

## Research



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## Animal behaviour

# No evidence for future planning in Canada jays (*Perisoreus canadensis*)

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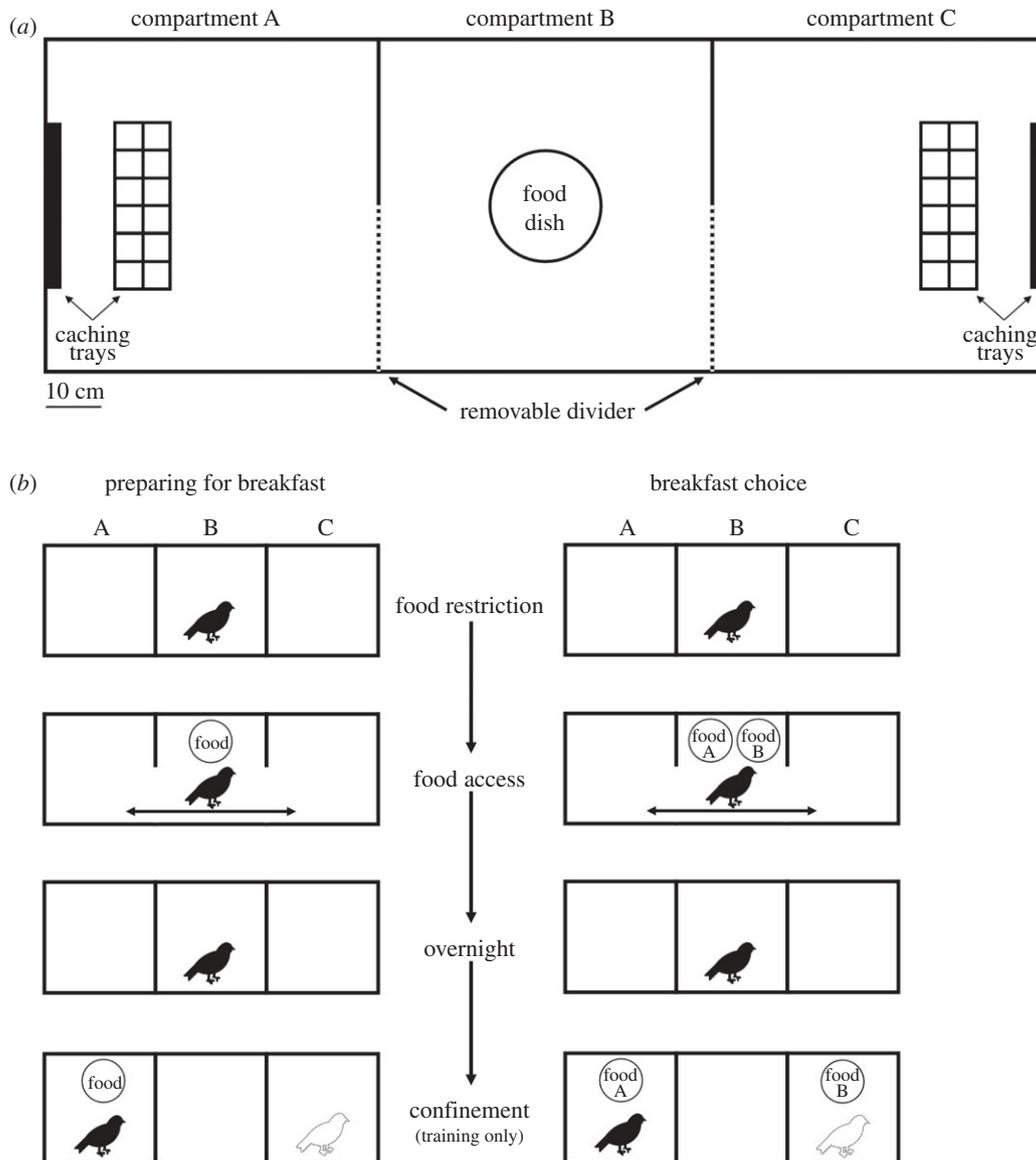
In the past 20 years, research in animal cognition has challenged the belief that complex cognitive processes are uniquely human. At the forefront of these challenges has been research on mental time travel and future planning in jays. We tested whether Canada jays (*Perisoreus canadensis*) demonstrated future planning, using a procedure that has produced evidence of future planning in California scrub-jays. Future planning in this procedure is caching in locations where the bird will predictably experience a lack of food in the future. Canada jays showed no evidence of future planning in this sense and instead cached in the location where food was usually available, opposite to the behaviour described for California scrub-jays. We provide potential explanations for these differing results adding to the recent debates about the role of complex cognition in corvid caching strategies.

## 1. Introduction

Intentional future planning is a complex learned cognitive ability (reviewed in [1]). This ability is historically thought to be unique to humans [2,3] as suggested by the Bischof–Köhler hypothesis [2] which 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 intentional future planning in animals (e.g. [4,5]; and reviewed in [6,7]).

Studies attempting to show non-human planning have focused on food caching birds, particularly corvids, because they cache food in the present and consume it days to months later, and because they rely on memory to find their caches (e.g. [4,8–10]). There have been critiques of these claims, however (e.g. [2,3,11]), with one of the most common criticisms being that there are explanations for the results that do not involve future planning, but instead, rely on simpler cognitive processes (e.g. [11–13]). Despite these criticisms, complex intentional future planning is widely accepted as a corvid ability.

One well-known (see [14,15]) study of future planning by corvids assessed the ability of California scrub-jays (*Aphelocoma californica*; formerly Western scrub-jays) to anticipate their future access to food and plan for it accordingly [16]. Individuals were found to anticipate their future needs by caching more food in the location in which food was predictably unavailable. When food of a particular type was only available in one location, and food of a different type only available in another location, individuals distributed their caches so that both food types were available in both locations. The researchers concluded that the California scrub-jays anticipated their future state, and, motivated by the anticipated future need for food, acted in advance to provide food for the future. These findings directly challenge the Bischof–Köhler hypothesis.



**Figure 1.** (a) The three compartment ( $0.6 \times 0.6$  m) experimental cage. Compartments A and C each contained two caching trays, one mounted vertically and one flat on the ground. Dashed lines indicate removable dividers, solid lines indicate non-removable barriers. (b) A flow chart for both the experiments shows 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. The confinement phase was not included in test trials.

The purpose of our study was to test whether Canada jays (*Perisoreus canadensis*) would exhibit the same caching patterns as California scrub-jays, using the methods of Raby *et al.*'s [16] original study of future planning. Canada jays are year-round residents of the Nearctic boreal and sub-alpine forests. Canada jays rely on cached food, in the form of saliva covered boluses [17], to survive periods of food scarcity in winter [18] and use memory to recover their caches [19]. We, therefore, expected Canada jays to exhibit the same caching patterns observed in California scrub-jays.

## 2. Method and materials

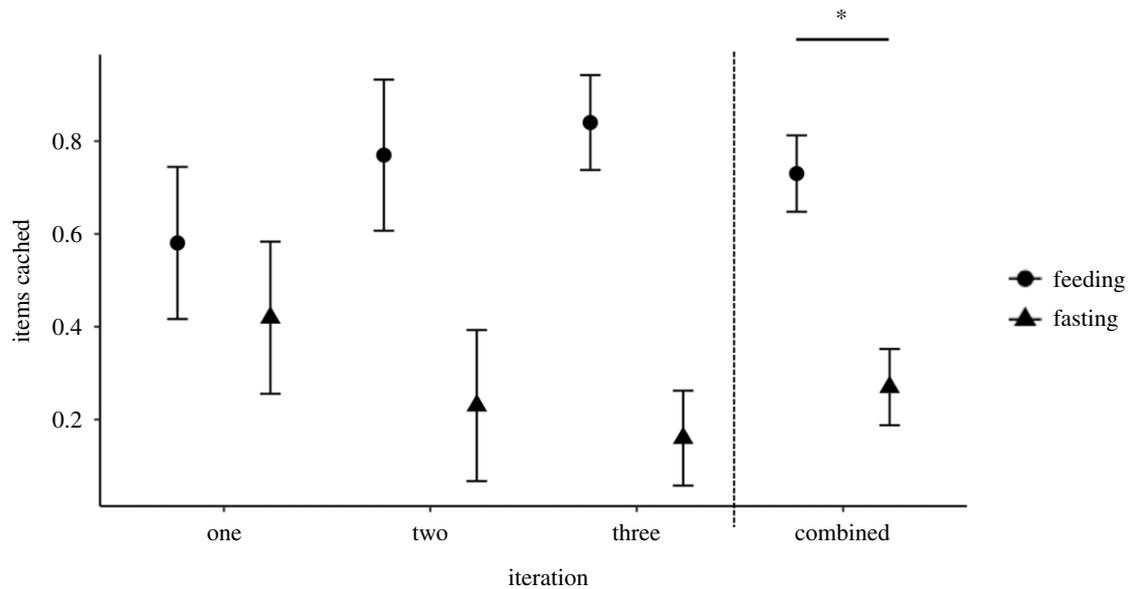
### (a) Subjects

Six wild-caught adult 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 and had captive caching experience prior to this experiment.

Birds were held on a 10 h L:14 h D photoperiod and housed individually in free flight home cages ( $1.0 \times 1.5 \times 2.0$  m) and experimental cages ( $0.6 \times 1.8 \times 0.6$  m) as described below. Birds were physically, but not visually or acoustically isolated regardless of cage. Home cages and experimental cages were in separate rooms. While in their home cages, birds had access to ad libitum food and water. Experimental cages were divided into three compartments, A, B and C, separated by removable barriers (figure 1). Compartment B was kept empty while Compartments A and C each had two standard 12-cube ice-cube trays for caching: one mounted vertically on a wall, and the other laying horizontally on the ground. In the experimental cages, food was available as described below and water was available ad libitum.

### (b) General procedure

We conducted the experiments during four consecutive weeks. During the first week, we conducted the *Preparing for Breakfast* experiment, followed by the *Breakfast Choice* experiment in the second week. We then repeated the *Preparing for Breakfast*



**Figure 2.** The mean proportions of items cached by individuals ( $n = 6$ ) in the Feeding and Fasting compartments across the three iterations of the *Preparing for Breakfast* experiment, with combined values at right. Asterisk indicates a significant difference,  $p < 0.001$ .

experiment two additional times during weeks 3 and 4. All food introduced was novel at the time of first introduction. Powdered food was non-cacheable, while whole food items could be cached. No obvious preferences were observed between foods. Except where noted below, we followed the procedures of Raby *et al.* [16] exactly. See electronic supplementary material for detailed methods, including the rationale for repetitions of *Preparing for Breakfast*.

### (c) Preparing for breakfast procedure

Birds were food deprived in Compartment B of the experimental cage for 1.5 h, after which we provided 10 g of powdered cat food (IAMS Proactive Health Adult Hairball Care, Mars Incorporated, USA) and allowed birds access to the entire apparatus; 0.5 h later food was removed, and birds were re-confined to Compartment B where they remained overnight. The following morning, birds were confined to either Compartment A or C for 2 h and provided with either 10 g of cat food (Feeding) in one compartment, or no food at all (Fasting) in the other compartment. Individuals were then returned to their home cages. Birds completed six consecutive training trials, alternating between the Feeding and Fasting conditions, experiencing each three times. On the seventh day, test day, birds were given 15 g of whole cat food, not powdered, and allowed to cache for 0.5 h. Birds were then returned to their home cages, without the opportunity to recover their caches.

### (d) Breakfast choice procedure

*Breakfast Choice* followed the same procedure as above, except that the Fasting condition was replaced with a second Feeding condition in which a different food item, Cheerios (Cheerios, General Mills, USA), was available. Birds were offered 10 g of both powdered cat food and powdered Cheerios in separate dishes placed equidistant from Compartments A and C during training but were offered only one food type when confined each morning. On test day, birds were provided with 15 g each of whole cat food and whole Cheerios to cache.

### (e) Alterations to original procedures

Canada jays experienced two fewer light hours than the scrub-jays used by Raby *et al.* [16], so experimental times were shifted. The duration of all phases remained the same. Birds were isolated at 16.00 (17.00 in the original study) each evening and were confined to their chambers at 08.00 (07.00 originally). Additionally, we used cat food and Cheerios in place of original food items. It is unlikely that these minor alterations affected our ability to accurately replicate the Raby *et al.* [16] experiment.

### (f) Statistical analysis

Cached food items were collected. No caches were made outside the ice-cube trays. Items on the floor were not counted. For the *Preparing for Breakfast* experiment, we compared the proportion of caches and number of items in each compartment with separate two-way repeated-measures ANOVAs performed in R v. 1.1.456 [20] with compartment and iteration as factors ( $n = 6$ ,  $\alpha = 0.05$ ). One trial was excluded as the bird made no caches. Two cache types were recorded for *Breakfast Choice*: same, a food item cached in the compartment where birds had encountered that item, and different, a food item cached in the compartment where birds had encountered the other food type. Data are presented for information, were not formally analysed because three birds made a total of zero caches.

## 3. Results

### (a) Preparing for breakfast

Over three iterations of the *Preparing for Breakfast* experiment, individuals cached a higher proportion of food items in the Feeding compartment than the Fasting compartment ( $F_{1,15} = 12.18$ ,  $p < 0.001$ ; figure 2). There was no interaction between compartment and iteration ( $F_{1,15} = 3.23$ ,  $p = 0.09$ ). The number of caches did not vary between iterations ( $F_{1,11} = 0.04$ ,  $p = 0.85$ ), with means of 8, 7.5 and 8.5 caches per bird per iteration.

## (b) Breakfast choice

Three birds did not cache. The other three birds averaged six caches as follows (same, different): Bird 1: two caches, one cache; Bird 2: four caches, eight caches; Bird 3: three caches, zero caches.

## 4. Discussion

We did not observe the behaviour described by Raby *et al.* [16] and found that with three iterations of the *Preparing for Breakfast* experiment, Canada jays cached significantly more food where they had previously found food, the opposite of the result obtained with California scrub-jays. These results provide no evidence that Canada jays plan for the future in the way California scrub-jays have been shown to.

Our results may differ from those of Raby *et al.* [16] due to species differences between Canada jays and California scrub-jays. The California scrub-jay genus *Aphelocoma* belongs to the monophyletic clade of New World jays, while *Perisoreus* is a Holarctic genus in a corvid group that includes the genera *Corvus* and *Garrulus* [21,22]. California scrub-jays are found in oak and oak–pine woodlands [23], and Canada jays in boreal forest dominated by white and black spruce [18]. California scrub-jays cache in the ground, whereas Canada jays cache arboreally. Both consume caches for survival, but Canada jays require cached items to gain weight prior to breeding, and to provision their offspring [18]. Despite these differences, there are similarities between the species. Both are non-migratory omnivores. Both recover some stored food soon after caching but leave much of their cached food in place for months [18,23]. Both remember the spatial locations of caches [19,24,25]. These similarities mean 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 be high for California scrub-jays, but the cost for Canada jays would be as high, or higher. As Canada jays rely on cached food for survival and provisioning young, failure to ensure resource access could have dramatic impacts on Canada jay population dynamics and future success. Thus, if continuous access to resources motivated the future planning observed in Raby *et al.* [16], we would expect Canada jays to be at least equally motivated to ensure access. While it is possible that California scrub-jays have evolved the ability to ‘plan for the future’ in response to some constraint Canada jays do not encounter, or that Canada jays have alternative mechanisms for coping with such a constraint, we find this unlikely given both species reliance on cached food. In addition, it is argued that prospection is a trait of corvids in general [26,27], further suggesting that species differences do not explain the behavioural differences observed.

Although we were able to closely follow the design of Raby *et al.* [16], one notable difference was the history of the birds participating. The Canada jays in this study were wild caught and had been in captivity for 8–18 months. The California scrub-jays used in previous research were part of a captive population, with potentially extensive caching experience in similar experimental procedures. It is possible that with more experience, Canada jays would have cached in a manner consistent with previous findings. It is also possible that the results obtained previously by Raby *et al.* [16] are a product of experience in captivity, and thus not generalizable to wild corvids.

Other results from studies with California scrub-jays, Eurasian jays (*Garrulus glandarius*) and other corvid species have been interpreted as evidence of future planning ([28–31] but see [32]). Many of these studies, however, have faced criticisms like those of the Raby *et al.* [16] study [12,28] including the requirement for pre-training, the assumption that birds learned a complex task in few trials, and that simpler mechanisms explain the behaviour. It is possible that birds rely on what–where–when memory: remembering details of past events, rather than planning for the future [8,33]. Although it is suggested that what–where–when memory and future planning share common cognitive processes, one does not necessarily imply the other. A bird that remembers it had no access to food in one location yesterday may cache that food now motivated by past events, not the anticipation of future events. This more closely resembles an association than any complex cognitive process involving future planning. Associations like these have been noted before, formed through episodic-like recall of past actions and their subsequent outcomes (or vice versa), leading to what appears to be future-oriented behaviours [29,34]. Notably, evidence for future planning in New Caledonian crows [31], potentially addresses these issues, though this evidence in a tool-use context.

Recent work in computational modelling has also demonstrated that apparent future planning behaviours can result from associative processes [35]. As such, we suggest the Canada jays formed an association between a chamber and access to food. Thus, when allowed to explore the full apparatus, cached more in that chamber. This observation matches caching patterns in the wild. [36]. This explanation, paired with the results of the Raby *et al.* [16] study and the individual variation observed during the *Breakfast Choice* experiment (at least one individual cached: (i) not at all, (ii) relatively evenly, (iii) favouring the ‘same’ compartment and (iv) favouring the ‘different’ compartment), leaves us with numerous questions. If both patterns result from associations, what factors drive the observed differences in behaviour? Are captive studies of this nature biologically relevant? How do other jays, and corvids in general, behave in these experiments? Answering these questions will help identify the reasons for differing outcomes of an important experiment in animal cognition.

**Ethics.** Birds were caught under the 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.

**Data accessibility.** Data for the replication of this work are available from the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.x0k6djhkn> [37]. The data are provided in the electronic supplementary material [38].

**Authors’ contributions.** R.J.M. contributed to conceptualization, data acquisition, data analysis and wrote the manuscript. G.K.M. contributed to data acquisition, and critically reviewed the manuscript. W.A.R. contributed to conceptualization, funding acquisition and critically reviewed the manuscript. D.F.S. contributed to conceptualization, data analysis, funding acquisition and critically reviewed the manuscript. All authors approve the final version and agree to be held accountable for the work performed therein.

**Competing interests.** We declare we have no competing interests.

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