

An observational analysis of Canada Jay (*Perisoreus canadensis*) foraging and caching ecology in Denali National Park and Preserve, Alaska, USA

K.N. Swift, E.J. Williams, and J.M. Marzluff

Abstract: Arctic and subarctic wildlife are among the most vulnerable species to climate change. Canada Jays (*Perisoreus canadensis* (Linnaeus, 1776)) are generalist residents of northern boreal forests and scatter-hoard food to insulate against food scarcity during winter. Unlike most scatter-hoarders, however, Canada Jays primarily cache perishable food, rendering their caches more susceptible to climate change induced degradation and loss. Here we use a mostly noninvasive approach to document Canada Jay foraging ecology among a population in interior Alaska, USA, including the types of food acquired, foraging and caching rates, and cache longevity and loss. We also tested for associations between foraging and caching rates with reproductive metrics to assess possible relationships among food and productivity. We found that Canada Jays have a varied diet that changed seasonally, and responded to a record-setting warm spring by directing foraging efforts away from cache recovery and towards the emergence of fresh food. We did not find evidence for relationships between foraging and caching rate with reproductive output, possibly owing to small sample sizes. We found that caches were recovered quickly (<4 weeks) and frequently lost to conspecific and heterospecific competitors. Our study suggests that Canada Jays may be better poised to respond to changes in cache integrity and food availability than has been previously recognized.

Key words: Canada Jay, *Perisoreus canadensis*, climate change, scatter-hoarding, cache theft, hoard-rot hypothesis, foraging ecology.

Résumé : Les espèces sauvages des régions arctiques et subarctiques sont parmi les espèces les plus vulnérables aux changements climatiques. Les mésangeais du Canada (*Perisoreus canadensis* (Linnaeus, 1776)) sont des résidents généralistes des forêts boréales nordiques qui utilisent la mise en cache dispersée pour se prévaloir contre les pénuries de nourriture durant l'hiver. Contrairement à d'autres espèces ayant recours à cette stratégie, les mésangeais du Canada mettent principalement en cache des aliments périssables, leurs caches étant donc plus vulnérables à la dégradation et aux pertes induites par les changements climatiques. Nous utilisons une approche principalement non invasive pour documenter l'écologie de la quête de nourriture de mésangeais du Canada dans une population de l'intérieur de l'Alaska (États-Unis), dont les types d'aliments obtenus, les fréquences de quête et de mise en cache de nourriture et la longévité et les pertes de caches. Nous tentons également de déterminer s'il existe des associations entre la fréquence de la quête de nourriture et la fréquence de la mise en cache de nourriture et des paramètres associés à la reproduction, afin d'évaluer l'existence éventuelle de liens entre la nourriture et la productivité. Nous constatons que les mésangeais du Canada ont un régime alimentaire varié qui change avec les saisons, et qu'ils ont réagi à des chaleurs printanières records en redirigeant leurs efforts de quête de nourriture de la récupération de nourriture mise en cache vers l'émergence d'aliments frais. Nous ne relevons aucun indice d'une relation entre les fréquences de quête et de mise en cache de nourriture et l'efficacité de la reproduction, possiblement en raison de la petitesse des échantillons. Nous relevons que les caches sont récupérées rapidement (<4 semaines) et qu'elles sont fréquemment pillées par des concurrents conspécifiques ou hétérospécifiques. Notre étude donne à penser que les mésangeais du Canada pourraient être mieux en mesure de réagir aux variations de l'intégrité des caches et de la disponibilité de nourriture que ce qui était reconnu auparavant. [Traduit par la Rédaction]

Mots-clés : mésangeai du Canada, *Perisoreus canadensis*, changement climatique, mise en cache dispersée, pillage de cache, hypothèse de la pourriture de la nourriture mise en cache, écologie de la quête de nourriture.

Introduction

Climate change has had global consequences on ecosystems and the organisms that live within them, from coral bleaching to large-scale population declines in insects (Reaser et al. 2000; Baranov et al. 2020). Continued warming impacts wildlife through

direct and indirect effects. Direct effects include pushing species beyond their thermal neutral zone, whereas indirect impacts include changes to resources, disease, and habitat structure or quality (Virkkala et al. 2008). For example, range shifts have been observed among American pika (*Ochotona princeps* (Richardson, 1828)) likely because of both direct physiological intolerance for

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Fig. 1. Image of study area and Canada Jay (*Perisoreus canadensis*) territory proximity to permanent, or seasonally permanent, discrete, spatially limited anthropogenic food sources, including garbage cans, dumpsters, and the park's dog kennels. (A) Colored polygons depict territory boundaries for the eight focal territories. We created polygons using the aggregate point tool in ArcMap, using GPS locations from caches. White text boxes delineate relevant epicenters of anthropogenic activity and potential food supplementation. (B) Measurements reflect shortest distance between a cache observed during the focal follows and the nearest predictable anthropogenic food source. For Mile 3.5 and Air Quality territories, the food source was dog kibble available at the park kennels. For all other territories, the anthropogenic food source was garbage cans or dumpsters. Color version online.

small increases in air temperature and indirect changes to habitat requirements including forage availability (Millar et al. 2016; Yandow et al. 2015). The impacts of climate change are perhaps most pronounced in the Arctic, where temperatures are predicted to increase as much as twice the rate of global temperatures (Kaplan and New 2006). Changes in winter temperatures, precipitation patterns, and the cryosphere have already been observed. Impacts to the Arctic cryosphere are myriad and include changes to snow depth and structure, degradation and loss of permafrost, and losses of freshwater ice (Olsen et al. 2011). Likewise, subarctic regions are also undergoing changes to species composition, permafrost, and temperatures (Thibault and Payette 2009; Herrmann et al. 2012).

The ecological consequences of climate shifts are already evidenced by changes in the fitness and ecology of many arctic and subarctic species. For example, Greenland's migratory caribou (*Rangifer tarandus* (Linnaeus, 1758)) are increasingly mismatched from peak resource availability, resulting in higher offspring mortality (Post and Forchhammer 2008). For snowshoe hares (*Lepus americanus* Erxleben, 1777), decreasing and unpredictable snow cover has led to camouflage mismatch, causing hares to be much more vulnerable to predation (Kumar et al. 2020). In Alaska's Arctic coastal plain, earlier lay dates by shorebirds and passerines have been linked to the advancement of snow melt (Liebezeit et al. 2014). However, despite evidence of earlier arrival (Oliver et al. 2020) and earlier lay dates for some species (Both et al. 2004), the ability for many migratory species to accurately time annual activities is increasingly compromised with rapid climate change (Kwon et al. 2019). For resident birds in the Arctic and subarctic, the effects of climate change are often indirect; as migrants expand their ranges northward and delay leaving or forego migration altogether, greater potential for increased competition and other density-dependent effects results (Böhning-Gaese and Lemoine 2004). Understanding how resident species may respond to these changes and other predicted effects of climate change, however, is largely unknown.

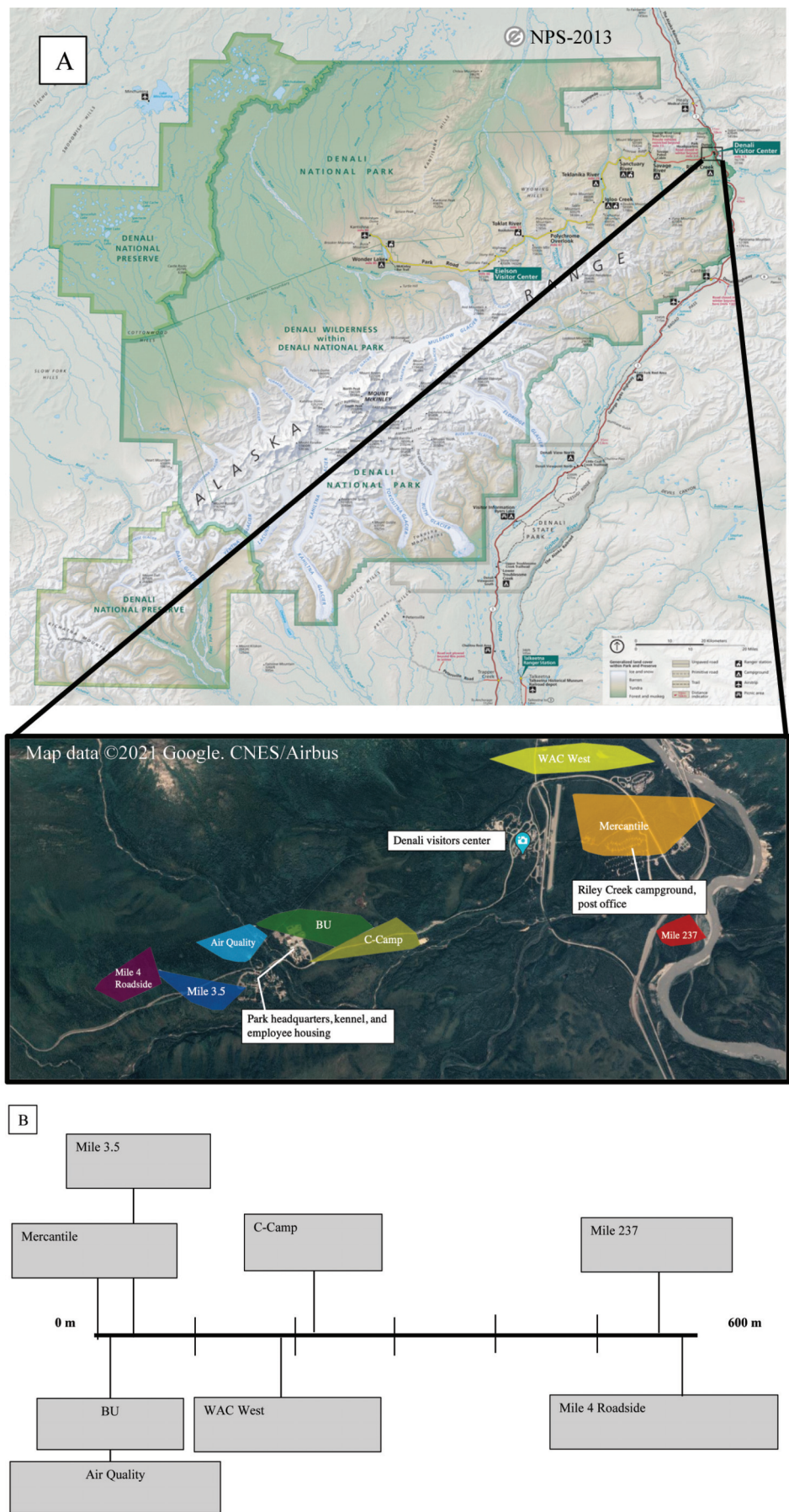
Canada Jays (*Perisoreus canadensis* (Linnaeus, 1776); subsequently referred to as "jays") are among the few birds that are found in boreal forests year-round, and are one of the region's earliest breeders, initiating nesting in the extreme cold of March (Handel et al. 2009; Strickland and Ouellet 2020). Canada Jays are dietary generalists that consume a range of foods including berries, animals, mushrooms, and anthropogenic items (Strickland and Ouellet 2020). To survive harsh winters and have food to provision nestlings during a time typically devoid of readily available food, Canada Jays scatter-hoard food throughout territories (Dow 1965). Scatter-hoarding has important ecological implications, as unrecovered seeds can help disperse trees, and stolen food items can supplement conspecific and heterospecific cache thieves (MacCluskie et al. 2005; Vander Wall and Beck 2012). Canada Jays coat food items in an adhesive saliva, turning it around in their mouths to create a compact bolus, which they place primarily within the bark or crevices of trees and shrubs (Dow 1965; Waite 1988). Canada Jays cache food year-round, but focus efforts in the late summer and autumn, and generally recover items in the winter and early spring, when fresh resources are most constrained (Waite 1988, 1991; Derbyshire et al. 2019). Unlike most other scatter-hoarders such as tits and many rodents, but similar to wolverines

(*Gulo gulo* (Linnaeus, 1758)) (Krott 1960), Canada Jays primarily hoard perishable foods (Strickland and Ouellet 2020). The boreal winter plays a crucial role in protecting caches from biological degradation through consistent subzero temperatures that freezes food and acts as a "natural refrigerator" (Haglund 1966; Inman et al. 2012).

Warming autumn and winter temperatures may impact the perishable food stores of long-term hoarders by degrading winter stores and reducing reproductive output via the hoard-rot hypothesis (Waite and Strickland 2006; Sechley et al. 2015). However, ecological niche theory predicts that, relative to specialists, generalists should better tolerate environmental changes that impact resource availability (Levins 1968). Among birds, community composition shifts that favor generalists have already been observed in Britain and France, though it is difficult to fully disentangle the impacts of climate change from ongoing changes in land use (Barnagaud et al. 2011; Davey et al. 2012). Relative to specialized hoarders, Canada Jays could be better equipped to respond to local changes in food availability by relying less on cached items and capitalizing on existing fresh food sources that are made available for greater portions of the year due to reductions in snowpack and increases in winter temperatures. Previous studies indicate, however, that cache degradation impacts reproductive success (Derbyshire et al. 2019). Accurately predicting the impacts of climate change on resident populations requires detailed understanding of the ecology and mechanisms by which environmental changes influence individual success (Stevenson and Bryant 2000; Sechley et al. 2015). We sought a comprehensive understanding of Canada Jay foraging ecology by studying a wild, but somewhat food-subsidized, population of Canada Jays in the front country of Denali National Park and Preserve in interior Alaska. Using hand-held video cameras and camera traps, we aimed to establish foraging and caching patterns by documenting the types of food that are acquired and cached, the rate of food acquisition and caching, and the location and duration of caches. We associated autumn 2018 and spring 2019 foraging and caching rates with clutch size, nestling mass, and date of clutch initiation of the following 2019 breeding season to investigate links between food and productivity. We predicted that clutch size and nestling mass would be positively associated with foraging and caching rate, but that later clutch initiation would be negatively associated with higher foraging and caching rates.

Materials and methods

We observed Canada Jays in the front country of Denali National Park and Preserve, Alaska, USA (63°44'14.7"N, 148°54'27.9"W; Figs. 1A and 1B). We identified Canada Jays (recently renamed from Grey Jay; see Chesser et al. 2018) by their size, plumage, and calls, which are distinct from all other birds in our study area (Sibley 2014). We also collected DNA from all marked birds in our study area as part of an ongoing study of jay productivity (E.J. Williams, unpublished data), ensuring taxonomic accuracy and reproducibility (Monckton et al. 2020). We define front country as outdoor park areas that are easily accessible by private vehicles, contain infrastructure, and are most frequently used by park visitors. We collected data in up to eight focal territories (Fig. 1A) over five field periods of peak foraging and caching activity including March of 2018 (three



territories), September–November of 2018 (seven territories), March–May of 2019 (seven territories), June of 2019 (seven territories), and August of 2019 (eight territories). We monitored more focal territories from March 2018 to August of 2019 as availability and experience levels of field staff increased. To identify individuals, we captured Canada Jays in baited potter traps (Third Wheel Ringing Supplies, Devon, UK) and mist nets (Avinet Research Supplies, Portland, Maine, USA) and placed a numbered U.S. Geological Survey band and a unique combination of three colored leg bands on each adult. All territories that we monitored comprised a pair of color-banded, breeding adults, though banded and unbanded offspring or non-breeders were often also present. We selected focal pairs based on their proximity to anthropogenic food sources and our ability to follow them (i.e., pairs whose territories comprised mostly steep hillsides were not selected; Fig. 1B). Although feeding wildlife is discouraged by park staff, all territories may have had access to at least some supplemental food. We assessed each territory's minimal distance to anthropogenic foods by measuring the distance from the nearest cache tree to a permanent, discrete, spatially limited food source, such as a garbage can, dumpster, or dog kennel using ArcMap 10.8.1 (Fig. 1B). Other less predictable and therefore less measurable sources of food, such as offal on roadways, food debris left at campsites, or handouts from visitors, were also nearby for all territories. We obtained information regarding timing of nesting and reproductive output including date of clutch initiation, clutch size, nestling mass, and nest fate from ongoing studies on jay productivity (E.J. Williams, unpublished data). We banded and measured all nestlings 13 ± 2 days from hatching, based on direct observations of clutch initiation.

Ethics approval

All research was conducted under approved ethical animal care and use protocols (University of Washington No. 3077-01 and National Park Service AKR_DENA_Williams_Corvids_2018.A3) and research permits from the North American Bird Banding Laboratory (No. 24141), the Alaska Department of Fish and Game (No. 19-138), and the Denali National Park and Preserve (DENA-2017-SCI-0004).

Follow procedure

Each day we visited up to three territories for approximately 2 h each. During all field seasons, we collected data in teams of 2–3 people. Upon arrival to the focal territory, if no jays were immediately visible, we played recordings of jay calls for ≤ 2 min using a portable Bluetooth speaker (Ultimate Ears Roll 2, USA) attached to an MP3 player (iPod Touch, Apple Inc., USA). If we were unable to recruit jays during the initial playback, then we walked the territory for 10–15 min before attempting a new playback. Once we saw or heard jays, we stopped using playback. While playback initially influences bird behavior via mimicking conspecific attraction, we ensured that it did not affect our observations of foraging or caching behavior by waiting until jays proceeded with normal activities (no longer acting vigilant, etc.) following audio recordings. Using a Nikon Coolpix P900, a videographer filmed all visually accessible activity from a mean distance of 15 m. If Canada Jays stopped foraging, consuming, or caching foods for more than 2 min, then we stopped recording until birds resumed relevant activity. The second (and when possible third) observer(s) used binoculars to keep track of bird movement. After we observed a bird deposit a cache, we used flagging tape and a handheld GPS (GPSmap 76Cx, Garmin Ltd., Olathe, Kansas, USA) to mark the cache tree or shrub. We attached flagging to the cache tree, but as far from the cache as we could reach without the aid of a ladder, so as not to draw attention by potential cache raiders. As most caches were more than 2 m above ground, the majority were at least 1 m away from flagging tape. While at the cache tree, we used a handheld compass to record the orientation of the cache. When the acquisition and subsequent caching of a food item were observed, we used a range finder (Bushnell Prime 1300, Overland Park, Kansas,

USA) to calculate the distance from the food acquisition site to the cache site. Individual follows lasted as long as maintaining visual contact with a bird was possible, generally between 1 and 30 min. Once we lost visual contact with the bird(s), we searched on foot and (or) used playback recordings to attempt to relocate them. After approximately 2 h on the territory, we stopped searching or data collection efforts. We limited the time on individual territories to 2 h to accommodate visiting three territories per field day.

Video analysis

We used VLC Media Player 2.1.4 to re-watch and manipulate video recordings (slow down, advance, and rewind) to better characterize and quantify foraging behavior, food acquisitions, and caching. Two to three observers analyzed all video footage, including one (K.S.) who was present throughout all analyses to ensure consistency. From video footage, we recorded the territory identity, the color band combination of focal birds, and the type of activity displayed. We described activity among four categories: (1) foraging (defined as active search and food acquisition time), (2) food handling (defined as the manipulation or consumption of a previously acquired food item), (3) caching (defined as the intentional storage of a food bolus), or (4) cache recovery (defined as the recovery of a stored food bolus) (Bunch and Tomback 1986). Generally, we defined a food acquisition as the observation of a bird collecting a single type of food (berries, invertebrates, vertebrate flesh, mushrooms, or anthropogenic foods) from a source in one trip. We define a foraging trip as an effort to acquire food that is uninterrupted by flight. For example, we characterized an individual Canada Jay flying to a blueberry bush to collect five blueberries from two adjacent bushes and then flying away as a single food acquisition. Likewise, a bird collecting three consecutive bites from a mushroom counted as a single food acquisition. Conversely, we would label footage of a jay that flew to a tree, collected a cached item, and then flew to a berry patch and collected berries as two separate food acquisitions and two distinct foraging trips. However, we counted different kinds of foods acquired in the same foraging trip (e.g., five blueberries followed by a live caterpillar) as separate acquisitions to account for the difference in search effort between food types. We took this approach to account for the conditional nature of food sources such as berry bushes, an animal carcass, or a mushroom, meaning the reduced search time between the initial discovery and the subsequent bites of food. We did not take this same approach to consecutively collected insects, however, given that unlike berries on a bush, individual insects are more independent from one another and each requires additional search effort. We did not observe jays feeding from insect nests or colonies. Food acquisitions could also include instances where we discovered a bird with a bill load of food without previously observing when the bird obtained the food item; however, this occurred rarely. Lastly, food acquisitions included instances when we suspected birds were recovering caches. We suspected cache recovery based on the identity of food (when possible) and where it was recovered from; for example, a blueberry pulled from a spruce tree.

We distinguished foraging behavior based on observations of the direction in which jays were looking (at food substrates such as the ground, in the bark, or foliage of trees and shrubs, etc.) combined with behaviors such as vegetation manipulation, gleaning, and probing. To determine foraging effort, we used the video clips to quantify how long birds spent searching or obtaining food during each follow. Search time included foraging for new food items and previously cached items. To characterize where Canada Jays most often looked for food, we recorded the amount of time spent foraging across three locations: at the ground (i.e., ground level and < 1 m high shrubs (mostly *Vaccinium* species)), arboreally (i.e., > 1 m tall shrubs and trees), or human-made surfaces such as picnic tables or grills. When searching trees and shrubs, we documented what substrate jays searched:

foliage or bark. We considered bark to be the trunk and any areas of a branch that were mostly uncovered by leaves or needles. We considered foliage to be areas of a branch that were mostly covered in leaves or needles. We also documented if the bird was searching the interior or exterior of the plant (which we will subsequently refer to as “spatial position”). We define interior as the trunk or the inner 50% of the branch as measured from the trunk to the branch’s midpoint. As substrates can be searched in either spatial position (i.e., bark can be searched in tree interiors and exteriors), we report substrate and spatial foraging efforts separately, where total substrate effort = 100% and total spatial effort = 100%. We included food acquisitions in foraging effort because they most often occurred too quickly for us to separate them from search time. We did not count time spent obtaining food from an animal carcass or large mushroom towards foraging time, as subsequent acquisition trips to the same source could take several seconds or minutes and required no additional search effort. Inclusion of these data with foraging effort would therefore meaningfully bias ground-based foraging effort. Given this strategy, we assume that our foraging effort calculations primarily reflect search effort and not acquisition effort.

We recorded the number and identity of food acquisitions from the video footage. We categorized food sources as berries, vertebrate flesh, invertebrates, mushrooms, anthropogenic foods, and miscellaneous items. Similar to our characterizations of foraging areas, we also used video recordings to identify relevant features of each cache site. These included the species of cache tree or shrub and the spatial position of the cache on the tree, which was classified as either exterior (outer 50% of the branch, measured from branch tip to branch midpoint) or interior (on the trunk or the inner 50% of the branch as measured from the trunk to branch midpoint). Lastly, we documented the substrate that caches were placed in or on (i.e., vegetation, including needles, lichen, or bark), and whether caches were concealed by wedging them under bark, setting them in needles, or by placing material over them. Throughout the paper, we refer caches as “on bark” to be interpreted only as the primary substrate and not implicating cache concealment.

Camera trapping

In cases where caches were low enough for us to identify ($n = 30$; maximum height = 177.8 cm), we deployed either a Bushnell Trophy Cam HD or a Reconyx Hyperfire HC600 camera at cache sites to record recovery. We used different camera models because of availability, but we ensured that photo quality and capture sensitivity was equivalent between each. We attached cameras directly opposite from cache locations onto trees or stakes placed in the ground distanced 1.5 m from the cache to increase detection (Randler and Kalb 2018). Given that cache recovery could take place hours or days from the time of camera deployment, it was not possible for us to directly observe jay behavior around the cameras. As Canada Jays are known to quickly habituate to human environments and do not appear to be especially neophobic once conditioned (Engeman and Wiloth 2014), we assumed that the presence of cameras did not influence their cache recovery behavior. In 2019, we deployed two cameras on each cache site to increase the probability of detecting a cache retrieval. We placed one camera directly opposite the cache as done previously and placed the second camera opposite the cache as well but at a 45° angle away from the first camera. We checked cameras every 3 days during field seasons and biweekly during the winter (November–March 2019) and summer (May–July 2019). The frequency of camera checks was based on the availability of project personnel or volunteers and site accessibility. During each camera check, we ensured the cameras were still working, changed batteries or SD cards as needed, and also checked whether the cache was present. We counted a cache as recovered if it was physically absent and if we captured an animal within 30 cm (as best estimated by K.S.) of the cache on camera. We saw

no evidence of multiple animal recoveries at the same cache. In cases where we saw that the cache was absent, but that no evidence of recovery was seen on camera, we recorded them as inconclusive.

Statistical analysis

To evaluate for seasonal differences in the number of acquisitions and caches of different food categories, we conducted χ^2 tests of independence using observations from all focal and incidental territories. Data collection was as follows: there were 17 collection days in March over 2 years, 18 days in April, 7 days in May, 1 day in June, 3 days in July, 21 days in August over 2 years, 23 days in September, and 21 days in October. Since data collection varied each month, we performed a traditional standardization (Kotze et al. 2012) to 23 field days as follows: for each food type, we divided the total number of acquisitions or caches by the number of field days and multiplied by 23. Since we observed only 27 acquisitions, and seven caches between June and July 2019, we did not include summer data in analyses of temporal changes in foraging behavior and instead included spring and autumn data, for which we had greater sample sizes. We had fewer summer observations due to our inability to locate and maintain contact with focal birds during a limited window for data collection (e.g., 1 week). To assess mean distances between cache trees within territories, we used ArcMap 10.8.1. To evaluate for proportional differences in foraging effort across substrates and microhabitats, we used proportional Z tests. To gauge nest success differences between 2018 and 2019, we calculated apparent nest success, which is a similar method to those that have been used in previous demographic studies of Canada Jays (Sutton et al. 2019). We define apparent nest success as the number of nests that fledged at least one young divided by the number of nesting attempts with known fates. We used a proportional Z test to evaluate for differences in apparent nest success. We used Pearson’s correlation to evaluate potential relationships between jay foraging efforts in the autumn (August–October 2018) and spring (March–May 2019) and reproduction, including clutch initiation (i.e., when the first egg was laid as described by the number of days since 1 January 2019), clutch size, and mean nestling mass among the seven territories for which we had data from the 2019 breeding season. Foraging efforts included recovered caches and the acquisition of fresh food items, as cache recovery alone was rarely identified due to the inherent difficulty of visually identifying stored food. We used a Rayleigh’s test of uniformity to determine whether jays showed a placement preference for the orientation of caches on vegetation. We completed all analyses in RStudio 1.3.1056 using the MASS (Venables and Ripley 2002), ggplot2 (Wickham 2016), and Circular (Agostinelli and Lund 2017) packages. We present means \pm SD for all analyses and considered p -values $\alpha \leq 0.05$ to be significant.

Results

Diet

We documented the acquisition of 1144 items of food, 40% of which ($n = 462$) we were able to identify as vertebrate flesh, berries, human food, invertebrates, mushrooms, or miscellaneous items. Miscellaneous items include unique items, such as toilet paper or slime mold, that we were able to identify but were only represented in the acquisition data a few times and did not fit within the five main food categories. All other items were unidentifiable. Among the six categories, we documented the acquisition of 29 specific food sources (Table 1). Across seasons, berries accounted for 28% of identifiable acquisitions ($n = 131$), invertebrates for 26% ($n = 121$), vertebrate flesh for 22% ($n = 103$), mushrooms for 15% ($n = 69$), human food for 6% ($n = 26$), and miscellaneous items accounted for 2% ($n = 11$). Consumption of different food types varied between spring (March–May) and autumn (August–October; corrected count data, $\chi^2_{[5]} = 145.37$, $p < 0.0001$;

Table 1. Categories for the 29 different food items that we documented Canada Jays (*Perisoreus canadensis*) to eat or cache.

Food source	Total acquisitions	Percentage of identified diet (%)	Total caches	Percentage of identified cached items (%)
Vertebrate flesh	103	22	51	21
Snowshoe hare (<i>Lepus americanus</i>)	83	18	44	18
Vole (Cricetidae species)	2	0	2	1
Berries	131	28	60	24
Bog blueberry (<i>Vaccinium uliginosum</i> L.)	60	13	39	16
Lingonberry (<i>Vaccinium vitis-idaea</i> L.)	11	2	8	3
Black crowberry (<i>Empetrum nigrum</i> L.)	4	1	0	0
False toadflax (<i>Geocaulon lividum</i> (Richardson) Fernald)	1	0	0	0
Soapberry (<i>Shepherdia canadensis</i> (L.) Nutt.)	6	1	3	1
Human food	26	6	42	17
Bread	7	2	6	2
French fry	2	0	4	2
Orange peel	1	0	1	0
Sausage	1	0	2	1
Pretzel	1	0	1	0
Invertebrates	121	26	53	21
Tiger moth caterpillar (Arctiinae species)	25	5	16	6
Spider	2	0	3	1
Slug	6	1	3	1
Moth	1	0	0	0
Unidentified caterpillar or grub	61	13	18	7
Yellow jacket (<i>Vespula</i> species)	1	0	1	0
Spider egg sac	1	0	0	0
Snail	3	1	4	2
Mushrooms	70	15	41	17
Fly amanita (<i>Amanita muscaria</i> (L.) Lam.)	7	2	3	1
Bolet (Boletales species)	19	4	15	6
Puffball (Agaricaceae species)	1	0	6	2
Miscellaneous	11	2	1	0
Toilet paper	2	0	1	0
Slime mold (possibly <i>Fuligo septica</i>)	2	0	0	0
Possible spruce seeds (<i>Picea</i> species)	1	0	0	0
Possible filamentous lichen	1	0	0	0
Urine snow	1	0	0	0
Total food sources: <i>n</i> = 29	Total identified acquisitions: <i>n</i> = 462		Total identified caches: <i>n</i> = 248	

Note: Foods that we could identify comprised only minima of items actually consumed or cached.

Fig. 2). For example, we found that among invertebrates, jays consumed $\sim 2.5\times$ more in the spring than what we observed in the autumn. Conversely, jays consumed $\sim 5.5\times$ more vertebrate flesh and $\sim 2\times$ more berries in the autumn than they did in the spring.

As a few of our acquisition observations (Table 1) can be considered novel or are rarely reported in the literature, they require further elaboration. In both cases of toilet paper consumption, we observed jays pulling shreds of toilet paper (which appeared to be clean) from the needles of spruce trees and consuming them over the course of several bites. In one case, the remaining pieces were re-cached in the tree and we were able to retrieve it and confirm that it was toilet paper. With respect to the slime mold, jays have only been observed consuming *Fuligo septica* (L.) F.H. Wigg. (see Sutherland and Crawford 1979). While we could not definitively identify to species, we suspect the same slime mold was consumed in our study based on our in-person inspections of the mold's color, texture, and the presence of *F. septica* in Alaska (Novozhilov et al. 2007). Unfortunately, our observations of the spruce (*Picea* species) seed and lichen were more limited. In both cases, jays were already holding or consuming them when

we observed them, so we do not know where they were obtained. For the spruce seed, our identification was based on its color and texture, but the jay flew off with it after only 2 s of video footage and we were not able to validate our identification any further. This observation should therefore be considered only as a possibility rather than as a definitive identification. While jays have not been observed to open spruce cones (Dow 1965), they have been observed acquiring seeds from the surface of snow (Strickland and Ouellet 2020). Likewise for the lichen, the jay was consuming something that had the form and texture of a filamentous lichen, of which there are several species in our study area (Stehn et al. 2015), but we cannot rule out the possibility that the lichen was simply "bycatch" for something hidden inside, especially given that we often documented jays to place caches in filamentous lichens. Finally, while the consumption of lepidopteran larvae is not rare, the pattern of jays consuming Arctiinae larvae that we observed warrants further detail. The observed species of Arctiinae larvae is covered in urticating setae, which is common defense among tiger moths (Wagner 2009). To clean the caterpillars of their setae, the jays rubbed them on the ground or a branch for up to several minutes (see Supplementary Video).¹

¹Supplementary video is available with the article at <https://doi.org/10.1139/cjz-20210-0053>.

Fig. 2. Seasonal differences in food acquisitions by Canada Jays (*Perisoreus canadensis*). Graph shows counts of different food categories between spring (March–May) and fall (August–October). We used a standardization technique to correct count data for unequal field days. Misc. is miscellaneous.

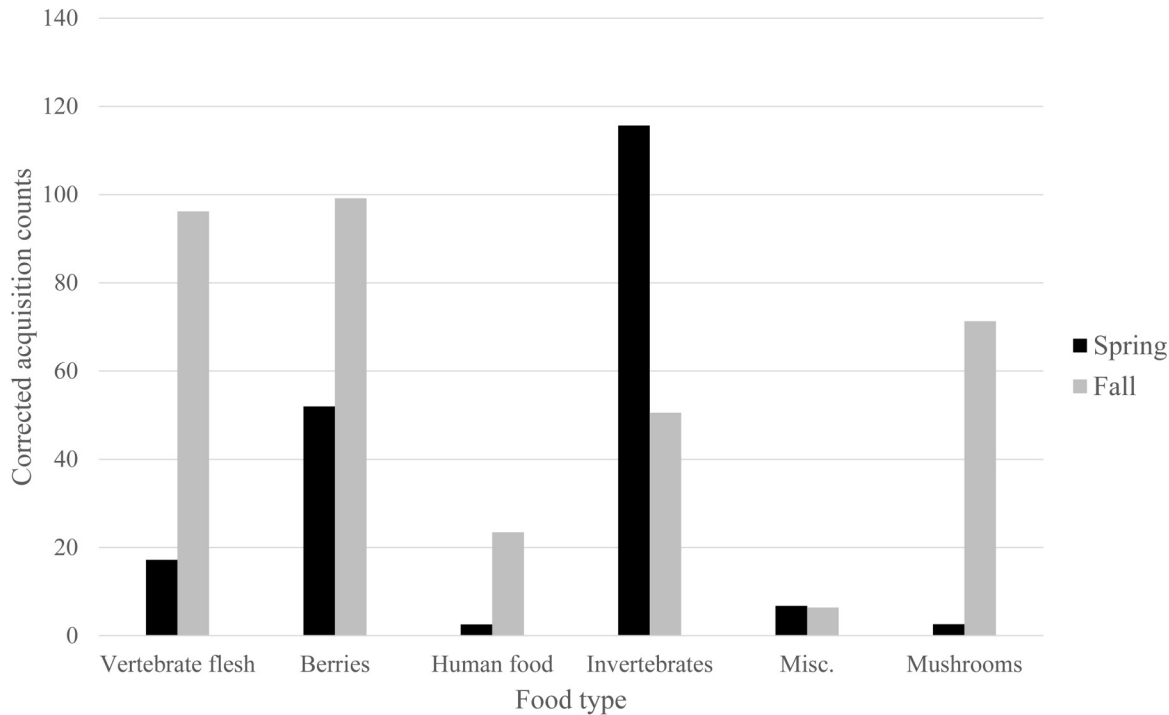


Table 2. Time (s) that Canada Jays (*Perisoreus canadensis*) spent foraging delineated by whether there was complete or incomplete snow cover.

	Complete snow cover	Incomplete snow cover
Total foraging time (s)	1518	30 830
Human surfaces (s)	0 (0%)	90 (0.29%)
Ground foraging (s)	2 (0.13%)	22 373 (73%)
Arboreal foraging (s)	1516 (100%)	8 367 (27%)
Spatial position		
Interior effort (s)	979 (65%)	3 769 (45%)
Exterior effort (s)	537 (35%)	4 598 (55%)
Substrate		
Bark effort (s)	1138 (75%)	5 449 (65%)
Foliage effort (s)	378 (25%)	2 918 (35%)

Note: Total foraging time reflects combined ground, human surface, and arboreal search efforts. Percentages (in parentheses) indicate proportion of total foraging time. Arboreal search effort is further subcategorized by spatial position (interior and exterior) and substrate (bark and foliage). Total spatial position effort equals 100% of arboreal foraging time. Total substrate effort likewise equals 100% of arboreal foraging time.

Foraging behaviors

Across seasons, we documented 9 h and 22 min of foraging time, which accounted for 40% of total recorded footage (23 h and 16 min). Only the March 2018 field season had complete snow cover (Table 2). During that season, we observed Canada Jays spending all of their foraging effort searching in trees, rather than on the ground. With respect to substrate, they spent 75% of their search effort inspecting bark. With respect to spatial position, jays spent 64% of their time searching tree interiors. During March–May 2019, jays spent the majority (85%) of their total foraging time on the ground. When searching trees, they primarily searched bark substrates (85% of arboreal foraging effort across

substrates). With respect to spatial position, they primarily searched the interiors of trees (58% of arboreal foraging effort across spatial position). During the autumn (August–October 2018, August 2019), jays again mostly searched the ground (54% of total foraging effort). When they foraged in trees, they still primarily searched bark (55% of arboreal foraging efforts across substrates) but more often searched tree exteriors (61% of arboreal foraging effort across spatial position). Across all spring and autumn seasons with only intermittent, partial snow cover, jays spent the majority (73%) of their foraging effort looking for items on the ground, as opposed to in trees ($Z = -112.80$, $p < 0.0001$). Of the 27% of time that they foraged arboreally, they spent less time searching the interior (45%) than the exteriors (55%) of trees ($Z = -12.81$, $p < 0.0001$). With respect to substrate, they spent more time (65%) searching bark on trunks and branches, relative to foliated areas (35%; $Z = 39.13$, $p < 0.0001$). In the autumn, jays spent <1% of their time searching anthropogenic surfaces such as picnic tables, garbage cans, and camp grills. They did not search these surfaces in the spring.

Caching

We documented 504 caches across all seasons. Of those, we were able to identify the food type in 248 (49%) cases. As with acquisitions, jays cached items from our six food categories. Among items that we could identify, berries accounted for the most frequently cached item (24%, $n = 60$), followed by vertebrate flesh (21%, $n = 51$), invertebrates (21%, $n = 53$), human food (17%, $n = 42$), mushrooms (17%, $n = 41$), and miscellaneous items (<1%, $n = 1$; Table 1). We found that most caches consisted of a single food item (e.g., one berry or one slug), but in two cases, jays prepared two different items as a single cache. We found seasonal differences in when the six different food categories were most frequently cached (corrected count data, $\chi^2_{[5]} = 277.35$, $p < 0.0001$; Fig. 3). Insects were the only food category that we documented a higher number ($\sim 1.5\times$) of spring caches relative to autumn. The mean (\pm SD) distance from food acquisition location to cache site was 10.43 ± 11.49 m (range = <1–101 m; $n = 233$ caches). Jays

Fig. 3. Seasonal differences in foods cached by Canada Jays (*Perisoreus canadensis*). Graph shows counts of different food categories between spring (March–May) and fall (August–October). We used a standardization technique to correct count data for unequal field days. Misc. is miscellaneous.

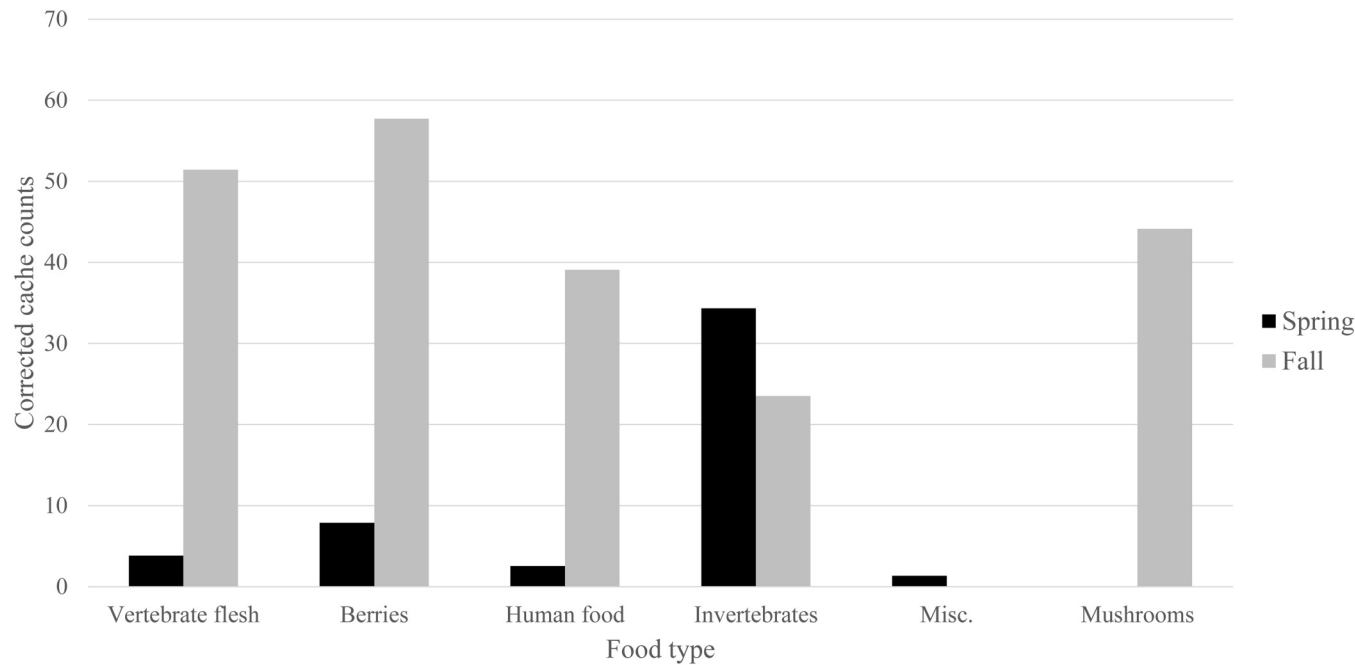
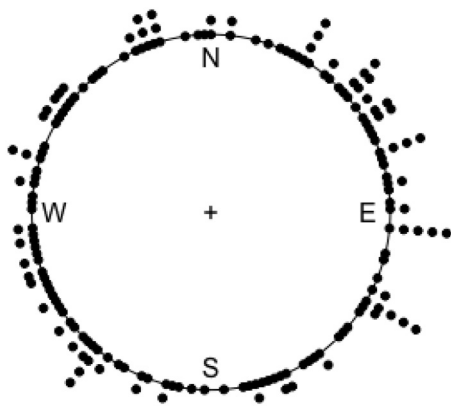


Fig. 4. Radial histogram of Canada Jay (*Perisoreus canadensis*) cache orientation for 174 measured caches during the 2019 spring, summer, and fall seasons. Jays did not show a preference for cache placement on trees with respect to cardinal direction (Rayleigh's test = 0.024, $p = 0.90$).



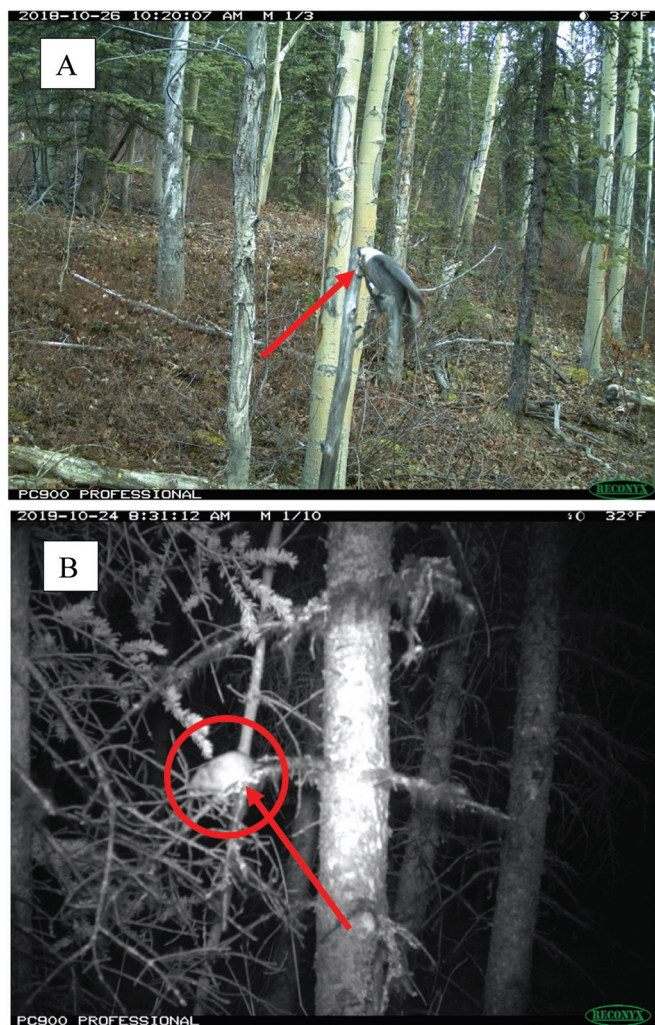
showed no preference for cache orientation ($n = 174$ measured caches, Rayleigh's test = 0.024, $p = 0.90$; Fig. 4). Most caches (92%) were deposited in spruce trees (white spruce (*Picea glauca* (Moench) Voss) or black spruce (*Picea mariana* (Mill.) Britton, Sterns and Poggenb.)), followed by quaking aspen (*Populus tremuloides* Michx.; 5% of caches). The remaining 3% were placed in a mix of willow (*Salix* species), alder (*Alnus* species), Alaskan paper birch (*Betula neoalaskana* Sarg.), and unidentified snags. Jays placed the majority of observed caches in the exteriors of trees (55%; $Z = -3.91$, $p = 0.0001$). Among interior caches, 33% were deposited directly on tree trunks. When selecting a substrate, the majority of caches (55%; $Z = 4.54$, $p < 0.0001$) were applied to bark, while 41% were placed in foliage including spruce needles and lichens, particularly filamentous lichens. Although we could not always verify the specific locations to which high or visually obscured

caches were placed, among the cache locations that we could observe, the majority were concealed (85%, $n = 430$). We documented 31 caches applied directly to the surface of bark, as opposed to concealing it under bark, within needles, or covered with lichen. Eight percentage ($n = 42$) of caches were deposited in trees with existing caches. The maximum number of caches observed in a single tree was 5. The majority (95%, $n = 40$) of caches deposited in previously used trees were made by the same bird that made the initial cache. Across our eight focal territories, the mean (\pm SD) distance between cache trees was 25.60 ± 30.63 m (range = 0.5–276.2 m). Of the 1144 food acquisitions that we documented, we suspected 40 (4%) to be recovered caches. The majority of those were recovered in the spring (March–May, 92%), although we documented three suspected recoveries in August 2019. Recovered food items included vertebrate flesh (20%), berries (8%), and anthropogenic food (5%). The remaining recovered caches could not be identified to food type (68%).

Camera traps

Of the 30 caches on which we deployed cameras, all caches eventually disappeared, though only 12 cameras successfully documented the cache fate. Of those 12, 9 caches comprised single, whole invertebrates including three snails, two slugs, three caterpillars, and one unidentified invertebrate. The remaining three caches included dog kibble and two puffball mushrooms. We considered 10 of the 12 to be concealed, as they were either nestled in needles, covered with lichen, or tucked into bark crevices or behind bark chips. We were better able to document cache fate when we deployed two cameras (67% success rate across 9 double camera deployments) than when we deployed only one camera (29% success rate across 21 single camera deployments). Among recovered caches, 25% ($n = 3$) were recovered by the jay that made the cache; 33% ($n = 4$) were recovered by a jay, but its color bands were obscured and so individual identity could not be determined; and 42% ($n = 5$) were not recovered by the initial cache maker. Among those, two were recovered by jays that did not make the cache (Fig. 5A) and three were recovered by

Fig. 5. Photos of cache recovery by (A) a conspecific, the Canada Jay (*Perisoreus canadensis*), and (B) a heterospecific, the northern red-backed vole (*Myodes rutilus*). Red arrows indicate cache placement. Color version online.



rodents (Fig. 5B). In all three cases, the rodents were voles, likely northern red-backed voles (*Myodes rutilus* (Pallas, 1779); identified by S. West and M. Flamme, personal communication), which are the most dominant rodent in our study area (Schmidt et al. 2018). Among the two confirmed cases of cache recovery by another bird, in one case it was recovered by the mate and in the other case it was recovered by a nonbreeder unaffiliated with the territory. Caches were present a mean (\pm SD) of 16 ± 17.2 days before being recovered or stolen (range = 24 h to 55 days).

Productivity

We monitored 24 and 30 nests in 2018 and 2019, respectively. We found that between 2018 and 2019 apparent nest success increased from 0.42 to 0.60, but not significantly so ($Z = -1.34$, $p = 0.18$). Among the seven territories where we had autumn (August–October 2018) and spring (March–May 2019) foraging data, pairs acquired a mean (\pm SD) of 2 ± 0.69 items/min of foraging effort. We did not find evidence for an association between acquisition rate and mean (\pm SD) nestling mass across our seven territories ($n = 19$ nestlings, 62 ± 4.64 g; Pearson's correlation test, $r_{[4]} = 0.32$, $p = 0.54$) or mean (\pm SD) clutch size (3.6 ± 1.27 eggs; Pearson's correlation test, $r_{[5]} = -0.16$, $p = 0.73$). We also found no evidence for our predicted negative relationship between

foraging effort and the date of clutch initiation (days since 1 January 2019, 80.57 ± 3.15 days (mean \pm SD); Pearson's correlation test, $r_{[5]} = 0.59$, $p = 0.16$). Onset of clutch initiation was not correlated with proximity to supplemental food sources, measured as the shortest distance between a cache tree and a consistent spatially limited source of anthropogenic food (231.43 ± 249.50 m (mean \pm SD) from food source; Pearson's correlation test, $r_{[5]} = 0.094$, $p = 0.84$). Among the seven territories where we had autumn (August–October 2018) and spring (March–May 2019) foraging data, pairs cached a mean (\pm SD) of 0.86 ± 0.42 items/min of foraging effort. We did not find evidence of any association between cache rate and nestling mass or clutch size (mean nestling mass: Pearson's correlation test, $r_{[4]} = -0.23$, $p = 0.66$; mean clutch size: Pearson's correlation test, $r_{[5]} = -0.41$, $p = 0.37$). We did not find an association between clutch initiation and cache rate (Pearson's correlation test, $r_{[5]} = 0.65$, $p = 0.23$).

Discussion

Across the Arctic and subarctic, climate change induced warming is having measurable impacts on a variety of species, from insects to large mammals (Post and Forchhammer 2008; Renner and Zohner 2018). Among birds, ecological ramifications have already been observed for both migratory and resident species and more is expected, but demographic models often fail to take phenotypic plasticity into consideration (Virkkala et al. 2008; Vedder et al. 2013; Wauchope et al. 2017). Warming temperatures are implicated to threaten Canada Jay fitness by degrading the integrity of autumn and winter caches and therefore constraining available resources for adults and nestlings (Waite and Strickland 2006; Derbyshire et al. 2015; Sechley et al. 2015). However, given that Canada Jays are resident, dietary generalists, they may be better equipped to respond to local changes in temperature and resulting food availability (Levins 1968; Barnagaud et al. 2011). Here we used an observational study to document Canada Jay foraging and caching ecology in a front-country population in Denali National Park and Preserve. Unexpectedly, snow accumulation was the lowest on record during our autumn 2018 season, resulting in only partial snow cover during this time (Sousanes and Hill 2018). Likewise, conditions during the 2019 spring season were unusually warm; March 2019 was 8°C warmer than mean March temperatures, and the snow melted out at our study area on 31 March, the earliest on record (Sousanes and Hill 2019). Jays appeared to respond to these unusually warm and snow-less conditions by focusing foraging efforts towards the ground, where fresh food was available.

As with previous studies, we found that Canada Jays in Alaska foraged and cached a variety of foods including berries, vertebrate flesh, invertebrates, mushrooms, and to a much lesser extent, anthropogenic foods and miscellaneous items. Berries, particularly *Vaccinium* species, appear to be among the most important food sources for jays as the most highly acquired and cached food. Peaking in the spring (March–May), invertebrates accounted for the second largest source of food, particularly during the observed April emergence of the Arctiinae caterpillars. Vertebrate flesh, primarily from snowshoe hares accounted for less than a quarter of all identified foods. These findings contrast those of stomach content analysis, which show that arthropods are the most common contents (82% of surveyed adults) and are highly represented even in winter (December–February), where they were found in 72% of surveyed adults (Strickland and Ouellet 2020). This difference may be owed to our difficulty of identifying captured invertebrates prior to consumption, relative to the ease of identifying berries or vertebrate flesh. This validates the need for additional or alternative approaches including DNA barcoding or isotopic analysis to better characterize diet.

In addition to these broad patterns in diet, we also documented several rare or previously undescribed foraging strategies. Of

particular note was the consumption and apparent caching of toilet paper. Whether this material might have initially been cached as future nesting material is uncertain, but our observations conclusively identified its repeated acquisition from trees and subsequent consumption by jays. We also identified the consumption of a slime mold, possibly *F. septica*, which has only rarely been reported (Sutherland and Crawford 1979). In addition, we documented a novel foraging strategy regarding a mechanically defended caterpillar.

Canada Jays are known to eat a wide variety of lepidopteran species, and in rare cases even those which are aposematically colored and generally regarded as unpalatable (Bowers and Farley 1990). While the observed species of consumed Arctiinae larvae are not aposematic, they are covered in urticating setae. Rubbing caterpillars to remove the irritating hairs has been observed in other birds including cuckoos (Cuculidae), Hoopoes (*Upupa epops* Linnaeus, 1758), Baltimore Orioles (*Icterus galbula* (Linnaeus, 1758)), Least Flycatchers (*Empidonax minimus* (W.M. Baird and S.F. Baird, 1843)), and Yellow Warblers (*Setophaga petechia* (Linnaeus, 1766)) (Payne 1997; Parry et al. 1997; Kristin 2001; Barbaro and Battisti 2011). Birds with strategies to consume insects with such defenses are considered to exhibit a moderate level of dietary specialization (Sherry 1990; Barbaro and Battisti 2011). Whether this behavior is unique to our study population or simply underreported elsewhere is unknown. Intraspecific specializations with respect to targeted food, feeding techniques, or foraging locations are not uncommon among generalists, including other corvids such as Western Jackdaws (*Corvus monedula* Linnaeus, 1758) and Blue Jays (*Cyanocitta cristata* (Linnaeus, 1758)) (Pietrewicz and Kamil 1979; Partridge and Green 1987; Bolnick et al. 2003).

Canada Jays have been observed caching food in a variety of aboveground locations including coniferous foliage, tree crevices, or directly to twigs (Waite 1988). In Denali, Canada Jays cached the majority of items on the exterior (the area from branch tip to branch midpoint) bark of white and black spruce trees, which are the most dominant trees in our study area. That spruce trees were most used by jays is consistent with a previous study showing Canada Jay preference for habitats with high proportions of coniferous trees (Norris et al. 2013). As with other studies, we found that caches were most often concealed either by wedging them under bark or in needles, or by covering them with an acquired substrate such as lichen (Strickland and Ouellet 2020). Although we found that jays most often used bark as the cache substrate, preferences for cache placement may differ among populations. For example, Canada Jays in Colorado, USA, primarily placed caches in foliage (Burnell and Tomback 1985). The observed bias for tree exteriors may be an artefact of the difficulty of confirming interior caching behavior or may be a strategy among jays to maximize accessibility. Likewise, the observed bias towards spruce bark as a substrate may be due to the availability of this surface relative to foliage or may be an intentional strategy such as cache preservation. For example, a study by Strickland et al. (2011) found that caches placed in pinaceous trees, including black spruce and white spruce, showed less degradation relative to those placed on other tree species. Although the exact mechanism underlying apparent tree preference by jays is not fully understood, Strickland et al. (2011) suggested that antimicrobial volatiles produced from the bark may act as a preservative for cached food. White-breasted Nuthatches (*Sitta carolinensis* Latham, 1790), Tufted Titmice (*Baeolophus bicolor* (Linnaeus, 1766)), and Black-capped Chickadees (*Poecile atricapillus* (Linnaeus, 1766)) and Carolina Chickadees (*Poecile carolinensis* (Audubon, 1834)) also predominately cache by wedging food times under bark or in crevices, rather than in foliage (Petit et al. 1989). Future microclimate and vegetation surveys may provide important validation and insights for these findings. That jays cached most items close to where they acquired them is consistent with previous reports on the trade-off between the energy investment in distributing caches and the potential for

cache theft (Waite and Reeve 1995). Like other arboreal caching songbirds, we did not find compelling evidence that jays are selective about compass aspect when choosing cache sites (Petit et al. 1989). Among ground caching corvids, Clark's Nutcrackers (*Nucifraga columbiana* (A. Wilson, 1811)) likewise do not show an orientation preference for cache location around large objects, possibly as a way of further concealing caches from competitors (Vander Wall 1982). Pinyon Jays (*Gymnorhinus cyanocephalus* Wied-Neuwied, 1841), however, appear to bias cache deposition on the southern side of trees, potentially to aid in earlier cache recovery through advanced south-facing snow melt (J.M. Marzluff, personal observation). That Pinyon Jays cache fewer perishable foods relative to Canada Jays may be an important factor in Pinyon Jays' tolerance of southern exposures.

Although our real-time follow technique allowed for substantive data collection regarding the nature of cache deposits, we made far fewer observations of cache recovery ($n = 40$). This is largely due to our inability to identify items foraged from trees because they were obscured by twigs and leaves or because the food source of the prepared bolus was unidentifiable. Our findings regarding cache recovery do not reflect that Canada Jays in our study area infrequently recover caches, but rather that it was difficult to identify recovery through our methods. Since we could not always reliably discern cache recoveries from novel food acquisitions in the field, our results are insufficient to make inferences about cache recovery strategies such as blind searching vs. memory-based recovery (see Strickland 1991). While our camera trap data likewise did not reveal insights regarding how jays recover or detect caches, they did provide interesting insights regarding cache theft and how quickly caches may be recovered.

Camera trap footage revealed that caches were present for 16 ± 17.2 days. Although this reflects a limited data set, this high turnover is interesting to consider. Unless jays cache substantially more food than they need, such a high turnover of caches is likely unsustainable through winter and so other explanations may dominate. One possibility is that the caches on which we deployed cameras were of low value and thus less hidden relative to caches placed higher in trees. However, 9 of the 12 documented caches were of intact, whole invertebrates including snails, slugs, and caterpillars, and the 10th was dog kibble — all ostensibly high calorie, high value food. Furthermore, the majority of those 12 caches were concealed. It is perhaps more likely that such caches were only temporary in nature and intended for redistribution. For example, Canada Jays are known to use a two-stage caching process when feeding from distantly sourced food, and (or) food bonanzas, initially making most caches close to the source and then redistributing them more widely (Waite 1991; Waite and Reeve 1997). It is also possible that our observations of cache recovery from camera trap footage resulted from the way that we designed this method. Perhaps the camera traps or flagging attracted potential cache robbers or catalyzed redistribution by the cache makers. Alternatively, if high cache turnover is truly representative of this population, then it may indicate that jays replace caches more frequently through access to food subsidies, which could mitigate the challenges of winter food scarcity.

Unexpectedly, we found that when Canada Jays foraged arboreally in the spring, they most often looked in tree interiors (on the trunk or inner 50% of the branch as measured from the trunk to the branch midpoint), despite depositing most caches in tree exteriors (area from branch tip to midpoint). Given that we did not collect data in the winter (November–February), we cannot address whether jays preferentially recover more exposed caches when conditions are still extremely cold, and then switch to more protected interior caches over the course of spring. Elucidating such a strategy would be important in understanding how Canada Jays may mitigate the effects of long-term storage under changing climatic regimes.

Given the unusually warm conditions of the autumn 2018 and spring 2019 field seasons, it is unsurprising that the birds spent the majority of their foraging efforts searching for food on the ground. Under normal circumstances, the disappearance of snow cover marks a shift from cache recovery to foraging for fresh food on the ground (Derbyshire et al. 2019). Here we found evidence for a similar shift when snow cover was significantly delayed or absent far earlier than usual. That high-quality fresh foods were available during these unique weather events was confirmed by our observations of the availability of foods like insects, berries, and mushrooms in 2018 and 2019 (K. Swift, personal observation). Still, we cannot rule out the possibility that our representation of ground foraging is biased because ground-based efforts were less obscured and therefore easier to track and identify than when jays were foraging in trees.

It is interesting that jay productivity trended upward from 2018 to 2019, given the unusually warm temperatures and lack of snowpack during our autumn 2018 and spring 2019 field seasons. Previous studies examining the influence of freeze–thaw events have found a negative correlation with fecundity (Sutton et al. 2019; Sutton et al. 2021). Of course, our observations were not of multiple freeze–thaw events, but rather delays or accelerations of seasonal temperature and snowpack changes. While findings from such a limited data set should be approached with caution, it does suggest the need for further study into how cache loss might be offset by the increasing availability of fresh food. One high-value food resource that we saw become available earlier than usual was insects, particularly caterpillars (E.J. Williams, personal observation), an observation in keeping with the well-documented advancement of insect emergence under current climate conditions (Valtonen et al. 2011; Høye et al. 2014; Renner and Zohner 2018). Such changes in peak insect abundance are predicted to shift the optimal breeding date for some Arctic breeding shorebirds and passerines (Tulp and Schekkerman 2008). While such phenological shifts pose challenges to migratory species through trophic mismatch, resident species may be better equipped to track environmental changes and respond through phenotypic plasticity (Vedder et al. 2013). For example, in Europe, while resident tits and migratory flycatchers both advanced clutch initiation, tits had progressively earlier dates than flycatchers, despite temperature cues being similar for both groups (Samplonius et al. 2018). How much Canada Jays have advanced laying in our study area remains unknown, but our results suggest jays are flexible with respect to foraging strategies. That they responded to a record-setting thaw event by primarily foraging on the ground, instead of arboreally where caches were located, suggests that cache degradation or loss could be offset by spring conditions that favor insect advancement and greater food availability revealed by rapid snow melt. However, the effects of climate change are complex and also unpredictable; so while conditions may allow animals to capitalize on new food resources in one year, they may have opposite, detrimental effects in the next year (i.e., increasing temperatures and precipitation (snow) leading to cache degradation and no available food). The complexities of how climate change will impact food webs, however, warrants further study to establish if what we observed in one unique year is representative, as well as adaptive.

Despite the potential for increased food availability to bolster productivity, we did not find any support for our predictions relating foraging and caching behavior to reproductive output. Given the importance of food to increasing body condition (Freeman et al. 2020) and reproductive performance (Sutton et al. 2019) in Canada Jays, it is possible that we would have found associations between foraging and productivity with greater sample sizes, and by incorporating more remote territories with fewer food subsidies. The high cache loss that we observed, however, may have important implications related to the lack of association between cache rate and the reproductive metrics that we tested. Rather than being indicative of robust future food stores, high cache rates may instead

indicate that a pair experiences high rates of cache loss. Carolina Chickadees, for example, cache significantly more food when they experienced $\geq 25\%$ cache losses to competitors relative to controls (Lucas and Zeleninski 1998). Future studies could examine the caloric value of cached biomass relative to the energetic needs of jays (47 kcal/day; Shank 1986) to verify whether jays cache more food than needed as a strategy to address high rates of cache loss. Although anthropogenic food accounted for only 6% of identified acquisitions, food subsidies provided by front-country living, including dog kibble and other anthropogenic foods, may have also influenced our results. This might be especially meaningful in the winter (December–February) when fresh food resources for remote living jays would be most constrained. As we did not collect data during this time, we cannot suggest to what degree winter-time acquisition and caching of anthropogenic foods subsidizes jay diet and how that might contrast with jays living farther from human-dominated areas.

Among food storing animals, defensive capabilities against food pilfering are thought to guide hoarding strategies, where animals that are unable to defend their caches scatter-hoard (as opposed to larder-hoarding; Stapanian and Smith 1978). The spatial distribution of caches is hypothesized to reflect the trade-off between the energetic costs of widely spacing caches and the risk of cache loss to competitors, though other explanations including the risks of predation, have also been proposed (Waite and Reeve 1992; Steele et al. 2014). Pilfering rates are reported to be 1.5%–27.6% reserves a day among long-term scatter-hoarders, with some reports of total losses as high as 50%–95% (Thompson and Thompson 1980; James and Verbeek 1983; Vander Wall 1990; 89%–91%; Vander Wall and Jenkins 2003); however, these studies base theft rates on observations at artificial caches. By using camera traps (especially two at each cache), we documented a substantial rate (42%) of cache theft from Canada Jay caches. This rate was higher than what was observed in another study of animal-made caches in red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)) (Gerhardt 2005). Of the cache theft that we observed, we found that a minority (40%) were taken by conspecifics. While a previous study reported that Canada Jays do not habitually steal from one another and do not steal from close relatives or mates (Burnell and Tomback 1985), our findings appear to support Vander Wall and Jenkins (2003), who describe Canada Jays as displaying a high tolerance for conspecific cache theft. Among corvids, conspecific caches may be stolen through random searches or observational recall, though in Clark's Nutcrackers, recall wanes after only 48 h (Kamil and Balda 1985; Bednekoff and Balda 1996; Bugnyar and Kotrschal 2002). Among other social hoarders such as tits and chickadees, or solitary hoarders with overlapping home ranges like many rodents, conspecific cache theft is thought to be tolerated because it is ultimately reciprocal (Vander Wall and Jenkins 2003; Dally et al. 2006; Dittel et al. 2017). We found that the majority of stolen caches (60%) were taken by heterospecifics, namely northern red-backed voles, which have been recently documented to climb trees (Nations and Olson 2015). As voles are only observed to climb up to 2 m, pilfering of jay caches by voles is likely overrepresented by our sample, which was limited to caches less than 2 m in height. If high levels of cache pilfering by voles is commonplace, then we should expect jays to adjust cache heights to limit such losses. Further replication is needed to better understand what proportion of a territory's caches are lost to competitors.

Given that focal territories all resided in the park's front country where people are most concentrated, it is unsurprising that we observed the consumption and caching of anthropogenic foods. Additionally, five of the eight focal pairs had access to high calorie kibble subsidies from the park's dog kennel. Canada Jays are well known for their recognition and recall of humans as sources of supplementary food (Rutter 1969). Such supplemental food resources are known to impact daily mass gain, time budgets,

and reproductive success in birds (Kristan et al. 2004; Goldenberg et al. 2016; Stofberg et al. 2019). For example, suburban Florida Scrub-jays (*Aphelocoma coerulescens* (Bosc, 1795)) that received experimentally supplemented food laid eggs earlier than their wildland counterparts (Reynolds et al. 2003; Schoech et al. 2004). Likewise, studies of supplemented Canada Jays demonstrate advanced clutch initiation, fledging date, and improved nestling body condition relative to controls (Derbyshire et al. 2015; Freeman et al. 2020). It is possible that our findings related to relationships between clutch size, mean nestling mass, clutch initiation, and acquisition and caching rate were decoupled by these food subsidies. However, because of low sample sizes, we had low power to detect differences in reproductive metrics and foraging behavior between territories closer to or farther from kennels. A future study with a larger sample size and that includes a comparative backcountry population (e.g., several miles from any human-habituated areas) would help elucidate the relative impact of anthropogenic food subsidies on foraging behaviors and reproductive success.

Climate change threatens wildlife and the ecosystems on which they depend in myriad direct and indirect ways. How animals may respond to this threat is therefore of considerable interest, particularly in Arctic and subarctic systems where climate change is advancing faster relative to other parts of the globe. In contrast to migrants, phenotypic plasticity among resident species, particularly generalists, may provide some degree of insulation against ongoing climate change. Assessing such plasticity and any possible adaptive consequences of such flexibility, however, requires a detailed understanding of a population's basal natural history, including demography, foraging, and reproductive ecology. Future studies examining cache longevity and foraging behavior under various climatic regimes and resulting demographic consequences will provide critical insight on how Canada Jays and other resident species may cope in a rapidly changing world.

Competing interests statement

The authors declare that there are no competing interests. The views and conclusions contained in the article are those of the authors and should not be interpreted as representing the opinions or policies of the U.S. Government. Mention of trade names or commercial products does not constitute their endorsement by the U.S. Government.

Contributors' statement

K. Swift: investigation, data curation, formal analysis, writing (original draft preparation). E.J. Williams: project administration, resources, investigation, writing (review and editing). J.M. Marzluff: conceptualization, funding acquisition, methodology, supervision, writing (review and editing).

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Data availability

The Excel data that supports these findings are available from the University of Washington's ResearchWorks Archive (<http://hdl.handle.net/1773/46685>).

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