

Investigating factors that set the lower elevational limit of Canada Jays (*Perisoreus canadensis*) on Vancouver Island, British Columbia, Canada

Nathaniel J. Quarrell, Dan Strickland, and D. Ryan Norris

Abstract: The biotic and abiotic factors responsible for determining ranges of most species are poorly understood. The Canada Jay (*Perisoreus canadensis* (Linnaeus, 1766)) relies on perishable cached food for over-winter survival and late-winter breeding and the persistence of cached food could be a driver of range limits. We confirmed that the Canada Jay's lower elevational limit on Vancouver Island, British Columbia, Canada, matches that of the subalpine zone (900 m) and then conducted simulated caching experiments to examine the influence of antimicrobial properties of subalpine tree species (biotic) and of temperature (abiotic) on the preservation of cached food. We found that two high-elevation species, yellow cedar (*Callitropsis nootkatensis* (D. Don) D.P. Little) and Amabilis fir (*Abies amabilis* Douglas ex J. Forbes), preserved cached blueberries and chicken flesh better than other trees, but they also occurred well below the lower limit of Canada Jays. The effect of temperature was similarly unclear; while food cached at 1150 m retained 17% more mass than food cached at 550 m, there was no difference in percent mass remaining of food placed 70 m above versus 120 m below the Canada Jay's lower elevational limit. Thus, we were unable to provide definitive evidence that either of the proposed abiotic or biotic factors was responsible for setting the lower elevational limit of resident Canada Jays.

Key words: food caching, range limit, distribution, climate change, altitudinal distribution, Canada Jay, *Perisoreus canadensis*.

Résumé : Les facteurs biotiques et abiotiques qui modulent les aires de répartition de la plupart des espèces ne sont pas bien compris. Le mésangeai du Canada (*Perisoreus canadensis* (Linnaeus, 1766)) recourt à de la nourriture périssable mise en cache pour sa survie hivernale et sa reproduction à la fin de l'hiver, et la persistance de la nourriture mise en cache pourrait moduler les limites de son aire de répartition. Nous avons confirmé que la limite d'altitude inférieure du mésangeai du Canada dans l'île de Vancouver (Colombie-Britannique, Canada) coïncide avec celle de la zone subalpine (900 m), puis avons mené des expériences de mise en cache simulée afin d'examiner l'influence des propriétés antimicrobiennes d'essences d'arbres subalpines (facteur biotique) et de la température (facteur abiotique) sur la préservation de la nourriture mise en cache. Nous avons constaté que deux essences de haute altitude, le cyprès jaune (*Callitropsis nootkatensis* (D. Don) D.P. Little) et le sapin gracieux (*Abies amabilis* Douglas ex J. Forbes), préservent mieux des bleuets et de la chair de poulet mis en cache que d'autres arbres, mais qu'ils se trouvent aussi bien en dessous de la limite inférieure des mésangeais du Canada. L'effet de la température est tout aussi mitigé; si la nourriture mise en cache à 1150 m d'altitude a conservé 17 % plus de sa masse que la nourriture mise en cache à 550 m, aucune différence n'a été relevée entre les pourcentages de masse restants de nourriture placée 70 m au-dessus et 120 m en dessous de la limite d'altitude inférieure des mésangeais du Canada. Nous n'avons donc pas été en mesure d'obtenir des preuves définitives d'un rôle des facteurs abiotique et biotique proposés dans l'établissement de la limite inférieure d'altitude des mésangeais du Canada résidents. [Traduit par la Rédaction]

Mots-clés : mise en cache de nourriture, limite de l'aire de répartition, répartition, changement climatique, répartition altitudinale, mésangeai du Canada, *Perisoreus canadensis*.

Introduction

With climate change expected to have major effects on the geographic ranges of many plants and animals (Parmesan and Yohe 2003; Oliver et al. 2012; Pearce-Higgins et al. 2017; Yu et al. 2019), it is increasingly important to identify factors responsible for determining their present distributions. Species' ranges are determined by a wide range of abiotic and biotic factors (Sexton et al. 2009). Abiotic factors, such as climate, can directly affect the distributions of plants and animals by imposing conditions that exceed their physiological tolerance (Canterbury 2002; Sorte and Hofmann 2004; Cahill et al. 2014; Gannon et al. 2014), while biotic factors,

such as competition (Repasky and Schluter 1994; Gross and Price 2000; Anderson et al. 2002; Pigot and Tobias 2013) and predation (DeRivera et al. 2005; Parlato et al. 2015), can also constrain species' distributions. Changes in abiotic or biotic factors may result in alterations to species' distributions as exemplified by the poleward shifts in some organisms in response to climate warming (Parmesan and Yohe 2003; Franco et al. 2006). While such shifts may be directly attributed to temperatures exceeding a species' physiological tolerance, temperature can also indirectly affect species' distributions by changing precipitation patterns causing shifts in food-plant distributions (McCain and Colwell 2011), by limiting food availability that negatively impacts prey habitat (Gross and Price

Received 25 May 2021. Accepted 11 September 2021.

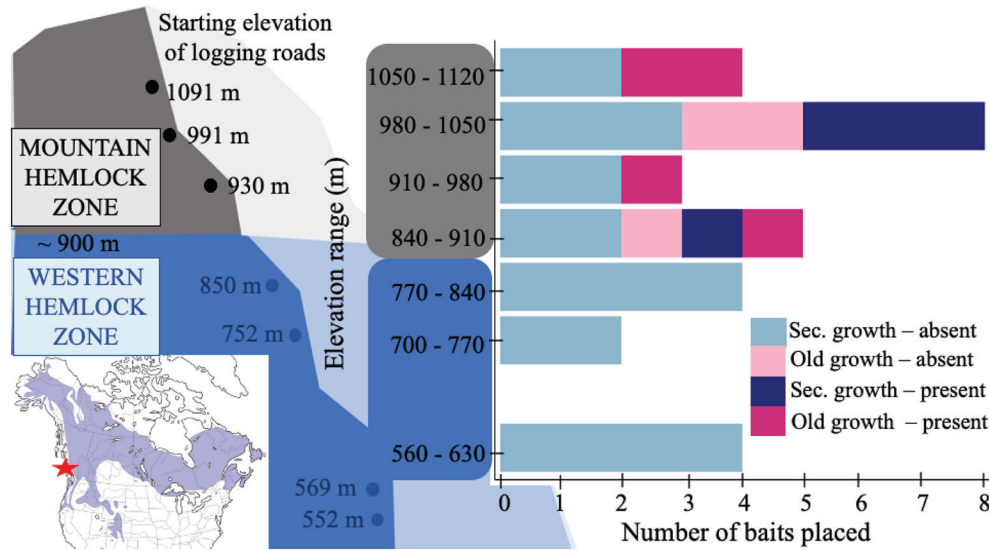
N.J. Quarrell and D.R. Norris. Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada.

D. Strickland. Dwight, Ontario, Canada.

Corresponding author: Nathaniel J. Quarrell (email: quarrellnj@gmail.com).

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Fig. 1. Presence or absence of Canada Jays (*Perisoreus canadensis*) along an elevational gradient on Mount Washington, Vancouver Island, British Columbia, Canada. The two biogeographic zones shown are the higher elevation mountain hemlock or “subalpine” zone (grey) and the lower elevation western hemlock zone (blue). Dots on the mountain indicate the elevations (552–1091 m) where caching experiments and most tree and lichen surveys were conducted and where most baits were deployed. The inset map from the [Cornell Lab of Ornithology \(2019\)](#) shows the range of Canada Jays with the red star indicating the location of Mount Washington. The graph depicts the results of presence or absence surveys of Canada Jays from baits deployed at the different elevations on Mount Washington (22 baits in 2019, 8 baits in 2010). The dark blue and dark pink bars signify baits where two or more Canada Jays were seen in second-growth (Sec. growth) forest and old-growth (Old growth) forest, respectively, whereas the light blue and pink bars signify baits where no Canada Jays were seen. Colour version online.



2000), or by increasing the abundance of predators (Harley 2011). Determining how abiotic or biotic factors may influence a species’ range is challenging because it requires examining multiple factors simultaneously within the same study system (Gaston 2009; Louthan et al. 2015).

Montane ecosystems are ideal for studying factors that restrict species’ ranges due to the presence of well-defined, elevation-driven temperature and precipitation gradients (Jump et al. 2009). Species that inhabit montane ecosystems are generally thought to be limited at higher elevations by abiotic factors, especially low temperatures, that cause physiological stress to individual organisms, and to be limited at lower elevations by biotic factors (MacArthur 1972), especially competition (Bullock et al. 2000; Jankowski et al. 2013). Consistent with this, Hargreaves et al. (2014) found in a meta-analysis of outside-of-range transplant experiments that there was no decline in fitness when organisms were moved to elevations below their normal range. Because transplanted populations persisted over the short term, this supports the notion that lower limits are likely constrained by biotic factors, which would take longer to have detrimental effects than abiotic factors. While this analysis supports the notion that a species’ lower elevational limit can be determined by biotic factors, the precise mechanisms and their relative influences are not often well known for many species.

One species for which a latitudinal range-limiting mechanism has been proposed is the Canada Jay (*Perisoreus canadensis* (Linnaeus, 1766)), a monogamous, year-round territorial, and food-storing resident of the boreal and subalpine forests of North America (range shown in Fig. 1; Strickland and Ouellet 2020). Although Canada Jays are highly successful in seemingly foodless winter conditions, they do not inhabit seemingly more productive environments. Waite and Strickland (2006) suggested that this limitation stemmed from this species’ dependence on cold weather conditions to effectively store otherwise perishable food (arthropods, berries, vertebrate flesh, and mushrooms). Although a number of North American boreal species depend on cached food (Sutton et al. 2016), Canada

Jays are among a small number that exclusively store perishable food items for periods of up to several months before retrieval (Strickland and Ouellet 2020). Perishable food items are cached during the late summer and fall in trees, under bark, or within fruticose lichens. Caches must persist from the time of storage in sufficient quantity and quality to sustain Canada Jays over the winter, to aid females with the additional energetic costs of late-winter breeding (Sechley et al. 2014; Derbyshire et al. 2015), and especially in periods of bad weather, to allow adults to provision young in their late-winter nesting period (Derbyshire et al. 2019).

In coastal British Columbia, Canada, the Pacific morphotype of the Canada Jay (*Perisoreus canadensis obscurus* Ridgway, 1874/*Perisoreus canadensis griseus* Ridgway, 1899; van Els et al. 2012) is said to occur at elevations as low as 400 m (Campbell et al. 1997), but most commonly it is found in the subalpine zone; i.e., above 900 m on Vancouver Island (Meidinger and Pojar 1991; Forest Service British Columbia Research Branch 2020). Above 900 m, the snowpack abruptly increases, and winter precipitation almost always falls and remains as snow (Klinka and Chourmouzis 2001), and forests are characterized by an abundance of mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière), Amabilis fir (*Abies amabilis* Douglas ex J. Forbes), and yellow cedar (*Callitropsis nootkatensis* (D. Don) D.P. Little) (Klinka and Chourmouzis 2001). Of these three main subalpine tree species, Amabilis fir is also common in the wetter, high-elevation parts of the western hemlock zone below 900 m (Meidinger and Pojar 1991; Green and Klinka 1994; Klinka and Chourmouzis 2001) as are western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). At lower elevations of the western hemlock zone, western red cedar (*Thuja plicata* Donn ex D. Don) becomes more common (Meidinger and Pojar 1991; Green and Klinka 1994).

To the extent that the lower limit of Canada Jays on Vancouver Island coincides with the lower limit of the subalpine zone or one of the major subalpine zone tree species, one hypothesis to explain the lower range limit of this species is that the Canada

Jays are critically dependent on one or more floral elements present in the subalpine zone to preserve their cached food and that these elements are absent or insufficiently abundant at lower elevations. In addition to the potential importance of conifers, epiphytic lichens, especially the conspicuous fruticose lichen *Alectoria sarmentosa* (Ach.) Ach. (common witch's hair), constitute a major floral component of old-growth forests (McCune et al. 1997) and may also be critical for the successful storage and long-term preservation of cached perishable food items. One or more of these floral elements could explain the presence, and perhaps the confinement, of Canada Jays in the otherwise seemingly less climatically hospitable subalpine zone.

Abiotic factors, specifically temperature, might also be playing a direct role in setting the lower elevational limit of Canada Jays on Vancouver Island, British Columbia, Canada. Warming temperatures (Waite and Strickland 2006) and (or) an increase in number of freeze–thaw cycles (Sutton et al. 2019) could put the viability of caches at risk. The reduction of cache quality would limit food availability for Canada Jays and have a negative impact on late-winter and early-spring reproductive success (Derbyshire et al. 2015; Freeman et al. 2020). If Canada Jay caches are directly at risk through their vulnerability to warm temperatures, then an upward shift in the lower distributional limit of Canada Jays may be imminent even if it will take much longer for the tree distribution limits to exhibit a similar shift. Current predictions are that by 2055, the present temperature conditions, which are presumably currently suitable to maintain sufficient cache quality for late-winter breeding, will have moved upward to such a degree that the current climatic conditions will almost certainly no longer coincide with the present subalpine zone (Hamann and Wang 2006).

Studies from Algonquin Park, Ontario, Canada, suggest that similar factors may influence the distribution of Canada Jays on Vancouver Island. In a range-edge population in Algonquin Park, Strickland et al. (2011) provided experimental evidence that artificially cached perishable food items intended to simulate Canada Jay caches placed on coniferous trees, especially black spruce (*Picea mariana* (Mill.) Britton, Sterns and Poggenb.), maintained a higher mass and caloric content than similarly cached food placed on deciduous trees. Based on this result, Strickland et al. (2011) proposed that the volatile antimicrobial resins of conifers reduced the spoilage rate of perishable food items stored in contact with the bark of those conifers.

Notwithstanding this putative protection of cached food, the Algonquin study population has decreased by more than 50% since the 1970s (Waite and Strickland 2006; Strickland et al. 2011; Sutton et al. 2021). There has been no detected change in forest composition over this same time period, but correlational and experimental evidence supports the hypothesis that this decline has been caused by increases in fall temperatures (Waite and Strickland 2006) and (or) an increase in the number of freeze–thaw events (Sutton et al. 2019, 2021). These climatic changes likely accelerate the degradation of cached food (Sechley et al. 2015), leading to lower-than-average reproductive success (Waite and Strickland 2006; Sutton et al. 2019) and negative population growth rates (Sutton et al. 2021). The general finding from the Algonquin Park studies is that the preservation of perishable food stores, and hence the demographic fortunes of the park's range-edge Canada Jays, benefit from the antimicrobial properties of spruce species, but also that both are being negatively impacted by the rising temperatures and (or) an increase in the number of freeze–thaw events associated with climate change.

In this study, we collected observational data and conducted field experiments in an attempt to identify abiotic and biotic factors that might contribute to setting the lower distributional limit of Canada Jays on Mount Washington, Vancouver Island,

British Columbia, Canada. First, we sampled along an elevational gradient to estimate the lower limits of both resident Canada Jays and the tree species that define the subalpine zone. We then tested predictions stemming from three hypotheses that might explain the relationship between the lower elevation limit of the Canada Jay and the subalpine zone.

The first hypothesis we examined was that, compared with prominent tree species in the lower, western hemlock zone, one or more subalpine tree species have potent antimicrobial properties which correspondingly better preserve perishable food items stored in contact with their bark and that this accounts for the presence of Canada Jays. Following this biotic hypothesis, we predicted that food artificially cached on one or more common tree species found within the subalpine zone would lose significantly less mass than food artificially cached on other tree species tested at the same elevation. We also predicted that the Canada Jay's lower elevation limit would coincide with the lower limit of the tree species putatively found to preserve artificial caches of perishable food better than other tree species.

We also considered a second (biotic) hypothesis. Canada Jays are often seen caching food items in, or recovering items from, strands of *Alectoria sarmentosa*, which is an epiphytic fruticose lichen that is common in the subalpine zone and known to produce antimicrobial compounds (Ranković and Mišić 2007; Çobanoğlu et al. 2010). Reasoning that *A. sarmentosa* might be a key floral element permitting Canada Jays to successfully store perishable food, we predicted that lichen abundance would be significantly greater above the Canada Jay's lower elevation limit than below this limit.

Finally, we also considered a third (abiotic) hypothesis. Given the critical role of accumulating snowpack and therefore of sub-zero temperatures in creating the conditions favorable for the establishment of subalpine plant communities, we reasoned that there might exist a similar temperature-dependent dichotomy in the survival of perishable food caches above and below the lower elevational limit of Canada Jays. Following this hypothesis, we predicted that artificial perishable food caches placed at various elevations below the subalpine boundary would lose mass at a significantly faster rate than otherwise similar cached items placed above the subalpine boundary.

Materials and methods

Study area

We conducted our study 32 km west of Courtenay, British Columbia, Canada (49°41'9.59"N, 124°59'23.9"W; Fig. 1), along 33 km of the Mount Washington main access road, the Strathcona Parkway, that runs from the Inland Island Highway 19 to the Mount Washington Alpine Resort. This road permits the only year-round motorized access to the subalpine (mountain hemlock) zone on Vancouver Island. The subalpine zone begins at approximately 900 m elevation on Mount Washington, whereas the western hemlock zone, which covers most of Vancouver Island, occurs below 900 m (Meidinger and Pojar 1991). The forests adjacent to the Strathcona Parkway are owned by the forestry company TimberWest and managed for timber production and consequently consist of second-growth forest, which is composed of various-aged stands of planted trees, interspersed with small remnant patches (all <3 ha) of old-growth forest.

Seven logging roads departing from the Strathcona Parkway at 552, 569, 752, 850, 930, 991, and 1091 m (mean distance between sites = 90 m) provided convenient access to suitable sites for simulated caching experiments and for conducting surveys to determine the presence or absence of Canada Jays and estimate tree composition (Fig. 1; for location details see Supplementary Table S1¹). Because 850 m was the lowest elevation at which Canada Jays had been observed in an earlier survey (D. Strickland,

¹Supplementary tables and figures are available with the article at <https://doi.org/10.1139/cjz-2021-0108>.

unpublished data; for details see the next section), we chose the other six experimental sites to be distributed equally with three above and three below the 850 m elevation ($n = 7$ sites total).

Confirming the lower elevation limit of resident Canada Jays

To confirm the lower elevation limit of resident Canada Jays, we tied baits consisting of 150 g of cheddar cheese wrapped in steel hardware cloth (1 cm \times 1 cm mesh openings; see Supplementary Fig. S1A¹) to trees at the six highest of the above-cited experimental sites from 1 to 5 November 2019. The lowest elevation site was excluded from bait placement because it was not possible to check all sites in a single day. Three baits were placed at each of these Canada Jay survey sites such that one bait was 25 m away from the Strathcona Parkway and the other two baits were placed farther into the forest and separated from each other by at least 500 m (for bait elevations see Supplementary Table S1).¹ The distance between baits was chosen so that it was unlikely that any two baits would be placed within the same Canada Jay territory (mean size on Mount Washington = 19.8 ha; D. Strickland, unpublished data). Of the 18 total baits placed at the six highest elevation sites, 2 baits were within old-growth forest (1 bait each at 956 and 984 m) and the remainder baits were in second-growth forest. An additional four baits were placed opportunistically in small patches (<3 ha) of old-growth forest that were accessible from the Strathcona Parkway (baits placed at 899, 1016, 1088, and 1098 m elevation; Supplementary Table S2¹).

To estimate whether a given location was within a resident Canada Jay territory, baits were visited once every day over the course of 4 days. Based on data from Algonquin Park (D. Strickland and D.R. Norris, unpublished data), we considered that to be sufficient time for Canada Jays, if present, to discover the bait and begin to cache and (or) consume it. If on one of our monitoring visits we found the cheese to be fully or partially consumed, then we refilled the station and waited an hour to observe if Canada Jays were responsible. A territory was considered occupied by Canada Jays only if two or more individuals were observed at a bait at the same time because an observation of a single bird was more likely to represent an unpaired individual searching for a breeding vacancy (Strickland 1991) and thus not be holding a stable territory at that location.

We combined these data with a similar Canada Jay presence or absence survey collected by D. Strickland between 15 and 18 October 2010. In that survey, eight cheese baits were tied to utility poles or trees along the Strathcona Parkway at elevations of 588, 710, 795, 823, 858, 898, 997, and 1112 m (for location details see Supplementary Table S3).¹ Baits were visited repeatedly each day, but otherwise were surveyed as described above. In total, 30 baits (22 in 2019 and 8 in 2010) were deployed.

Describing tree distributions

To describe how tree species' presence and abundance varied with elevation, we conducted surveys near each of the experimental sites from 22 June to 4 December 2019, (see "Study area" section). In the forest near each site, an 800 m transect was laid out, beginning 25 m away from both the Strathcona Parkway and the logging road. Each transect was subdivided at intervals of 20 m, of which six locations were randomly selected for the placement of 20 m \times 20 m plots. In addition, we also placed four 20 m \times 20 m plots 25 m away from the forest edge in old-growth forest (see "Confirming the lower elevation limit of resident Canada Jays" section). Since all old-growth patches were located beside either a clear-cut forest or a road, the forest edge was distinct. In total, 46 plots (7 transects \times 6 plots/site + 4 old-growth plots) were surveyed. Within each plot, all trees with a diameter at breast height (DBH) >15 cm were identified to species ($n = 5227$ trees; 11 species). Identification of tree species was done by the primary author using the identification methods found in Pojar and MacKinnon (2016).

Tree species planting records were also obtained from TimberWest for the elevations where we conducted tree surveys (TimberWest, personal communication; Supplementary Table S1¹). Although there are government guidelines that suggest which tree species are most appropriate to plant for a given biogeographic zone (Green and Klinka 1994), forestry companies are under no obligation to follow these guidelines. We used TimberWest's planting records to determine if subalpine and western hemlock zone tree species were planted at supposedly appropriate (Meidinger and Pojar 1991; Klinka and Chourmouzis 2001) elevations (i.e., above 900 m for subalpine species or below that elevation for western hemlock zone trees).

Estimating lichen distribution

Percent lichen cover was estimated for every tree that was surveyed. Following McCune (1990), we visually inspected the tree from a location that permitted good visibility to the treetop. We considered anything part of the tree (e.g., branches, trunk) or growing on it (i.e., epiphytes) as "tree cover" and visually estimated the proportion of cover accounted for by lichens. Following McCune (1990), we then placed percent lichen cover into one of nine classes used to approximate an arcsine square root transformation: 0 = 0%; 1 = 0%–1%; 2 = 1%–5%; 3 = 5%–25%; 4 = 25%–50%; 5 = 50%–75%; 6 = 75%–95%; 7 = 95%–99%; 8 = 100% (McCune 1990).

Description of chambers used to simulate food caches

To examine the influence of both temperature and tree species on the mass loss of perishable food items over time, we deployed artificial food storage chambers (see Supplementary Fig. S1B)¹ designed to simulate a Canada Jay food cache in the wild and previously used by Strickland et al. (2011) and Sechley et al. (2015). Food chambers were made of 3.5 cm \times 4 cm \times 1.6 cm polyethylene blocks on one surface of which a 2 cm diameter circular "well" was drilled halfway through the block. A curved passage leading from the well to the bottom edge of the block allowed microbes, spores, and small invertebrates to enter the central well but prevented larger animals or water from entering. At the bottom of the well, a disk of bark from the same tree species (or tree slab or lumber) on which the food chambers would be deployed was placed. This was done so that, when the chamber was deployed, food items being tested would be sandwiched between the bark of a living tree and the bark disk, thus simulating caches made by Canada Jays under bark flakes on tree trunks. Tested foods consisted of either 1 g of half a cut-up blueberry (mean \pm SD from all samples: 1.16 \pm 0.08 g) or cut-up raw organic chicken breast (1.15 \pm 0.09 g). Blueberries and chicken breast were chosen because they represent two prominent types of food (berries and vertebrate flesh) cached by Canada Jays (Strickland and Ouellet 2020). All food items were weighed before deployment and after retrieval with an Ohaus SP-202 Scout Pro Balance scale (Ohaus, Dundas, Ontario, Canada) to the nearest 0.01 g.

Depending on the experiment and treatment within an experiment, food chambers were directly fastened into one of three chamber substrates: living trees, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) lumber, or western red cedar tree slabs (see next section). All food chambers were deployed on the north-facing side of trees, with the lowest food chambers being 2 m above the ground. This placement minimized the effect of solar radiation on the food chambers and ensured that none of the chambers would be buried in snow by the time the last food chambers were removed in December.

Experiment to determine if cache preservation varied by tree species

To determine if cache preservation varied by tree species, from 22 July to 4 December 2019, we conducted a simulated caching experiment at 930 m elevation on Mount Washington. Five of the six most common native conifer species on Mount Washington

were present at this sampling site. Of these tree species, three were typical of the subalpine habitat of Canada Jays (mountain hemlock, Amabilis fir, and yellow cedar), whereas two were typical of the lower elevation western hemlock zone (western hemlock and Douglas-fir). For the absent western red cedar, we used tree slabs of that species. At a lower elevation where western red cedar was common, we conducted a side experiment that confirmed these tree slabs had preservation abilities similar to those of live western red cedars (for details see [Appendix A](#)).

For each of the five conifer species that were present at this site (mountain hemlock, Amabilis fir, yellow cedar, western hemlock, and Douglas-fir), we selected seven individual trees to which we temporarily fastened food chambers. In the local absence of live western red cedars, we fastened food chambers to slabs of that species and tied those slabs to other trees. We deployed two food chambers, one containing a blueberry and one containing raw chicken breast, on all 42 trees or slabs on three different occasions: 22–25 July (retrieved on 4–5 September), 7 September (retrieved on 18 October), and 20–22 October (retrieved on 4 December). Thus, caches deployed in July were exposed to the environment for 41–44 days, caches deployed in September were exposed to the environment for 42 days, and caches deployed in October were exposed to the environment for 45–47 days. In total, 252 food chambers were deployed (3 deployment periods \times 6 tree substrates [5 living trees + 1 slab] for each period \times 7 trees/period \times 2 food types/tree) for this experiment. After retrieval, the content of each food chamber was immediately weighed to determine the wet mass.

Experiment to determine if cache preservation varied with elevation

From 20 July to 5 December 2019, we conducted a second simulated caching experiment on Mount Washington to test if there might exist a temperature-dependent dichotomy in the survival of perishable food caches above and below the lower elevational limit of Canada Jays. Food chambers were deployed at different elevations (see “Study area” section), resulting in their being exposed to different temperatures. Temperature differences between sites were confirmed by placing iButtons (iButtonLink Technology, Whitewater, Wisconsin, USA) at each cache deployment site, which allowed us to record temperature every 2 h over the course of the experiment.

To control for potential differences in the antimicrobial properties of different tree species, food chambers were attached to 5 cm \times 2 cm \times 30 cm boards of kiln-dried Engelmann spruce lumber (see Supplementary Fig. S1C)¹ tied to trees ($n = 49$ boards in total). To determine if elevation affected mass loss, we investigated how the time of year food was stored affected mass loss while controlling for exposure time. To do this, we deployed two food chambers, one containing blueberry and one containing chicken breast, on all 49 boards on three different occasions: 20–22 July (retrieved on 3–4 September), 6–7 September (retrieved on 18 October), and 20–22 October (retrieved on 4–5 December). Thus, caches deployed in July were exposed to the environment for 43–46 days, caches deployed in September were exposed to the environment for 41–42 days, and caches deployed in October were exposed to the environment for 44–45 days. In total, 296 food chambers were deployed (3 deployment periods \times 7 experimental sites for each period \times 7 boards/site per period \times 2 food types/board) for this experiment. After retrieval, the content of each food chamber was immediately weighed to determine the wet mass.

Statistics

For Canada Jay presence or absence surveys conducted in 2019, for which we had data on the tree species near baits, we did not run any statistical models to examine which tree species influenced the presence of Canada Jays due to the low number of Canada Jays observed at baits.

To examine how date and elevation influenced mean daily temperature ($^{\circ}\text{C}$; recorded from iButtons), we fitted generalized linear models with Gaussian distribution and an identity link using the following predictors: (i) elevation (552–1091 m), (ii) the day that temperature was recorded (23 July – 5 December), and (iii) the interaction of elevation \times day that temperature was recorded; we used Akaike’s information criterion corrected for small sample size (AIC_c) for model selection of all permutations, i.e., model that best fit the data ([Burnham and Anderson 2002](#)). We included this interaction term because we were interested in examining whether the effect of elevation on mean daily temperature varied with the day temperature.

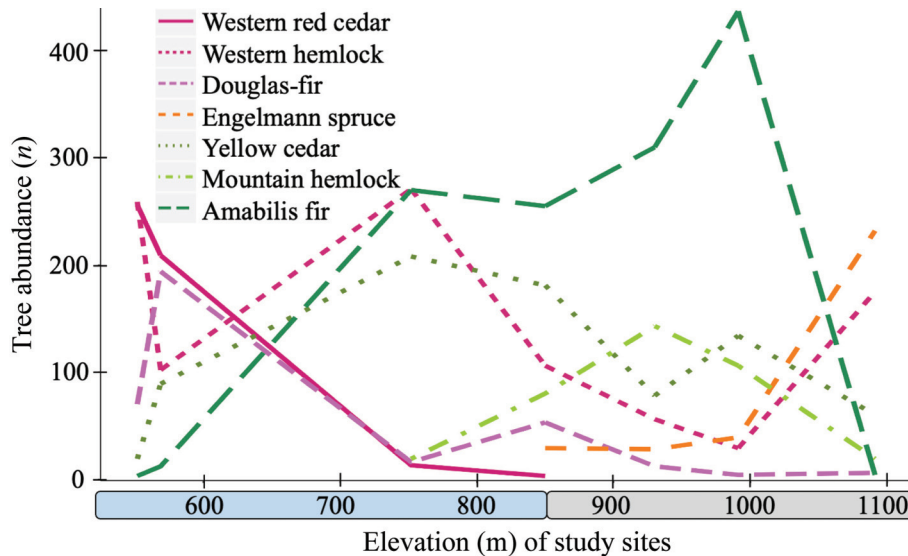
To examine how tree species influenced mass remaining per food type (blueberry, chicken), we fitted generalized linear models with a Gamma distribution and log link to each food type using the following predictors: (i) tree species (mountain hemlock, Amabilis fir, yellow cedar, western hemlock, Douglas-fir, western red cedar), (ii) deployment date (July, September, October), and (iii) the interaction of tree species \times deployment date; we used AIC_c for model selection of all permutations. We included this interaction term because we were interested in examining whether the effect of deployment date on mass loss differed according to tree species. For all models, the reference value for tree species was western hemlock. For blueberry models, the reference value for deployment date was 20–25 July. Chambers containing chicken breast that were deployed in July had a high proportion of food loss (81% of food chambers were empty upon retrieval), so caches deployed at this time were excluded from analysis. Thus, the reference value for deployment date of these models was 6–7 September.

To examine if temperature influenced the mass loss of simulated caches above and below the lower elevational limit of Canada Jays, we used a two-sample t test to compare the percent mass of food remaining from chambers fastened to Engelmann spruce boards that were placed below the Canada Jay’s lower elevation limit, at 742 m, to chambers on Engelmann spruce boards placed directly above this elevation limit, at 930 m.

To examine how elevation influenced mass remaining per food type (blueberry, chicken), we fitted generalized linear models with a Gamma distribution and log link to each food type using the following predictors: (i) elevation (552–1091 m), (ii) deployment date (July, September, or October), and (iii) the interaction of elevation \times deployment date; we used AIC_c for model selection of all permutations. We included this interaction term because we were interested in examining whether the effect of deployment date on mass loss differed according to elevation. For blueberry models, the reference value for deployment date was 20–22 July. Similar to the above experiment, chambers containing chicken breast that were deployed in July had a high proportion of food loss (41% of food chambers were empty upon retrieval), so caches deployed at this time were excluded from analysis. The reference value for deployment date of these models was 6–7 September.

For each of the above simulated caching model sets (tree species and elevation), we used AIC_c to evaluate models that best fit the data ([Burnham and Anderson 2002](#)). Models within $2 \Delta\text{AIC}_c$ of the top model were considered to be strongly supported by the data ([Burnham and Anderson 2002](#)), but if multiple models fit this criteria, then the model parameters were averaged across competing models. For the candidate model or models, we calculated 85% confidence intervals (85% CI) for each parameter ([Arnold 2010](#)) and considered the parameter to be above or below zero if the confidence interval did not overlap with zero. [Arnold \(2010\)](#) argued that 85% CI, not 95% CI, should be used with best-approximating models that are supported by lower AIC values because AIC selects models at $p < 0.157$, which is consistent with 85% CI, not at $p > 0.05$, which is consistent with 95% CI. All statistical tests were performed with R version 3.5.2 ([R Core Team 2019](#)) using the lme4 ([Bates et al. 2015](#)) and MuMIn ([Bartoń 2019](#)) packages, whereas ggplot2 was used to visualize the data ([Wickham 2016](#)).

Fig. 2. Estimated abundance (number of individuals/plot) of the seven most common tree species at different elevations (552–1091 m) on Mount Washington, Vancouver Island, British Columbia, Canada. At each elevation, 6 plots (0.04 ha in area) were randomly placed along a transect ($n = 42$ total plots) and sampled between 6 June and 4 December 2019. Along the x axis, the two biogeographic zones are shown in blue (western hemlock zone) and gray (mountain hemlock zone or “subalpine zone”). Colour version online.



Results

Estimating the distribution of Canada Jays along an elevation gradient

The lowest elevation at which apparently resident groups of Canada Jays were observed was at 858 m. At and above this elevation in subalpine zone forest, Canada Jays were seen at 4 of the 7 baits near (<50 m) old-growth patches and at 4 of the 13 baits near second-growth forests (Fig. 1). No Canada Jays were observed at any of the 10 baits placed between 560 and 840 m (Fig. 1).

Tree species' presence and abundance in relation to the Canada Jay's lower elevation limit

Of the major subalpine zone tree species, mountain hemlock was abundant at high elevations near and above the lower subalpine zone boundary (900 m). The majority of mountain hemlock (95%) was located above the lower elevation limit of Canada Jays (>850 m; Fig. 2). Both yellow cedar and Amabilis fir were abundant throughout the subalpine zone and at upper elevations of the western hemlock zone (Fig. 2). The proportions of yellow cedar and Amabilis fir near the lower elevation limit of Canada Jays (850 m; 26% yellow cedar, 36% Amabilis fir) were similar to those observed 100 m below this point (752 m; 26% yellow cedar, 34% Amabilis fir). Among the tree species associated with the western hemlock zone, Douglas-fir was rare at the zone's high elevations, whereas western red cedar was absent. Western hemlock was common at all elevations in its eponymous zone. At the highest elevation site (1091 m), Engelmann spruce (a non-native, planted species) was common. The observed distribution of planted western hemlock and Engelmann spruce matched the tree planting records obtained from TimberWest (Supplementary Table S1).¹

Within old-growth patches ($n = 6$), all of which were located in the subalpine zone (above 900 m elevation), 317 trees were identified to species. Among trees found in old-growth patches, 45% were mountain hemlock, 28% were yellow cedar, 20% were Amabilis fir, and 7% were other tree species.

Description of elevational temperature profile

From July to December 2019, mean daily temperature at the highest elevation site (1091 m) ranged from -7.6 to 17.7 °C (6.8 ± 5.5 °C, mean \pm SD), whereas mean daily temperature at the

lowest site (552 m) ranged from -3.2 to 20.2 °C (9.2 ± 5.6 °C; Fig. 3). Two top models ($\Delta\text{AIC} \leq 2$) explained variation in mean daily temperature (Supplementary Table S4).¹ The top-ranked model included elevation and date, whereas the second-ranked model ($\Delta\text{AIC} = 1.6$) included elevation, date, and the interaction between elevation and date. The confidence intervals of the model-averaged parameter estimate of elevation and date did not overlap with zero, whereas the model-averaged parameter estimates for the interaction did overlap with zero (Supplementary Table S5),¹ suggesting that elevation and date independently affected mean daily temperature.

Description of elevational lichen profile

Of all the trees surveyed for lichen coverage, 85% had <1% lichen coverage. Trees with >25% lichen coverage were only found in old-growth plots; all of which were above 900 m elevation. Within old-growth plots, 15% of trees had >25% lichen coverage, and among these, 65% were mountain hemlock, 13% were Amabilis fir, and 6% were yellow cedar.

Experiments comparing cache preservation on different tree species

The top model explaining variation in percent mass remaining of blueberries included both deployment date and tree species as predictors (Table 1). In the top model, the confidence intervals for yellow cedar, mountain hemlock, and deployment date estimates did not overlap with zero (Table 2), suggesting that blueberries deployed in September and October retained more mass than those deployed in July. Blueberries on yellow cedar retained more mass than those on western hemlock, and blueberries on mountain hemlock lost more mass than those deployed on western hemlock.

Two top models ($\Delta\text{AIC} \leq 2$) explained variation in percent mass remaining of chicken breast deployed in different months (October, December) and on different tree species (Table 1). The top-ranked model included tree species and deployment date, whereas the second-ranked model ($\Delta\text{AIC} = 1.8$) included only tree species. The confidence intervals of the model-averaged parameters for yellow cedar, Amabilis fir, and deployment date did not overlap with zero (Table 2), suggesting that chicken breast deployed in

Fig. 3. The mean daily temperature (°C) from July to December 2019 measured at seven elevations (552–1091 m) on Mount Washington, Vancouver Island, British Columbia, Canada. The vertical blue lines represent food chamber deployment dates (20–25 July, 6–7 September, 20–22 October), whereas the red lines represent food chamber retrieval dates (3–5 September, 18–19 October, 4–6 December) for the simulated cache experiments. The green arrows represent deployment duration. Colour version online.

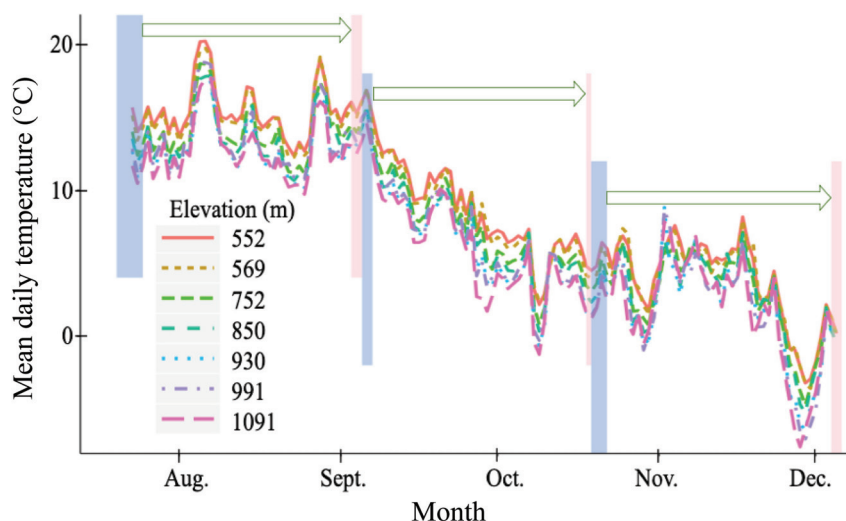


Table 1. Top competing models within $2 \Delta AIC_c$ explaining variation in the percent mass remaining of simulated blueberry and chicken breast caches deployed in different months on different tree species.

Food cached	Models predicting percent mass remaining				
		K	AIC _c	ΔAIC_c	ω_i
Blueberry	Deployment date + tree species	9	-213.7	—	1.0
	Tree species	7	-110.8	1.8	0.2
Chicken	Deployment date + tree species	8	-112.6	—	0.5
	Tree species	7	-110.8	1.8	0.2

Note: We considered all combinations (including interactions) of two variables: deployment date (food chambers were deployed on three different occasions: 20–25 July (July data for chicken was not used), 7 September, or 20–22 October; food chambers were retrieved 41–44 days later) and tree species ($n = 6$ species). The null model was an intercept-only model. The number of model parameters (K), Akaike's information criterion corrected for small sample size (AIC_c), ΔAIC_c scores, and AIC_c weight (ω_i) are presented for each model.

Table 2. Model coefficient outputs for top competing models explaining percent mass remaining of blueberry and chicken breast caches deployed in different months and on different tree species ($n = 6$) on Mount Washington, Vancouver Island, British Columbia, Canada.

Food cached	Variable	Estimate	SE	85% CI
Blueberry	Amabilis fir (<i>Abies amabilis</i>)	-0.16	0.10	-0.34, 0.02
	Mountain hemlock (<i>Tsuga mertensiana</i>)	-0.28	0.13	-0.46, -0.09
	Western red cedar (<i>Thuja plicata</i>)	0.12	0.13	-0.06, 0.30
	Yellow cedar (<i>Callitropsis nootkatensis</i>)	0.51	0.13	0.33, 0.70
	Douglas-fir (<i>Pseudotsuga menziesii</i>)	0.03	0.13	-0.16, 0.22
	Deployment date (6–7 September)	0.76	0.09	0.62, 0.90
	Deployment date (19 October)	0.50	0.09	0.36, 0.63
Chicken	Amabilis fir	0.23	0.15	0.02, 0.44
	Mountain hemlock	0.96	0.15	-0.12, 0.31
	Western red cedar	-0.06	0.17	-0.31, 0.18
	Yellow cedar	0.36	0.14	0.14, 0.57
	Douglas-fir	-0.17	0.16	-0.40, 0.06
	Deployment date (19 October)	0.19	0.12	0.06, 0.32

Note: If multiple models were supported (within $\Delta AIC_c \leq 2$; Table 1), then model averaging was used to infer the parameters. The reference value for deployment date in the blueberry model was 20–25 July and for the chicken breast model was 6–7 September (July data for chicken was not used). The reference value for tree species in both models was western hemlock (*Tsuga heterophylla*). Values in boldface type represent variables with 85% confidence intervals (85% CI) that did not overlap with zero.

October retained more mass than chicken breast deployed in September and that chicken breast deployed on yellow cedars and Amabilis fir retained more mass than those deployed on western hemlock (Fig. 4).

Experiments comparing cache preservation at different elevations

Two top models ($\Delta AIC_c \leq 2$) explained variation in percent mass remaining of blueberries deployed in different months (July,

Fig. 4. Percent mass remaining of blueberry (top panels) and chicken breast (bottom panels) caches deployed on different tree species (*Amabilis fir*, *Abies amabilis* (AF); mountain hemlock, *Tsuga mertensiana* (MH); yellow cedar, *Cupressus nootkatensis* (YC); Douglas-fir, *Pseudotsuga menziesii* (DF); western hemlock, *Tsuga heterophylla* (WH); western red cedar, *Thuja plicata* (RC)) on Mount Washington, Vancouver Island, British Columbia, Canada. Food chambers for each deployment period were retrieved 42–45 days after deployment. Blue dots represent the percent mass of individual caches ($n = 7$ caches deployed on each tree species per food type), with the red dot showing the mean and whiskers showing the standard deviation. Colour version online.

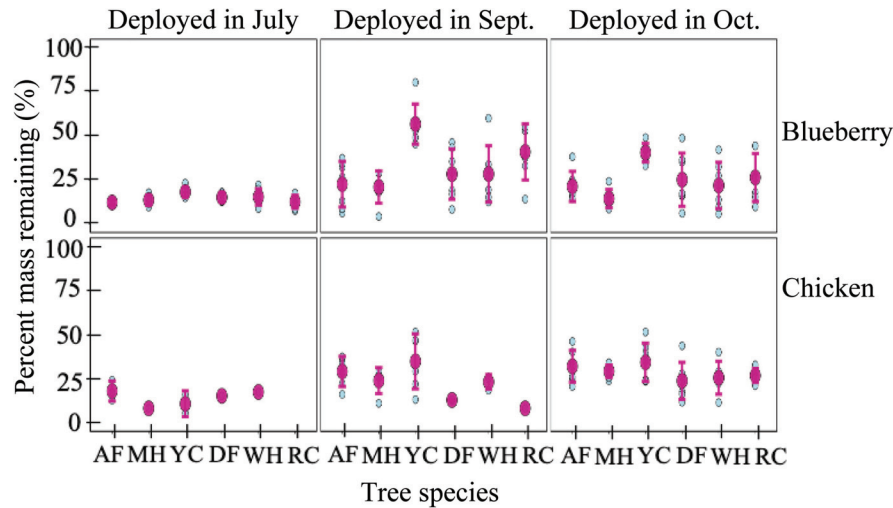


Table 3. Top competing models within $2 \Delta AIC_c$ explaining variation in the percent mass remaining of simulated blueberry or chicken breast caches deployed in different months and at different elevations.

Food cached	Models predicting percent mass remaining				
		K	AIC_c	ΔAIC_c	ω_i
Blueberry	Deployment date	4	-227.4	—	0.6
	Deployment date + elevation	5	-226.2	1.2	0.3
Chickent	Elevation	3	-109.6	—	0.6
	Deployment date + elevation	4	-108.6	1.0	0.3

Note: We considered all possible combinations (including interactions) of two variables: deployment date (food chambers were deployed on three different occasions: 20–22 July (July data for chicken was not used), 6–7 September, or 20–22 October; food chambers were retrieved 41–45 days later) and elevation (552–1091 m). The null model was an intercept-only model. The number of model parameters (K), Akaike's information criterion corrected for small sample size (AIC_c), ΔAIC_c scores, and AIC_c weight (ω_i) are presented for each model.

September, October) and elevations (Table 3). The top-ranked model included just deployment date, whereas the second-ranked model ($\Delta AIC = 1.2$) included both deployment date and elevation. The confidence intervals of the model-averaged parameter estimate of elevation overlapped with zero, whereas the confidence intervals of the model-averaged parameter estimate for deployment date did not overlap with zero (Table 4), suggesting that elevation had no effect on blueberry mass loss but that food chambers deployed in September and October retained more mass than those deployed in July.

Two top models ($\Delta AIC \leq 2$) explained variation in percent mass remaining of chicken breast deployed in different months (September, October) and elevations (Table 3). The top-ranked model included just elevation, whereas the second-ranked model ($\Delta AIC = 1.0$) included both deployment date and elevation. The confidence intervals of the model-averaged parameter estimate for elevation did not overlap with zero, whereas the confidence intervals of the model-averaged parameter estimate for deployment date overlapped with zero (Table 4), suggesting that chicken breast deployed at higher elevations retained more mass than at lower elevations, but there was no difference in mass loss between food chambers deployed in September and October (Fig. 5).

Mass loss of simulated caches placed at the site below the Canada Jay's lower elevation limit (elevation = 742 m) and caches placed at the site immediately above the Canada Jay's lower elevation limit (elevation = 930 m) did not differ (blueberry caches: two-sample t test, $t_{[68]} = 0.18$, $p = 0.85$; on chicken breast caches: two-sample t test, $t_{[45]} = -0.92$, $p = 0.36$).

Discussion

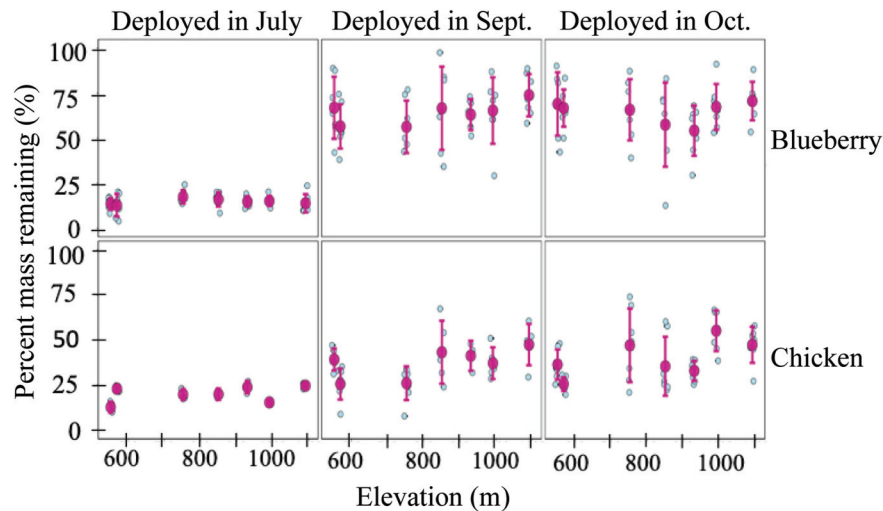
The first objective of our study was to estimate the lower elevation limit of Canada Jays on Mount Washington. The lowest site where we found pairs or larger social groups of Canada Jays was at 858 m (Fig. 1) and the forest at this elevation (measured at 850 m) was composed primarily of Amabilis fir, yellow cedar, mountain hemlock, and western hemlock (Fig. 2). This suite of tree species along with the similarity in abundance between western hemlock and mountain hemlock indicate that this location is near the lower edge of the subalpine zone (Klinka and Chourmouzis 2001). Thus, our results indicate that the lower limit of resident, territorial Canada Jays on Mount Washington likely occurs in the transition zone between the higher elevation subalpine community and the lower elevation western hemlock community.

Table 4. Model coefficient outputs for top competing models explaining percent mass remaining of blueberry and chicken breast caches deployed in different months and different elevation ($n = 7$ elevations) on Mount Washington, Vancouver Island, British Columbia, Canada.

Food cached	Variable	Estimate	SE	85% CI
Blueberry	Elevation	0.00004	0.00009	-0.00005, 0.003
	Deployment date (6–7 September)	1.47	0.05	1.39, 1.54
	Deployment date (20–22 October)	1.47	0.05	1.40, 1.54
Chicken	Elevation	0.0007	0.0002	0.0005, 0.001
	Deployment date (20–22 October)	0.03	0.06	-0.03, 0.19

Note: In both cases, multiple models were supported (within $\Delta\text{AIC} \leq 2$; Table 3) and model averaging was, therefore, used to infer the parameters. The reference value for deployment date in the blueberry model was 20–22 July and for the chicken model was 6–7 September (July deployment data for chicken was not used). Values in boldface type represent variables with 85% confidence intervals (85% CI) that did not overlap with zero.

Fig. 5. Percent mass remaining of blueberry (top panels) and chicken breast (bottom panels) caches at different elevations (552–1091 m) on Mount Washington, Vancouver Island, British Columbia, Canada. Food chambers for each deployment period were retrieved 41–45 days after deployment. Blue dots represent the percent mass of individual caches ($n = 7$ caches deployed per elevation per food type), with the red dot showing the mean and whiskers showing the standard deviation. Colour version online.



Consistent with our first prediction from the biotic tree species hypothesis, our results provide evidence that two major subalpine zone tree species, yellow cedar and Amabilis fir, preserved cached food better than other tree species tested, although in the case of Amabilis fir, this only applied to raw chicken breast caches. Many studies have shown that compounds extracted from yellow cedars, such as carvacrol and nootkatone, inhibit the growth of microbes and fungi and deter insects due to the presence of distinct secondary compounds (Johnston et al. 2001; Rosales-Castro et al. 2014; for a summary of all compounds identified in yellow cedar see Karchesy et al. 2018). Furthermore, a study that investigated the antimicrobial properties of trees whose wood is commonly used in animal bedding, including yellow cedar, western red cedar, and Douglas-fir, found that only extracts from yellow cedars significantly reduced the activity of all four microbial species tested (Johnston et al. 2001). In our study, the antimicrobial properties of Amabilis fir were dependent on food type, which is consistent with Xian-Wen et al. (2008) who found that various *Abies* species produce unique chemical compounds with species-specific antimicrobial properties.

The results of our caching experiments provide some support for the biotic tree species hypothesis, but we are hesitant to conclude that the antibiotic properties of yellow cedar or Amabilis fir are the critical factor allowing Canada Jays to inhabit the subalpine zone because both of these trees occurred well below the lower limit of Canada Jays on Mount Washington (i.e., ca. 850 m).

It could be that higher temperatures at lower elevations override the preservative abilities of both tree species and mask their importance in setting the lower elevation limit of Canada Jays. Alternatively, the relevant factor may not be the presence or absence of either yellow cedar or Amabilis fir, but rather the abundance of *Alectoria sarmentosa*, the epiphytic lichen that was especially associated with old-growth mountain hemlock in the subalpine zone. Unfortunately, the results of our temperature experiments and lichen surveys provide weak support at best for either of these possibilities.

While our results also provided evidence that temperature impacted the preservation of perishable food, we did not detect a critical threshold above which significantly better food preservation occurred. The lack of difference in mass loss of simulated caches placed above and below the Canada Jay's lower elevation limit (930 versus 742 m) does not support our prediction that food lost mass at a significantly faster rate below the Canada Jay's lower elevation limit than above it. However, our results do suggest that, at least for chicken breast caches, elevation-related temperature differences are likely important in determining how well food is preserved across a broader elevational range. The generalized linear model estimating percent mass remaining of chicken breast caches (Table 4) predicted that Canada Jays occupying a territory at 1150 m elevation would have, on average, 17% more food remaining compared with Canada Jays at 550 m elevation and this could be important, particularly because

Canada Jays rely almost exclusively on caches during the winter months. Perishable food exposed to colder temperatures would be expected to retain more mass than food exposed to warmer temperatures presumably because microbial activity is slower in colder temperatures (Brackett 1987; Rawat 2015). The delaying of microbial growth due to colder temperatures would imply that higher elevation sites would be of higher quality because they preserve cached food better.

Our results provided minimal support for our prediction from the biotic lichen hypothesis because the vast majority of trees throughout the study site had <1% lichen cover due to the effects of forestry at Mount Washington. Due to the slow growth rate and low dispersal capability of *A. sarmentosa*, after a forest has been harvested, it may take hundreds of years for lichen abundance to build up to previous old-growth levels (Lesica et al. 1991; Sillett et al. 2000; Botting and Fredeen 2006). The lack of lichen throughout areas where Canada Jays were present would suggest that lichens do not play a significant role in restricting Canada Jays to the subalpine zone. However, Canada Jays tended to occur most frequently near old-growth patches (Fig. 1) where *A. sarmentosa* was abundant. Within these old-growth patches, which were all located in the subalpine zone, the majority of trees with >25% lichen coverage was mountain hemlock whose lower range limit closely coincided with the observed lower limit of Canada Jays. This could imply that Canada Jays must have, at least, some portion of their territory within lichen-rich, old-growth mountain hemlock forest. Detailed information on territory boundaries and (or) areas used for foraging and food storage would be required to support this claim. Furthermore, before any robust conclusions can be made concerning the importance of lichens to Canada Jays on Mount Washington, data are needed on how well epiphytic lichens preserve cached food. We attempted to examine this using the simulated cache chambers, but we encountered methodological problems related to the difficulty of separating lichens from the food items when caches were retrieved several months after they were deployed (for more details see Appendix B).

Despite the lack of evidence on whether lichens play a role in food preservation, our results shed light on how different food types cached by Canada Jays might degrade over time. In general, we found that blueberry caches retained more mass than chicken breast caches. The likely reason for this is that, within fruits, the cuticle is more resistant to microbial degradation than the fleshy interior (Lara et al. 2014), whereas chicken breast is composed of muscle fibre. Accordingly, upon the retrieval of food chambers containing cut-up blueberries, we typically found the cuticle remaining intact in the chamber, which likely contributed to a substantial portion of the final mass. In contrast, upon retrieval of chicken breast, we normally found a fairly small piece of either dehydrated or mouldy chicken. Another difference seen between the two food types was that a high percentage of caches contained no chicken breast at all upon retrieval, especially when they were deployed in the summer, whereas there was always some blueberry present upon retrieval, regardless of the deployment period. Chicken breast was likely consumed or removed from the chamber by invertebrates, or other non-endothermic organisms, such as bacteria or fungi whose metabolic activity is linked to ambient temperature (Wolda 1988). These points of speculation, along with our findings from the experiments, suggest that fleshy fruits, such as blueberries, may be a more dependable cached food source than vertebrate flesh because they are less susceptible to degradation and loss. However vertebrate flesh is likely the higher quality food source (Freeman et al. 2021), which is likely why Canada Jays will readily cache this food type, despite the diminishingly positive effects of doing so.

Although the specific biotic or abiotic factors that ultimately restrict the altitudinal range of Canada Jays on Mount Washington remain unclear, our experimental results suggest that climatic warming will eventually cause the lower elevation limit of Canada Jays to shift upwards. The pace at which this happens will

depend, at least in part, on whether biotic or abiotic factors have a greater effect on maintaining cache quality. If the lower range limit of Canada Jays is primarily restricted by biotic factors, then an upward shift in distribution will be extremely slow given that, even though conditions would no longer be suitable for the regeneration of dominant subalpine tree species at the lower edge of what is now the subalpine zone, it would be decades, if not centuries, before the old trees died out and the lower subalpine, therefore, became unsuitable for Canada Jays. However, if abiotic factors are responsible for setting the lower elevation limit of Canada Jays, then the lower elevation limit may shift at a faster pace as climate becomes more variable and warmer at lower elevations. Since the subalpine zone climatic envelope is predicted to no longer coincide with current subalpine zone vegetation by 2055 (Hamann and Wang 2006), in the near future Canada Jays would no longer be expected, under the abiotic hypothesis, to be found at their present lower elevational limit. In either scenario, the lower elevation limit of Canada Jays is expected to rise in elevation, shrinking the amount of available habitat to Canada Jays, although compensated for, at least in part, by a presumed upward expansion of the subalpine zone into what is now the treeless alpine zone.

In summary, although we did find that Canada Jays were restricted to the subalpine zone, we did not find definitive evidence supporting the hypotheses that temperature or the antimicrobial properties of subalpine tree species or their associated lichens played a role in setting the lower elevation limit of Canada Jays on Mount Washington via their impact on cache quality. However, the widespread planting of both yellow cedar and Amabilis fir may have resulted in extending their lower elevation limit and, therefore, complicating any conclusions on whether tree species limit the distribution of Canada Jays. It may be possible that the lower elevation limit of Canada Jays is set by the antimicrobial properties of yellow cedar or Amabilis fir, but that higher temperatures at lower elevation where these two tree species are abundant could prevent Canada Jays from occupying these areas. Ultimately though, the abiotic or biotic factor that sets the Canada Jay's lower elevation limit remains to be determined. Based on our results related to the effects of temperature on cached food and climate models that predict future conditions will no longer favour the growth of subalpine zone tree species across much of its present range (Hamann and Wang 2006), it is therefore likely that the lower elevation limit of Canada Jays will be increasingly vulnerable to the effects of climate change.

Funding statement

This research was funded by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada to D.R.N.

Acknowledgements

For insights into biogeoclimatic zone classification and additional information on Mount Washington, we thank E. McClaren of the British Columbia Ministry of the Environment and Climate Change Strategy and S. Saunders and H. Klassen of the British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development. We also thank L. Maingon for his help with lichen presence and absence; B. Gates, A. Martell, and C. Hughes for further insights into Canada Jay distribution on Vancouver Island; and TimberWest for allowing us access to their property to conduct our research.

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Appendix A

Experiment to determine if western red cedar slabs could be used to represent living western red cedar trees.

Background

To determine if cache preservation varied by tree species, ideally, we would have found a single site containing the six most common tree species found throughout the subalpine and western hemlock zones. However, we could find no such site, so we conducted a simulated caching experiment at 930 m that had five of the six most common tree species found at Mount Washington present, with western red cedar being the lone exception. As a substitute for living western red cedars, western red cedar slabs, which were sections of lumber that still possessed bark (30 cm × 60 cm), were used. However, how the ability of slabs to preserve cached food compares with that of living western red cedars is unknown.

Methods

To confirm that western red cedar slabs were an appropriate substitute for living trees, we conducted an additional artificial caching experiment at 569 m where western red cedars were common. We deployed two food chambers, one containing blueberry (Supplementary Fig. S1B)¹ and one containing raw chicken breast, on seven red cedar trees and seven slabs on three different occasions: 24–25 July, 7 September, and 22 October; food chambers were retrieved on 5 September, 19 October, and 6 December, respectively. Thus, caches deployed in July were exposed

to the environment for 42–43 days; caches deployed in September were exposed to the environment for 42 days, and caches deployed in October were exposed to the environment for 45 days. Food chambers deployed on western red cedar trees were temporarily fastened to the tree, while food chambers deployed on tree slabs were screwed into the bark of a tree slab that was tied to a randomly selected tree. In total, 84 food chambers were deployed (3 deployment periods × 2 tree substrates [living, slab] × 7 replicates for each substrate/period × 2 food types/replicate) for this experiment. After retrieval, the content of each food chamber was immediately weighed to determine the wet mass.

To examine how the western red cedar substrate influenced per food type (blueberry or chicken), we fitted generalized linear models with Gamma distributions and log link to each food type using the following predictors: (i) tree substrate (western red cedar live tree versus western red cedar slab) and (ii) deployment date (July, September, or October), and (iii) the interaction of substrate × deployment date; we used AIC_c for model selection of all permutations. We included this interaction term because we were interested in examining whether the effect of deployment date on mass loss differed according to substrate. For models in which blueberries were placed in the chamber, the reference value for deployment date was 24–25 July. Chambers containing chicken breast that were deployed in July had a high proportion of food loss, so caches deployed at this time were excluded from analysis. The reference value for deployment date of these models was 5 September.

Results

There was no evidence that the percent mass of food was influenced by substrate type (generalized linear model; blueberry: 85% CI of −0.39, 0.098; chicken: 85% CI of −0.093, 0.29). We used these results as a post hoc justification that western red cedar slabs could be used to represent live western red cedar trees.

Appendix B

Experiment to determine if cache preservation varied with lichen.

Background

In addition to caching perishable food items in trees, Canada Jays have frequently been seen storing food within *Alectoria sarmentosa* (D. Strickland and N.J. Quarrell, personal observation), which is an abundant lichen in old-growth forest of the subalpine zone. Lichens have two properties that make them a potentially useful location for cache placement by Canada Jays. First, various lichen species are known to produce volatile chemicals that have antimicrobial and antifungal properties (Gollapudi et al. 1994; Ranković and Mišić 2007; Çobanoglu et al. 2010) which potentially could prevent food from spoiling for longer periods of time than would otherwise be expected. Second, lichens are a structural suitable location for cache placement, contributing to both concealment from competitors and protection from wind and rain. We examined whether the lower elevation limit of Canada Jays was set by the distribution of epiphytic lichens whose antimicrobial properties preserve cached food items. Following this hypothesis, we predicted that food embedded within lichens would lose less mass than food not embedded in lichens.

Methods

To determine if the presence of lichen affected the mass loss of simulated caches, we investigated if food that is embedded within lichens (*A. sarmentosa*) retained more mass than food that is not embedded in lichens. To examine the effects of lichen on cache preservation, we modified a subset of food chambers ($n = 294$) to have a transparent covering to allow sunlight to reach the lichen and keep it alive (Supplementary Fig. S2).¹ To simulate Canada Jay caches in lichen, approximately 1 g of half a cut-up

blueberry (mean \pm SD from all samples: 1.18 ± 0.08 g) or cut-up raw chicken breast (1.16 ± 0.09 g) was wrapped in lichen and placed in a modified food chamber. We deployed two of these modified food chambers, one containing cut-up blueberry and one containing cut-up raw chicken breast, on all 49 previously placed Engelmann spruce lumber (see "Experiment to determine if cache preservation varied with elevation" section) at the seven experimental sites (see "Study area" section) on three different occasions: 20–22 July, 6–7 September, and 20–22 October; food chambers were retrieved on 3–4 September, 18 October, and 4–5 December, respectively. Thus, caches deployed in July were exposed to the environment for 43–46 days, caches deployed

in September were exposed to the environment for 41 – 42 days, and caches deployed in October were exposed to the environment for 44–45 days. In total, 294 food chambers were deployed (3 deployment periods \times 7 experimental sites/period \times 7 boards/site per period \times 2 food types/board) for this experiment. However, upon the retrieval of the modified food chambers, the blueberry and chicken breast could not be separated from the lichen. Since some of the food remained embedded within the lichen and the initial mass of lichen was never weighed, the final mass of all lichen-embedded food items was underestimated. Because of this, no further analyses were conducted with this datum.