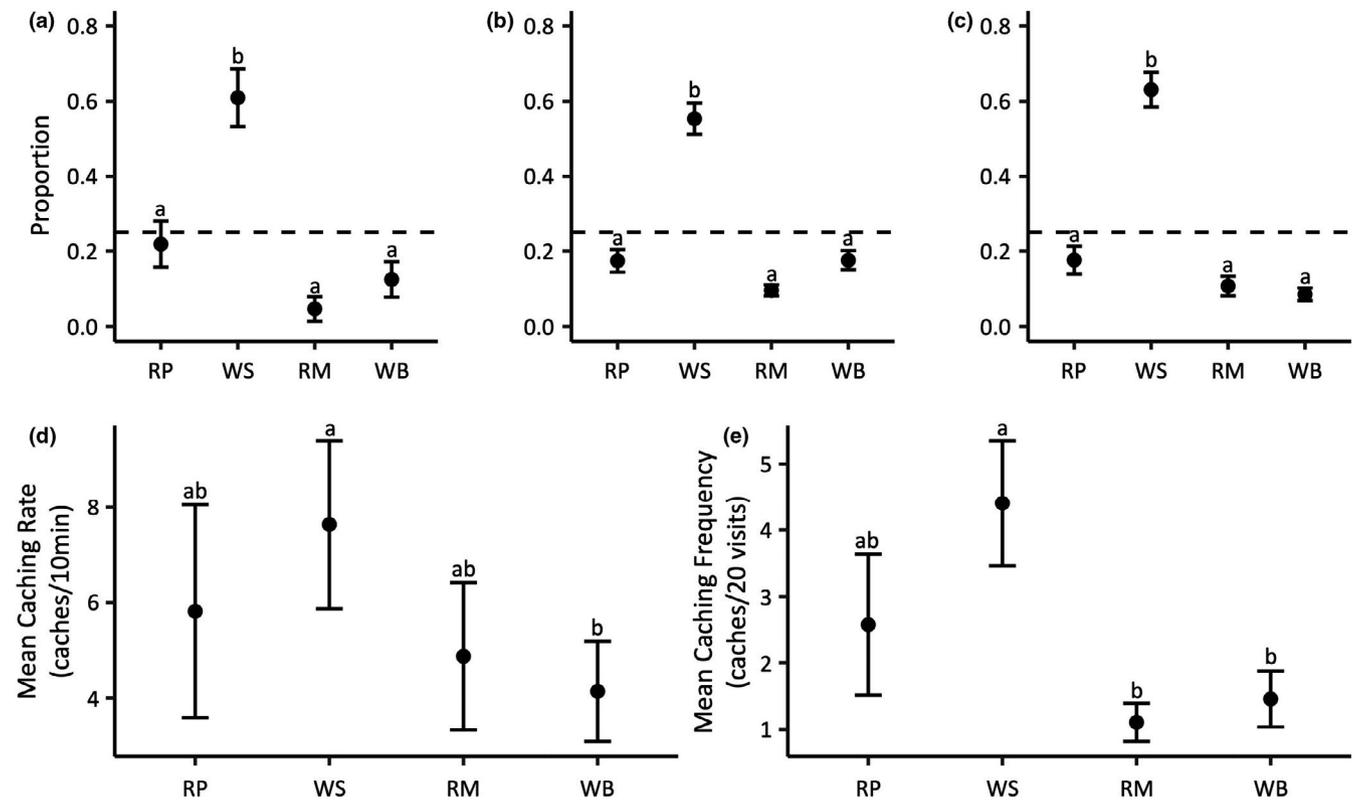


FIGURE 2 Top row: mean proportion of (a) first visits, (b) time spent and (c) caches in branches of each tree species. Bottom row: mean number of (d) caches deposited per 10 min block and (e) caches deposited per 20 visits in branches of each tree species. Dashed lines represent the 0.25, chance level. 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 $p < .05$

preferred the white spruce over the red pine (Tukey's: $p = .0011$), red maple ($p < .0001$) and white birch ($p = .0001$). All other comparisons were nonsignificant (Tukey's: $p > .05$ for all).

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 ($F_{3,1} = 38.3$, $p < .0001$; Figure 2b). As with cache location, jays spent the most time in the white spruce (51.63% of all time) compared to red pine (20.01%; Tukey's: $p < .0001$), red maple (10.70%; $p < .0001$), or white birch (17.66%; $p < .0001$) but showed no preferences between the other three trees (Tukey's: $p > .05$ for all remaining comparisons).

3.2.3 | Cache location

Canada jays demonstrated a strong preference for tree species when caching ($F_{1,3} = 50.6$, $p < .0001$; Figure 2c). Jays preferred to cache in white spruce (63.08% of all caches) over red pine (17.64%; Tukey's: $p < .0001$), red maple (10.74%; $p < .0001$) and white birch (8.54%; $p < .0001$) but showed no preferences between the other three trees (Tukey's: $p > .05$ for all remaining comparisons).

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 ($X^2_3 = 9.56$, $p = .023$; Figure 2d). Canada jays cached more frequently in the spruce tree over the white birch (Tukey's: $p = .027$); however, all other comparisons were not statistically significant.

Canada jays' propensity to deposit a cache on a given visit also varied by tree species ($X^2_3 = 19.96$, $p < .0001$; Figure 2e). 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: $p = .001$) or the white birch ($p = .006$). We found no difference for how likely individuals were to deposit a cache when visiting either the spruce or pine trees.

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, whilst 1 ended with bird on the ground. Of the 24 trials in which birds became inactive whilst perched, 18 (75%) occurred whilst 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.

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.

We next attempted to determine how birds can identify these trees. We tested whether the cue differentiating the preferred conifer species was olfactory.

4 | EXPERIMENT TWO: OLFACTORY IDENTIFICATION OF CACHE-SITES

In this experiment we assessed birds' abilities to identify, and subsequently exploit cache-sites based on olfactory cues. Because the suspected mechanism of increased cache preservation is volatile compounds in conifer resin (Strickland et al., 2011), we expected olfactory cues to be a strong indicator of potential cache preservation. As Canada jays demonstrated a preference for conifer species in Experiment One, and because deciduous trees lack volatiles used to produce strong scents, we used only conifer odours in this experiment. Additionally, it has been shown that even within conifers, some species preserve caches better than others (Strickland et al., 2011), making the distinction between conifer trees important.

4.1 | Methods

4.1.1 | Flight room

Stimuli for Experiment Two were custom made caching boards. Boards were made from commercially available SPF dimensional lumber and were cut, drilled and allowed to dry indoors for at least 10 days to reduce existing scent cues. Each board was 1.6 m × 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 it. The lowest hole in the centre 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; Alikir Essential Oils) 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.

We selected oils from four coniferous species because 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.

4.1.2 | Statistical analysis

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 ($n = 11$). We used linear mixed effects models to analyse birds' tree species preferences for number of visits, time spent in each tree and for cache location. We did not analyse the exploitation of site due to the low number of trials in which caches were deposited.

4.2 | Results

Canada jays did not differ in the number of visits they made to a location ($F_{3,93} = 0.86, p = .47$; Figure 3a), or the time they spent interacting with each of the scented caching boards ($F_{3,93} = 0.95, p = .42$; Figure 3b). Additionally, Canada jays did not preferentially cache in any of the scented boards ($F_{3,30} = 0.88, p = .46$; Figure 3c).

4.3 | Discussion

We found no evidence to suggest that Canada jays use olfactory cues to discriminate between potential caching sites. Whilst it is possible that olfaction does play a role in the discrimination process, olfactory cues alone do not appear sufficient to elicit a behavioural response. We suggest that olfactory cues may be indistinguishable in a mixed forest, or that the birds simply rely on more obvious visual cues to identify trees.

5 | EXPERIMENT THREE: STRUCTURAL IDENTIFICATION OF CACHE-SITES

Inherently, with different tree species, different structural configurations are common. For example, typical conifer trees have many branches protruding perpendicularly from a central trunk in all directions whilst deciduous trees often have fewer branches protruding at angles. There are also obvious foliage differences, adding to the visual information available to caching birds. In this experiment we assessed birds' abilities to identify, and subsequently exploit cache-sites based on structural cues. For our purposes, we focused on the branchiness of a tree most closely resembling a conifer configuration.

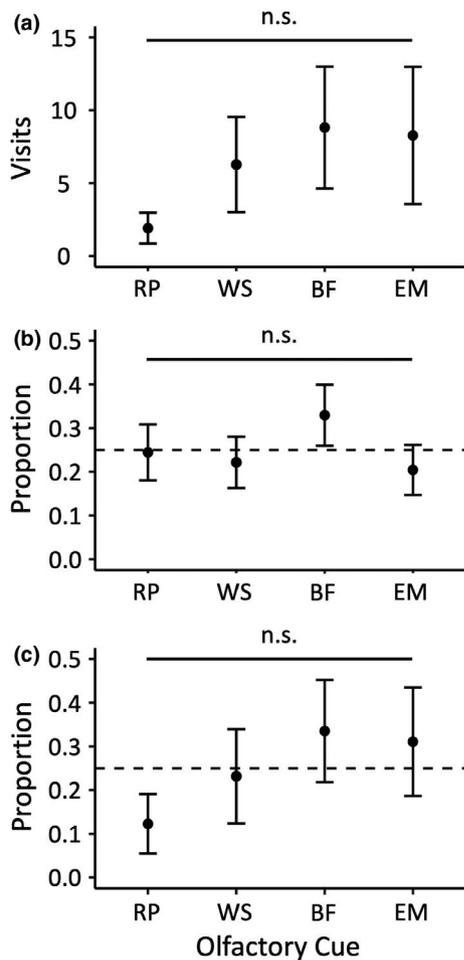


FIGURE 3 (a) number of visits, (b) mean proportion of time spent and (c) mean proportion of caches deposited by birds in each of the four scented caching boards. The dashed line indicates chance, 0.25. Olfactory cues are identified by two-letter abbreviations: RP, Red pine; WS, White spruce; BF, Balsam fir; EH, Eastern hemlock. Alpha for all tests was set at 0.05, 'n.s.' indicates nonsignificant differences

5.1 | Methods

5.1.1 | Flight room

Stimuli for Experiment Three were custom made artificial trees. Trees were composed of a $0.05 \times 0.05 \times 2.0$ 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 as the lowest two branches that were perpendicular to one another. No branch protruded in the same direction as the branch either immediately above or below it. For each testing day,

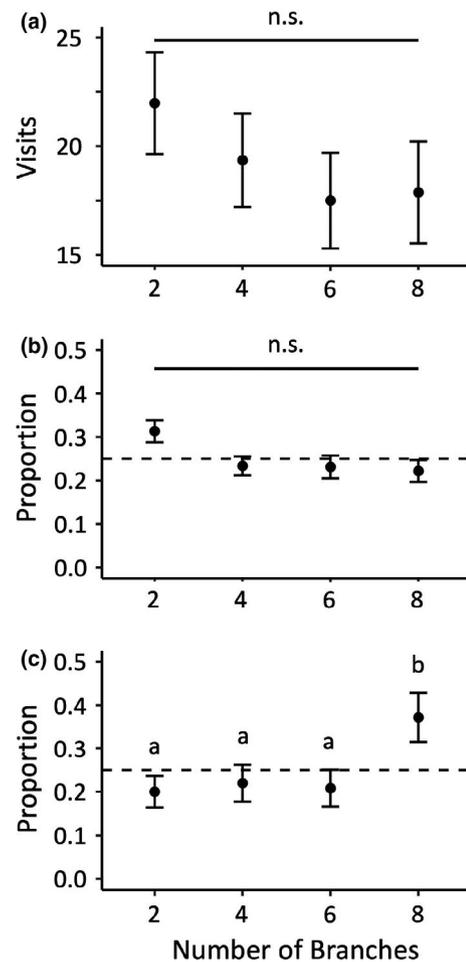


FIGURE 4 (a) number of visits and mean proportions of (b) time spent and (c) caches deposited by birds in each of the four artificial trees. The dashed line indicates chance, 0.25. Structural cues are the number of branches on each tree (e.g. 2, two-branch). Lowercase letters that are not shared indicate a significant difference at $p < .05$, 'n.s.' indicates a nonsignificant difference

a new spatial configuration of trees was used to control for spatial preferences.

5.1.2 | Statistical analysis

Birds interacted with at least one artificial tree in all trials ($n = 49$) and deposited at least one cache in 98% of those trials ($n = 48$) were analysed. We used linear mixed effects models to analyse birds' preferences for individual artificial trees for time spent, number of visits and caches deposited.

5.2 | Results

Birds demonstrated no preferences in the number of times they visited a particular tree ($F_{3,144} = 1.61$, $p = .19$; Figure 4a). There was a main effect of location on time spent ($F_{3,144} = 0.289$, $p = .04$;

Figure 4b), but post hoc tests revealed no significant pairwise differences (Tukey's: all comparisons >0.05). Birds did, however, demonstrate a preference for the proportion of caches they deposited in each location ($F_{3,141} = 3.86, p = .01$; Figure 4c). 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).

5.3 | Discussion

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

6 | GENERAL DISCUSSION

The overall aim of our study was two-fold. First, we assessed Canada jays' ability to identify and exploit beneficial cache locations. Second, we aimed to evaluate two potential factors that individuals could be using to decide between potential caching locations. We 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, we found evidence to suggest that Canada jays use structural features of trees when making caching decisions.

Conifer species, specifically spruce trees, preserve cached perishable food better than other tree species (Sechley et al., 2015; Strickland et al., 2011). Additionally, as Canada jays' caches are most at risk from acute pilferage at the time of caching (Burnell & Tomback, 1985; Rutter, 1972), caching amongst an abundance of branches (and needles) may help to disguise the location of caches (broadly reviewed in Dally et al., 2006). Whilst the forest composition of territories jays inhabit has long been assumed to be related to food-caching preferences, our results provide a key empirical link showing 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 provides a potential explanation for the link between conifer density and Canada jay territory occupancy described by Strickland et al. (2011), especially considering that Canada jays do not consume conifer seeds (Dow, 1965; Strickland & Ouellet, 2020). That is, territories with a higher proportion of spruce provide higher quality caching locations for long-term food storage and individuals are exploiting these locations, leading spruce-dominated territories to be occupied more than other habitat types.

Additionally, we have shown that Canada jay's process and use trees' 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 mature 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 and exposed ends of branches, there were more caching sites available. Although birds cached along the entire length of branches in Experiment Three, the intersection of the branches and the trunk, and the exposed end of the branch were used by multiple individuals as caching locations. Previous research has shown that the number of potential nesting sites in a location plays an important role in determining the level of nest predation, and thus nest location choice (Martin, 1993), and the same could be true for cache-site selection; the more potential sites available the less likely a cache is to be pilfered.

Interestingly, Canada jays only preferred the 8-branch tree when caching, but not when entering the room (first tree visited) or when making decisions where to perch. We suspect this is because whilst the structural characteristics of the tree appear important for caching, they are less important or useful for discriminating tree species when other visual cues (e.g. foliage) might be more salient. 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.

Though we have found evidence that Canada jays actively exploit their environment to their potential benefit, we acknowledge that our sample could be biased. Despite efforts to limit potential biases within our sample, based on the STRANGE framework (Webster & Rutz, 2020) our sample could have been biased in four of the seven STRANGE factors. Birds that participated in this study were captured in the same general area, using a single trapping method, and thus, could be biased in the (1) Trappability and self-selection and (2) Genetic make-up factors. Additionally, our sample remained in captivity for approximately 12 months between Experiment One and Experiments Two and Three resulting in possible biases in the (3) Natural changes in responsiveness factor. Finally, our sample participated in other captive experiments whilst in captivity, which could have resulted in bias in the (4) Experience factor. As noted, steps were taken to minimize potential biases, including ensuring that birds were collected as far apart as possible (within the permitted area), housing birds in semi-natural conditions when possible and providing environmental enrichment. As such, we feel as though our sample is a representative of Canada jays living in the southern portion of their range. Regardless, we encourage caution when generalizing our results and suggest that any interpretations be made with the identified potential biases in mind.

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, 2021) and could have long-term effects on populations of food-caching birds, especially those that are already food limited (Derbyshire et al., 2015).

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). Our results suggest Canada jays can actively evaluate and process information about cache-sites prior to caching and use this information to inform caching decisions. The results 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 (Sechley et al., 2015; Strickland et al., 2011).

ACKNOWLEDGEMENTS

We would like to thank Francis Boon and Michela Rebuli for their assistance with animal husbandry and maintenance. Additionally, we would like to thank Dr. Leanne Grieves for suggestions made to improve these experiments.

AUTHOR CONTRIBUTIONS

RJM and MF conceived and designed the study, with input from DFS. RJM completed behavioural trials, analysed data and wrote the first draft of the manuscript. MF and DFS contributed significantly to subsequent versions of the manuscript.

CONFLICT OF INTEREST

We have no conflicts or competing interests.

CONSENT FOR PUBLICATION

All authors have given consent for publication.

DATA AVAILABILITY STATEMENT

The data are publicly available at <https://doi.org/10.5061/dryad.4j0zpc89w>.

ORCID

R. Jeff Martin  <https://orcid.org/0000-0002-1155-6704>

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How to cite this article: Martin, R. J., Furst, M., & Sherry, D. F. (2022). Canada jays (*Perisoreus canadensis*) identify and exploit coniferous cache locations using visual cues. *Ethology*, 00, 1–10. <https://doi.org/10.1111/eth.13273>