

Linking the availability of cached food to climate change: an experimental test of the hoard-rot hypothesis

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Abstract: Understanding how long-term changes in climate influence populations requires knowledge of the mechanisms by which climate influences individual success and population abundance. We explored the implications of warmer falls and winters on a nonmigratory, food-caching bird, the Gray Jay (*Perisoreus canadensis* (L., 1766)), in Algonquin Park, Ontario, by experimentally examining the influence of temperature on the caloric content and mass of simulated cached food. Using three sites in, north of, and south of Algonquin, we examined the hypothesis that warmer temperatures would negatively influence the preservation of cached food by accelerating decay. Food cached at the highest latitude site retained the greatest mass and caloric content over 180 days of exposure, but there was no difference between the intermediate and the low latitude sites. We also show that Algonquin experienced a winter climate similar to our northernmost site as recently as 1990, and our results suggest that food availability in Algonquin has likely decreased since then, due to a warming climate. Interestingly, this coincides with a decline in territory occupancy by Gray Jays in Algonquin. Our results point to a unique mechanism by which climate warming may influence the persistence of a boreal species through its influence on winter food availability.

Key words: *Perisoreus canadensis*, Gray Jay, habitat quality, food caching, climate change.

Résumé : La compréhension de l'influence des changements climatiques à long terme sur les populations nécessite une connaissance des mécanismes par lesquels le climat influence le succès individuel et l'abondance des populations. Nous nous sommes penchés sur les conséquences d'automne et d'hivers plus chauds sur un oiseau non migrateur qui cache sa nourriture, le mésangeai du Canada (*Perisoreus canadensis* (L., 1766)) dans le parc Algonquin (Ontario), en examinant de manière expérimentale l'influence de la température sur le contenu calorique et la masse de la nourriture cachée simulée. En nous servant de trois sites, à l'intérieur, au nord et au sud du parc, nous avons vérifié l'hypothèse voulant que des températures plus élevées aient une incidence négative sur la préservation des aliments cachés en accélérant la décomposition. La nourriture cachée au site à la plus grande latitude conservait la plus grande masse et le plus grand contenu calorique durant 180 jours d'exposition, mais il n'y avait aucune différence entre les sites de latitudes intermédiaire et plus faible. Nous démontrons également qu'un climat semblable à celui du site le plus septentrional régnait encore au parc Algonquin en 1990, et nos résultats indiqueraient que la disponibilité de nourriture dans le parc a vraisemblablement diminué depuis en raison du réchauffement climatique. Fait à noter, cela coïncide avec une baisse de l'occupation du territoire par les mésangeais du Canada dans le parc Algonquin. Nos résultats indiquent qu'un mécanisme unique expliquerait l'influence du réchauffement climatique sur la persistance d'une espèce boréale, qui découlerait de l'influence de ce réchauffement sur la disponibilité de nourriture en hiver. [Traduit par la Rédaction]

Mots-clés : *Perisoreus canadensis*, mésangeai du Canada, qualité de l'habitat, dépôt de nourriture en cache, changement climatique.

Introduction

Predicting the effects of climate change on populations requires detailed knowledge of the mechanisms by which long-term changes in the environment can influence individual success (Stevenson and Bryant 2000; Moss et al. 2001; Both et al. 2006). Climate change has been linked to population decline through its influence on the availability of seasonal food resources (Post and Stenseth 1999; Pearce-Higgins et al. 2010) and phenological changes that can lead to a mismatch between timing of reproduction and food abundance (Dunn and Winkler 1999; Both et al. 2006; Møller et al. 2008). Northern and boreal species living at the southern edge of their range could be particularly susceptible to changes in climate because they are typically living on the extreme edge of their environmental tolerance (Thomas and Lennon 1999; Franco et al. 2006). For example, nonmigratory species that

depend on cached food to survive during the winter months may rely on cold environments to preserve their caches and prevent decay (Stuebe and Andersen 1985; Careau et al. 2008; Morrison et al. 2009). In these populations, long-term warming of the environment could limit the availability of winter resources by increasing cache decay (Post and Urban 1993; Inman et al. 2012), which in turn may lead to a decrease in reproductive success (Waite and Strickland 2006) or survival.

Gray Jays (*Perisoreus canadensis* (L., 1766)) are year-round residents of northern coniferous and boreal forests in North America and rely on cached food to provide sustenance during the winter months (Strickland and Ouellet 2011). Among caching birds, Gray Jays are unique in that they hoard exclusively perishable food items, such as berries, fungi, insects, and carrion (Strickland and Ouellet 2011). In Algonquin Park, Ontario, Canada, at the southern edge of their range, a marked population of Gray Jays has been

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declining over the past three decades (Waite and Strickland 2006; Strickland et al. 2011). Waite and Strickland (2006) hypothesized that the cause of this decline was due to warming fall temperatures causing an increase in the rotting of stored food (the “hoard-rot hypothesis”; Waite and Strickland 2006). Although Waite and Strickland (2006) demonstrated a negative correlation between fall temperatures and reproductive success, there is no experimental evidence that higher fall temperatures have a negative impact on the quality or quantity of cached food.

To address the hoard-rot hypothesis, we conducted an experiment by placing and systematically retrieving simulated caches across three latitudes with different fall and winter temperature profiles. Following the hoard-rot hypothesis, we predicted that the quantity (percentage of the original mass remaining) and quality (caloric content) of cached food would be positively related to latitude (i.e., inversely to temperature). In addition to temperature, the availability of suitable caching habitat can also influence cached food preservation (Strickland et al. 2011; Inman et al. 2012). In Gray Jays, experimental evidence suggests that coniferous trees are better able to preserve cached food compared with deciduous species, potentially due to the antimicrobial properties of coniferous bark (Strickland et al. 2011). Gray Jays have higher reproductive success on (Strickland et al. 2011) and higher rates of dispersal into (Norris et al. 2013) habitats with a high proportion of conifers. Thus, we hypothesized that higher temperatures would exacerbate the decay of food on tree species that are already less capable of preserving cached food, such that the influence of tree species on cached food preservation would vary with site. We predicted that the difference in preservation between food cached on coniferous and deciduous species would be greatest at the southernmost site and least pronounced at the northernmost site.

Materials and methods

Field methods

From Sept. 2011 to Mar. 2012, we conducted a simulated caching experiment at three sites in Ontario, Canada, located at different latitudes: Cochrane (49°3'31"N, 81°1'27"W), Algonquin Provincial Park (45°33'9"N, 78°31'49"W), and Guelph (43°32'33"N, 80°16'8"W). Cochrane lies within Canada's boreal region (Power and Gillis 2006) and has abundant Gray Jays (Strickland 2008). Algonquin, 450 km south of Cochrane near the southern edge of the Gray Jay range in Ontario, is our long-term Gray Jay study site. Guelph is located outside of the Gray Jay range to the south (250 km south of Algonquin) and was selected to act as the lowest latitude site. At each site, temperature readings were taken every 2 h over the course of our experiment using iButton Thermochron temperature recorders (Maxim Integrated Products, San Jose, California, USA) placed on trees. Mean temperature each month between Sept.–Mar. varied between sites (repeated-measures ANOVA: $F_{[2,12]} = 30.0$, $p < 0.001$; Fig. 1a), with the mean of the mean temperature each month being higher in Guelph than in Algonquin (Tukey' contrasts for comparison of means: $\beta = 4.21 \pm 0.95$, $z = 7.7$, $p < 0.001$) and higher in Algonquin than in Cochrane ($\beta = 3.11 \pm 0.95$, $z = 3.3$, $p = 0.003$). The three sites also differed in mean fall temperature (defined as the mean of the mean daily temperatures in Oct. and Nov.; $F_{[2,115]} = 1367.7$, $p < 0.001$), which is the “fall temperature” measurement used by Waite and Strickland (2006) in their analysis of the influence of climate warming on reproductive success. The lowest latitude site, Guelph, exhibited a significantly higher mean fall temperature (mean \pm SD: 7.1 ± 0.5 °C) than the intermediate latitude site, Algonquin (4.3 ± 0.3 °C; $t_{[63]} = 28.3$, $p < 0.001$), and mean fall temperature in Algonquin was in turn higher than that in Cochrane (2.6 ± 0.2 °C; $t_{[71]} = 28.0$, $p < 0.001$), the highest latitude site (Fig. 1b).

In Sept. 2011, at each of the three sites, we deployed 6 simulated food caches (Strickland et al. 2011; Figs. 2A–2C and see description

below) on the north face of 45 trees, 15 each of black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), jack pine (*Pinus banksiana* Lamb.), and white birch (*Betula papyrifera* Marshall; also referred to as “paper birch”), for a total of 810 caches (6 caches/tree \times 45 trees/site \times 3 sites). Black spruce was selected because it is one of the most common tree species within Algonquin Park Gray Jay territories (Strickland and Ouellet 2011), and experimental evidence has suggested that raisins cached on this species retained the greatest mass compared with food cached on five other species of coniferous trees (white pine (*Pinus strobus* L.), white spruce (*Picea glauca* (Moench) Voss), red pine (*Pinus resinosa* Aiton), white cedar (*Thuja occidentalis* L.), and balsam fir (*Abies balsamea* (L.) Mill.)) and three deciduous species (species of the aspen genus *Populus* L. (also referred to as cottonwood), sugar maple (*Acer saccharum* Marsh.), and white birch) (Strickland et al. 2011). We chose to also include jack pine in our caching experiment, as it is common in the boreal forest, has a bark structure likely to facilitate food storage by Gray Jays, and was present at all three of our sites. White birch was similarly selected because of its appropriate bark structure, its presence at all three sites, and because it is known to be used, at least on occasion, by Gray Jays for food storage (D. Strickland, unpublished data).

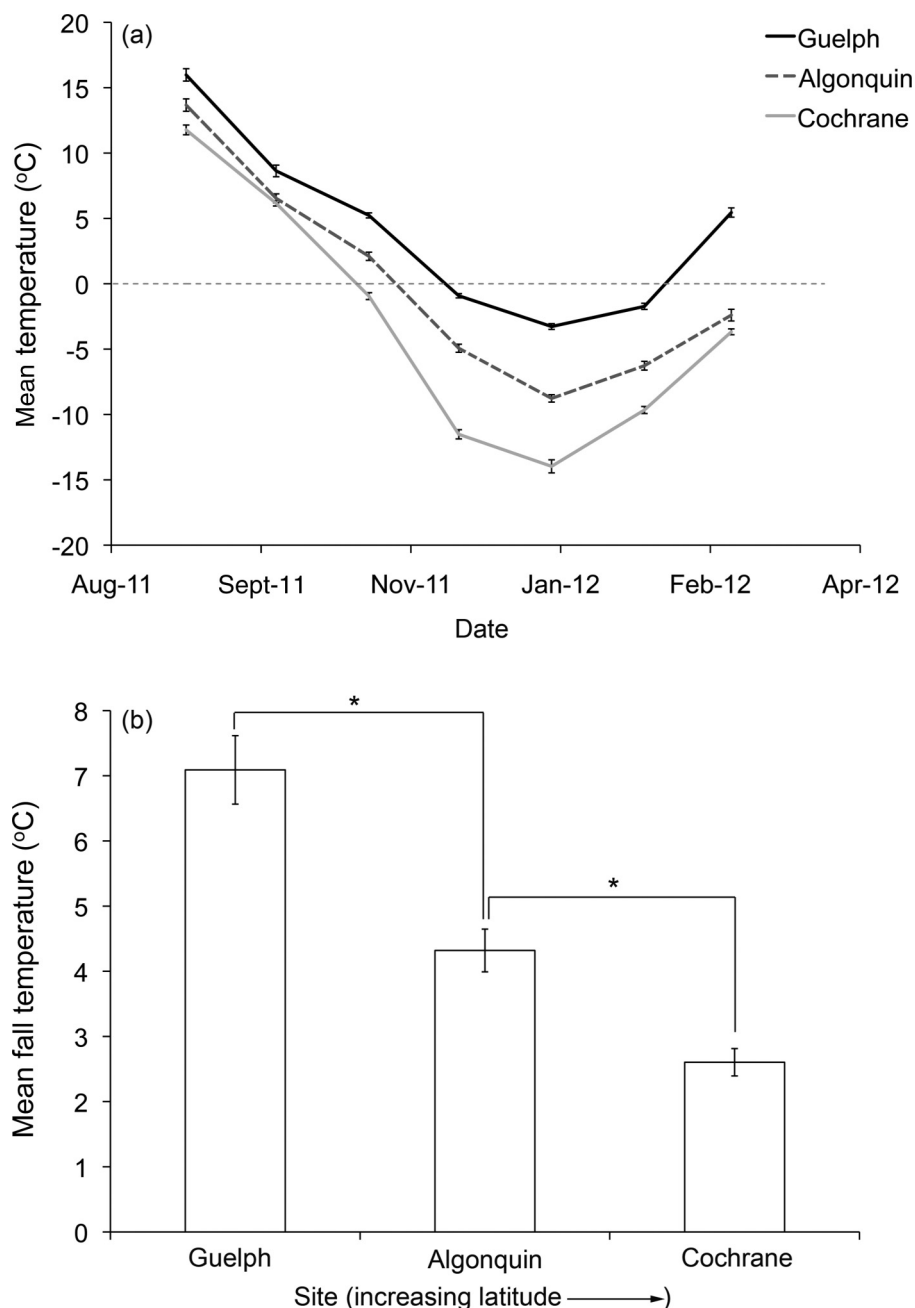
As described in Strickland et al. (2011), each simulated cache consisted of a plastic chamber that contained a hollow well on one side with a small canal that allowed for airborne microbes to enter the chamber but prevented the accumulation of water by acting as a drain. A disc of bark (originating from the same species of tree on which the cache was deployed) was placed in the well of each cache, and then the food item was placed on top of the disc of bark before being affixed to the tree (Fig. 2A). This approach was intended to simulate the way in which Gray Jays wedge food items into bark crevices on trees (Strickland and Ouellet 2011). On each tree, three caches contained one jumbo mealworm (*Tenebrio molitor* L., 1758) each (killed prior to placement in the cache by crushing the head with tweezers) and the other three caches contained three Sultana raisins each (Figs. 2B, 2C). These food items were chosen to represent two common types of food (insects and fruit) that Gray Jays cache in the wild, and have been used in a previous caching experiment (Strickland et al. 2011). Prior to assembling the caches, the food contents of each cache were weighed to the nearest 0.001 g. On average, each mealworm weighed 0.40 ± 0.12 g (mean \pm SD) and the three raisins weighed 0.99 ± 0.16 g.

To simulate jays using the caches throughout the late fall and winter, we retrieved one cache of each food treatment from each tree in mid Nov., mid Jan., and mid Mar. (total number of caches retrieved at each 2-month interval = 270). There was no indication of substantial insect activity in the caches at the end of the caching period. The contents of each cache were weighed to the nearest 0.001 g immediately after retrieval to determine the fresh mass. Cache contents were subsequently freeze-dried and weighed again to determine the dry mass. Freeze-drying the samples served to remove the potentially misleading influence of moisture on mass measurements, as the moisture present in the samples may reflect the environmental conditions at the time of retrieval (i.e., if it had recently rained or snowed) and bias the mass of the sample. Each sample was then heated in a bomb calorimeter (1271 Oxygen Bomb Calorimeter; Parr Instruments, Moline, Illinois, USA) to determine the caloric content (kcal, where 1 cal = 4.18 J).

Statistical analysis

Three-way analysis of variance (ANOVA; type I sum of squares) tests were conducted to determine the effect of site (Guelph, Algonquin, Cochrane), exposure time (60, 120, or 180 days), and tree species (white birch, jack pine, black spruce) on both (i) the freeze-dried mass (percentage of original mass remaining) and (ii) caloric content (kcal) of cached mealworms and raisins. An interaction

Fig. 1. (a) Mean (\pm SD) monthly temperature ($^{\circ}$ C) from Sept. 2011 to Mar. 2012 and (b) mean (\pm SD) fall temperature ($^{\circ}$ C; defined as the mean of mean daily temperatures in Oct. and Nov.; Waite and Strickland 2006) in Guelph, Algonquin, and Cochrane. Asterisks represent significant differences between sites ($\alpha = 0.05$) based on Tukey's honest significant difference (HSD) tests.



between site and tree species was included in all four models to investigate the hypothesis that the influence of tree species on decay of cached food varied with site (i.e., with temperature). Also in all four models, an interaction between exposure time and tree species was included to account for the fact that the rate of cache decay may vary between tree species. In the analyses of raisins (both mass and caloric content), the response variable was log-transformed owing to skew in the data, which improved normality. Following the ANOVA models, Tukey's honest significant difference (HSD) tests were carried out to assess significant differences between sites, exposure times, and tree species. All analyses were conducted in R version 2.12.0 (R Development Core Team 2010).

Results

For raisins, the models with site, exposure time, tree species, and interactions between tree species and site and between tree species and exposure time explained 39% of the variation in freeze-dried mass remaining and 32% of the variation in caloric content (Table 1). For mealworms, the models with the same factors explained 38% of the variation in the freeze-dried mass remaining and 14% of the variation in caloric content (Table 1).

Site

Site was a strong predictor of both mass remaining and caloric content in raisins and mealworms (Table 1; Figs. 3a–3d). At the end of the 180-day period, mealworms cached at Cochrane retained a

Fig. 2. Example of the experimental set-up showing (A) cache placement on a tree, and cache chambers containing (B) a mealworm (*Tenebrio molitor*) and (C) three raisins. Figure appears in colour on the Web.



significantly greater percentage of their initial mass than those cached in Algonquin or Guelph (Fig. 3a; Supplementary Table S1¹). Raisins also retained a significantly greater mass in Cochrane compared with those in Algonquin or Guelph (Fig. 3b; Supplementary Table S1¹). There was no significant difference between the freeze-dried mass of mealworms or raisins stored in Algonquin and Guelph (Figs. 3a, 3b; Supplementary Table S1¹). Similarly, caloric content of mealworms and raisins cached in Cochrane was significantly higher than in those cached in Algonquin (Supplementary Table S1¹) and Guelph (Figs. 3c, 3d; Supplementary Table S1¹). However, we found no significant difference in caloric content remaining between mealworms or between raisins cached in Algonquin and Guelph (Figs. 3c, 3d; Supplementary Table S1¹).

Exposure time

Freeze-dried mass in both mealworms and raisins also significantly declined with increasing exposure time (Table 1; Figs. 4a–4d). Mealworm mass declined between 60 and 120 days of exposure, but did not continue to decline after 120 days of exposure (Fig. 4a; Supplementary Table S1¹). Raisin mass declined across the 180 days of exposure, and raisins lost mass more slowly than mealworms, as indicated by significant differences in raisin mass remaining between 60 and 120 days of exposure and between 120 and 180 days of exposure (Fig. 4b; Supplementary Table S1¹). The caloric content of raisins also declined over time (Table 1; Fig. 4d), following the same pattern as the decline in raisin mass with significant decreases in caloric content between 60–120 days of exposure and 120–180 days of exposure (Supplementary Table S1¹). However, there was no effect of exposure time on the caloric content of mealworms (Table 1; Fig. 4c).

Tree species

Tree species significantly influenced the mass remaining in both raisins and mealworms over the course of the caching period

(180 days; Table 1). Raisins cached on jack pine retained significantly less of their initial mass than those cached on black spruce or white birch (Supplementary Table S1¹). There was no significant difference in the mass remaining between raisins cached on white birch and raisins cached on black spruce (Supplementary Table S1¹). Mealworm mass did not show as much variation between tree species; the only significant trend was that mealworms cached on jack pine had less mass remaining than those cached on black spruce or white birch (Supplementary Table S1¹). Caloric content in raisins and mealworms varied significantly between tree species in much the same way as mass (Table 1). Similar to the trend seen in mass, raisin caloric content was lowest when cached on jack pine compared with white birch or black spruce (Supplementary Table S1¹), and there was no significant difference in the caloric content remaining between raisins cached on black spruce and raisins cached on white birch (Supplementary Table S1¹). Caloric content of mealworms was significantly lower on jack pine compared with white birch, but caloric content did not differ significantly between mealworms cached on jack pine and black spruce or between white birch and black spruce (Supplementary Table S1¹).

Tree species interaction with site and exposure time

For raisins, there was also a significant interaction between tree species and site in both the mass remaining and caloric content models (Table 1). At Guelph, raisins cached on black spruce retained significantly more mass than those cached on white birch, while there was no significant difference in the mass remaining of raisins cached on white birch and jack pine at this site (Fig. 3b; Supplementary Table S1¹). Caloric content of raisins was also higher on black spruce at Guelph than on white birch (Fig. 3d; Supplementary Table S1¹). In Algonquin, however, mass and caloric content did not differ significantly between raisins cached on black spruce and white birch, while raisins cached on white

¹Supplementary Table S1 is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2015-0016>.

Table 1. Results from analysis of variance (ANOVA) tests examining the influence of site (Guelph, Algonquin, Cochrane), exposure time ("exposure"; 60, 120, 180 days), tree species ("tree"; black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), white birch (*Betula papyrifera*)), and interactions between tree and site and between tree and exposure on the mass remaining ("mass") and caloric content of cached raisins and mealworms (*Tenebrio molitor*).

Response	Predictor	R ²	F	df	p
Raisins					
Mass		0.39	19.2	14, 376	<0.001
	Site		35.9	2, 376	<0.001
	Exposure		41.2	2, 376	<0.001
	Tree		23.2	2, 376	<0.001
	Tree × site		15.6	4, 376	<0.001
	Tree × exposure		1.4	4, 376	0.250
Caloric content		0.32	12.2	14, 313	<0.001
	Site		14.9	2, 313	<0.001
	Exposure		26.6	2, 313	<0.001
	Tree		14.5	2, 313	<0.001
	Tree × site		3.6	4, 313	<0.001
	Tree × exposure		0.8	4, 313	0.531
Mealworms					
Mass		0.38	17	14, 358	<0.001
	Site		93.8	2, 358	<0.001
	Exposure		7	2, 358	0.001
	Tree		9.9	2, 358	<0.001
	Tree × site		2.8	4, 358	0.028
	Tree × exposure		1.2	4, 358	0.306
Caloric content		0.14	4.4	14, 278	<0.001
	Site		35.9	2, 278	<0.001
	Exposure		0.1	2, 278	0.928
	Tree		3.7	2, 278	0.027
	Tree × site		2.1	4, 278	0.078
	Tree × exposure		0.2	4, 278	0.953

Note: Adjusted R² (for whole model results), F values, df (shown as predictor variable df, residual df), and p values based on F values ($\alpha = 0.05$) are reported.

birch retained a greater mass than those cached on jack pine (Fig. 3b) but did not differ in caloric content (Fig. 3d; Supplementary Table S1¹). At Cochrane, the mass and caloric content remaining was higher in raisins cached on white birch than those cached on black spruce and jack pine (Figs. 3b, 3d; Supplementary Table S1¹). Mealworm mass was also influenced by the tree species × site interaction, but showed less variation than raisins (Table 1). The only significant trend between coniferous and deciduous tree species revealed that mealworms cached on jack pine retained less mass than those cached on white birch or black spruce at Guelph, while the three species did not differ in Algonquin or Cochrane (Supplementary Table S1).¹ There was no significant effect of the site × tree species interaction on the caloric content of mealworms (Table 1; Fig. 3c).

Finally, there was no significant effect of an exposure time × tree species interaction for mass or caloric content of either mealworms (Table 1; Figs. 4a, 4c) or raisins (Table 1; Figs. 4b, 4d), indicating that the rate of cache decay did not differ between tree species.

Discussion

Our findings provide some experimental evidence that climate likely plays a role in the decay of cached food, suggesting that long-term changes in climate may have a negative impact on species that cache perishable food, particularly at the southern edge of their range (Waite and Strickland 2006; Inman et al. 2012). At the end of the 5-month simulated caching period, food cached at our high latitude site, Cochrane, had a higher quality (0.2–0.3 kcal higher; measured as caloric content) and a higher quantity (10%–15% higher; measured as percentage of original mass remaining) compared with either the site at the southern edge of the Gray Jay

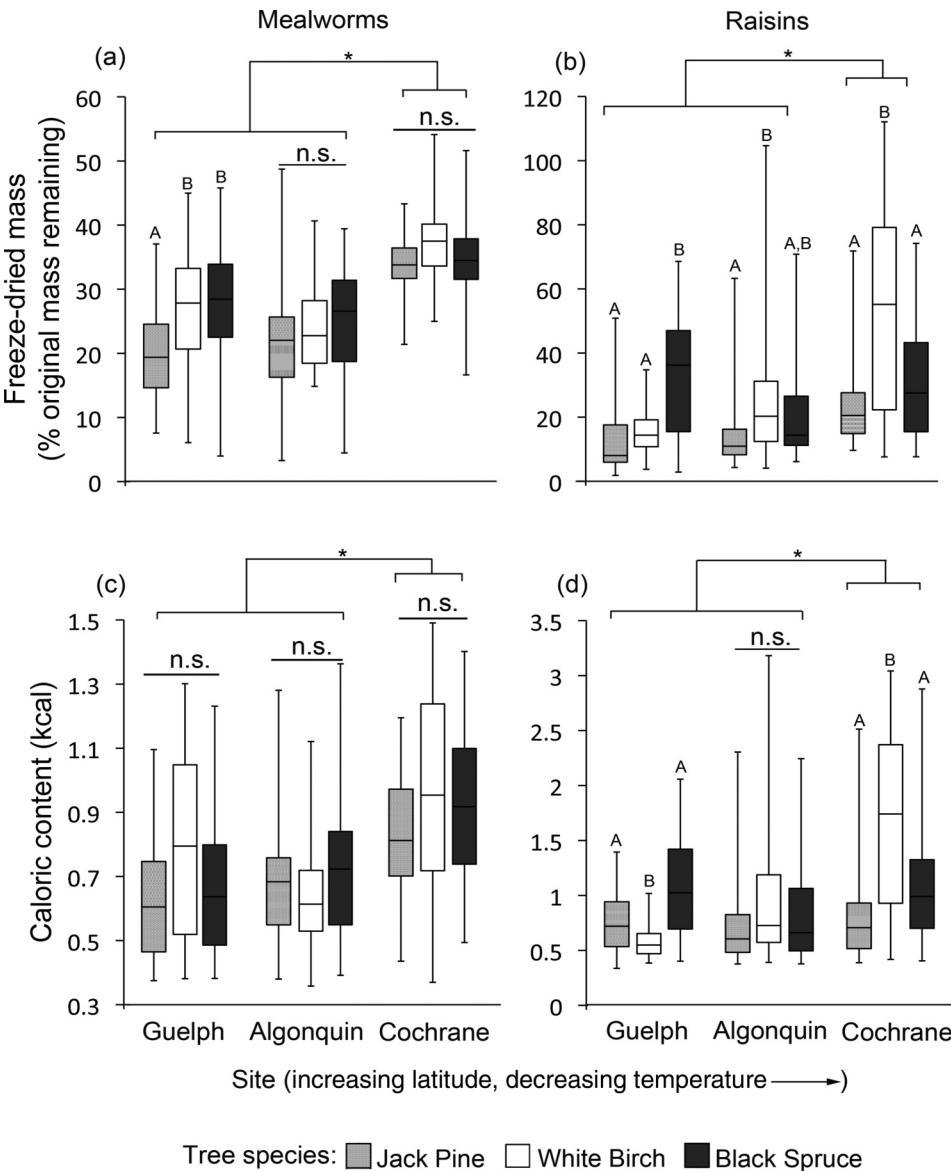
range, Algonquin, or the southernmost site, Guelph, which is outside of the Gray Jay range. These three sites likely vary in environmental and climatic factors other than temperature alone, as we discuss below, but by keeping the tree and cache treatments consistent between sites, we have attempted to isolate the influence of climate, specifically temperature. In addition, carrying out our experiment in the true fall and winter conditions experienced at these different latitudes, as opposed to imposing temperature treatments within a site, provides insight into the potential factors influencing the distributional boundaries for Gray Jays.

Based on these results, we can make some inferences about the historical winter food supply for Gray Jays in Algonquin Park. With a 7-year extension of the temperature–time series used by Waite and Strickland (2006), there is strong evidence that mean fall temperature over the last 35 years in Algonquin Park has been increasing (linear model: $\beta = 0.06 \pm 0.02$; $t_{[34]} = 2.9$, $p = 0.006$; Fig. 5a). From this linear model, we estimated that the current mean fall temperature in Cochrane (2.6 °C) could have been observed in Algonquin as recently as 1990 (Fig. 5a). Extrapolating linearly from the differences in cached food we found between Cochrane and Algonquin at the end of our experiment, our results suggest that mean mass and caloric content of caches may have declined by 10%–15% and 0.2–0.3 kcal, respectively, over the last 23 years (1990–2012). Of course, this is a crude estimate because it is not based on historical cached food data from Algonquin Park. Nevertheless, it does provide some indication that the quality and quantity of cached food for Gray Jays in Algonquin may have declined in the recent past due to changes in climate, and, interestingly, coincides with a general decline in the occupancy of low-quality territories by Gray Jays within Algonquin (Fig. 5b; see below for discussion).

A second result from our experiment that provides some insight into current versus past conditions in Algonquin Park is the interaction between site and tree species. We found that mass of cached raisins was higher on black spruce than on white birch and that caloric content of raisins was higher on both jack pine and black spruce than on white birch at Guelph, which supports the hypothesis that coniferous trees are better able to preserve cached food at warm temperatures (low latitudes) than deciduous trees. Recent work has shown that variation in habitat quality is, at least in part, driven by the proportion of coniferous trees on territories because they are better able to store food than deciduous trees (Strickland et al. 2011). Interestingly, in contrast to the results in Strickland et al. (2011), coniferous species included in our study did not show an increased capacity to preserve cached food overall compared with the deciduous species. One possible reason for this could stem from the fact that Strickland et al.'s (2011) experiment took place during June–Nov. while ours took place during Sept.–Mar. Since our findings indicate that deciduous species exhibit a decreased capacity for preservation at warmer temperatures, it is possible that the high degree of disparity in cached food preservation observed by Strickland et al. (2011) can be explained by the fact that their experiment was carried out in warmer ambient temperatures than our current study.

On the other hand, our experiment investigated cached food preservation on only one species of deciduous tree, while Strickland et al.'s (2011) study included a more comprehensive collection of the deciduous species found within Gray Jay territories. As such, our results may not accurately represent the capacity of deciduous-dominated territories to preserve food, which underlines the need for further experiments to examine factors causing differences in cached food preservation between tree species. Despite differences in our and Strickland et al.'s (2011) findings, the hypothesis that variation in habitat quality is influenced by the proportion of conifers on territories is supported by evidence of lower reproductive success on (Strickland et al. 2011) and

Fig. 3. Freeze-dried mass (% original mass remaining) of (a) mealworms (*Tenebrio molitor*) and (b) raisins, and caloric content (kcal, where 1 cal = 4.18 J) of (c) mealworms and (d) raisins cached on three tree species (black spruce (*Picea mariana*), white birch (*Betula papyrifera*), jack pine (*Pinus banksiana*)) across a latitudinal gradient in Ontario at the end of 180 days of exposure. Box plots represent median and 1st and 3rd quartiles. Error bars denote maximum and minimum observations within each category. Asterisks represent significant differences between sites ($\alpha = 0.05$) based on an ANOVA model; upercased letters denote significant within-site differences between tree species based on Tukey's honest significant difference (HSD) tests ($\alpha = 0.05$); "n.s." signifies nonsignificant differences.

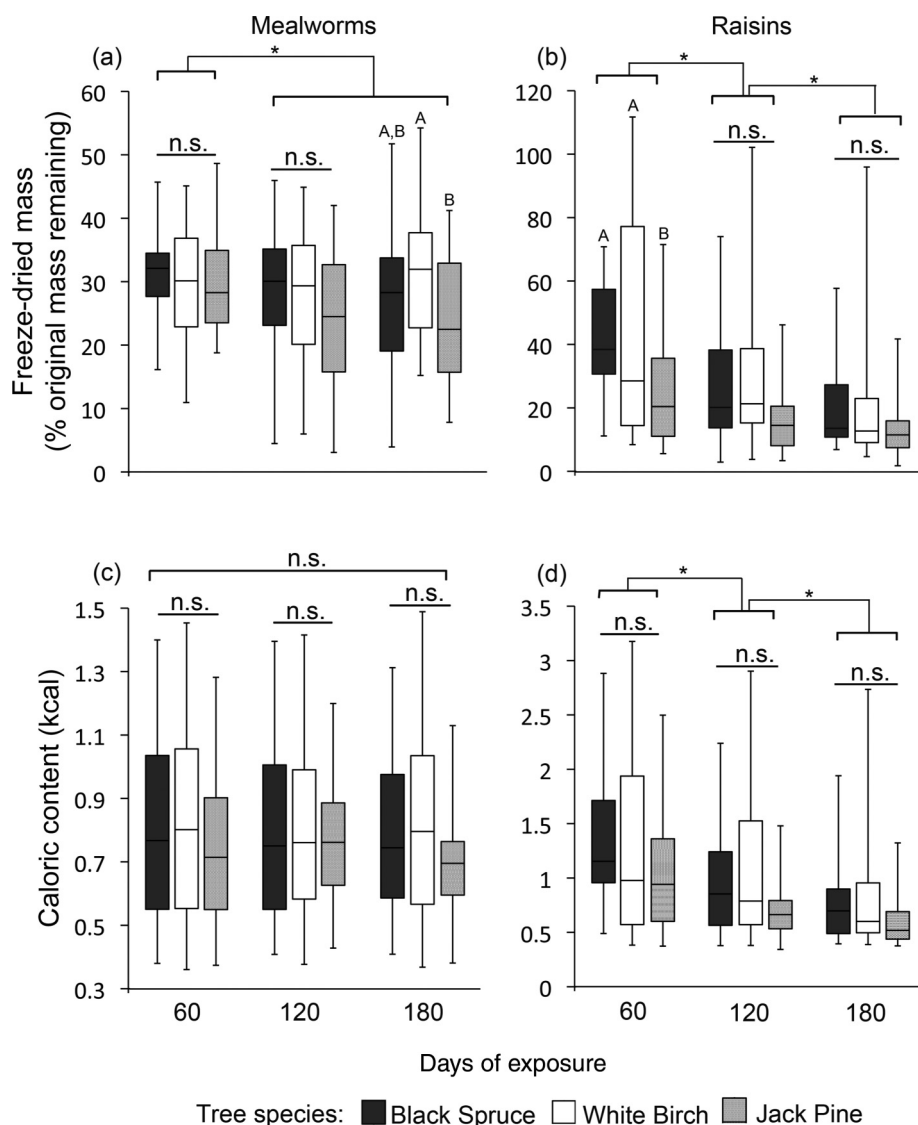


lower dispersal rates into (Norris et al. 2013) deciduous-dominated territories compared with coniferous-dominated territories. Not surprisingly, the decline of the Algonquin Gray Jay population appears to be primarily driven by a sharp drop in the occupancy of territories with a high percentage of deciduous trees (Fig. 5b; Strickland et al. 2011). For example, in 1990, when our long-term models suggest that Algonquin's fall climate resembled that of Cochrane, 47% of low-quality territories were occupied compared with the 7% currently occupied (Fig. 5b). Although declines in territory occupancy may be due to demographic processes that affect both high- and low-quality territories, the result of our experiment suggests a potential mechanism for the increased decline in low-quality territories, if the negative effect of warmer temperatures is more pronounced in deciduous tree species.

Although our work implies that there has been a decline in cached food in Algonquin over the past two decades, our experi-

mental results also suggest that further warming, at least to temperatures that currently occur 250 km south of the Gray Jay range in Ontario, may have little influence on cached food. We found no difference in the quality and quantity of cached food between Algonquin and Guelph despite the fact that the magnitude of the differences in mean monthly temperatures between these two sites was similar to the temperature differences between Algonquin and Cochrane (Figs. 1a, 1b). This lack of difference could imply that there is a threshold temperature for preservation. Zero degrees Celsius is known to be a threshold level for the decay of organic material (Carreiro and Koske 1992; Mikan et al. 2002; Sjørnsen et al. 2005), as freezing facilitates preservation by reducing decomposer activity. However, it is possible that an additional threshold exists that may explain the pattern that we observed. Sulkava and Huhta (2003) demonstrated that hard frost events, where temperatures reached -16°C , halted virtually all decom-

Fig. 4. Freeze-dried mass (% original mass remaining) of (a) mealworms (*Tenebrio molitor*) and (b) raisins, and changes in the caloric content (kcal, where 1 cal = 4.18 J) of (c) mealworms and (d) raisins cached on three tree species (black spruce (*Picea mariana*), white birch (*Betula papyrifera*), jack pine (*Pinus banksiana*)) over 180 days of exposure. Box plots represent median and 1st and 3rd quartiles. Error bars denote maximum and minimum observations within each category. Asterisks represent significant differences between exposure times ($\alpha = 0.05$) based on ANOVA; uppercased letters denote significant within-exposure differences between tree species based on Tukey's honest significant difference (HSD) tests ($\alpha = 0.05$); "n.s." signifies nonsignificant differences.

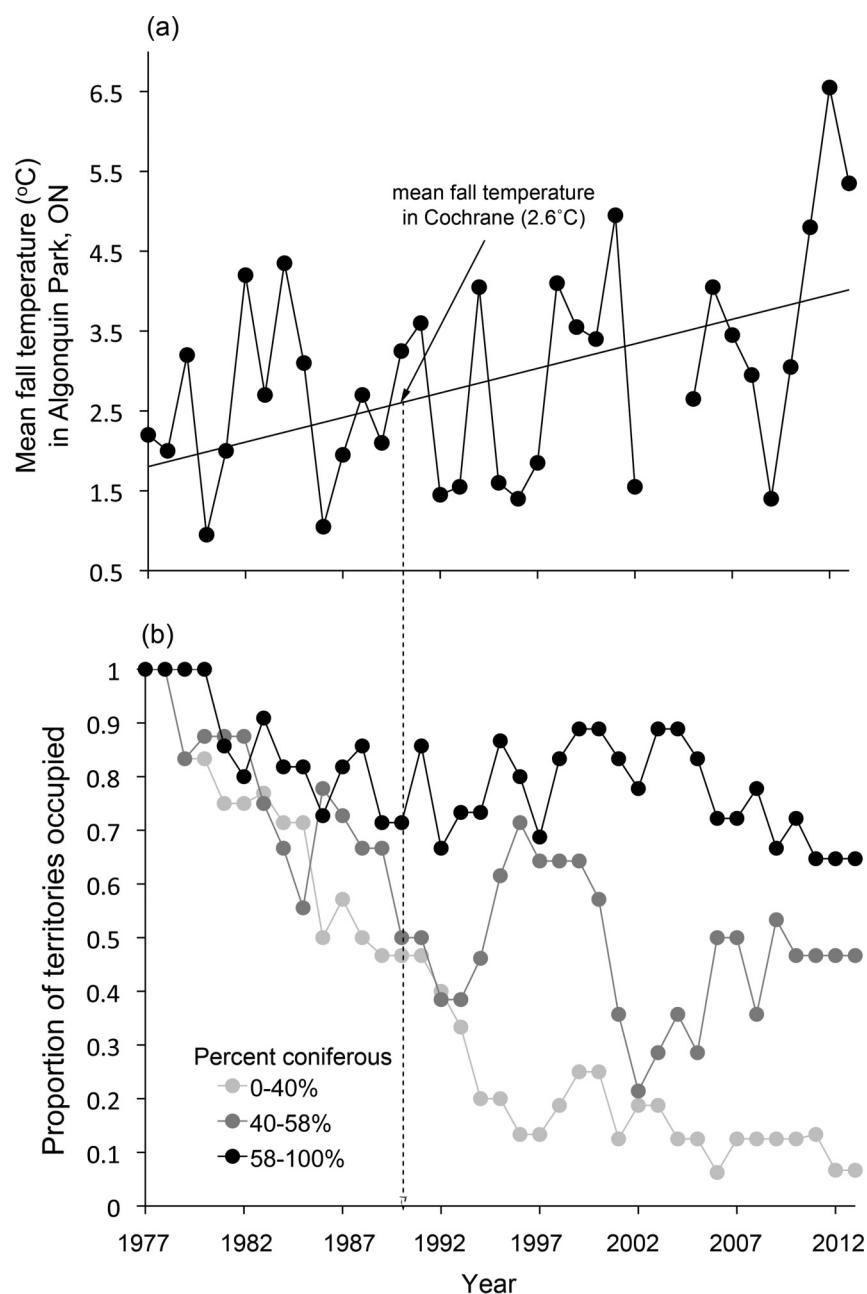


poser activity, while shallow freezing (-2°C) did not. In our experiment, mean monthly air temperatures in Cochrane reached -10 to -15°C during Dec.–Feb., while the coldest mean monthly temperature in Algonquin, recorded in January, did not go below -9°C (Figs. 1a, 1b) and mean monthly temperature in Guelph never fell below -5°C , indicating that only shallow frosts were consistently experienced at these sites (Figs. 1a, 1b). Thus, a “deep freeze” may be required to preserve a high percentage of cached food. The presence of a temperature threshold implies that Algonquin may already be experiencing conditions that are only minimally adequate for cached food preservation. It is possible that the level of decay in Algonquin would be maintained if conditions continued to warm to the level currently experienced at Guelph and may not change until mean monthly temperatures reach above 0°C regularly throughout the winter. Additional experimental work is needed to examine this “deep freeze” threshold hypothesis.

In addition to the environmental conditions, it is important to consider how different types of food might degrade over time and

how this might interact with a warming environment. In general, we found that raisins decayed more slowly than mealworms. This could be due to the fact that insects may initially decay very quickly if they are not frozen immediately, since the nonchitinous parts of arthropods are especially prone to rot (Baas et al. 1995). Because of this, warmer falls may particularly accelerate the decay of cached insects and cause these sources of winter food to become unreliable for Gray Jays. Our findings suggest that dried berries may be more dependable because they are less susceptible than insects to decomposition once they desiccate (Pitt and Hocking 2009). We also show that the mass of cached raisins and mealworms covaried closely with their caloric content, which suggests that the mass of these food sources can potentially be used as a proxy for the energy available to Gray Jays from them. However, it is possible that our results provide overestimates of the food energy available from arthropods in particular. For example, observations have suggested that Gray Jays cannot efficiently digest chitin (D. Strickland, unpublished data; chitin digestion in birds

Fig. 5. (a) Trend in mean fall temperature (mean of mean daily temperatures in Oct. and Nov.; updated from [Waite and Strickland 2006](#) with 7 additional years (2007–2013)) between 1977 and 2013 showing a significant increase over time. Line indicates linear best fit. Arrow indicates the current mean fall temperature in Cochrane (2.6 °C), which occurred in Algonquin in 1990 according to linear best fit. (b) Proportion of territories occupied between 1977 and 2013 in Algonquin Park, Ontario (ON), separated by territory quality (percent coniferous; updated from [Strickland et al. 2011](#) with 2 additional years (2012–2013)). Dotted vertical line indicates the proportion of territories occupied during 1990, when the line-of-best fit suggests that Algonquin mean fall temperature resembled Cochrane's current mean fall temperature.



generally ranges from 10% to 60%: [Weiser et al. 1997](#)), while the energy measurements of mealworms in our experiment included the caloric content of the exoskeleton. Berries and fruits, on the other hand, may retain a greater proportion of useful energy over winter, because calorie-rich sugars are concentrated in these items when they desiccate ([Pitt and Hocking 2009](#)). If, as our results imply, the nonchitinous, energy-rich parts of insects decay more quickly than fruit or berries, these latter foods might be a more reliable source of energy as warmer temperatures cause decay to accelerate.

In conclusion, our results point to a novel mechanism by which climate may be influencing Gray Jay populations at the southern

edge of their range. As fall and winter temperatures continue to rise in Algonquin, it is possible that the park may become unsuitable for Gray Jays due to an increased rate of cached food decay. However, as our results suggest, the decay of cached food might not increase further in Algonquin until an additional climate threshold, such as 0 °C, is surpassed. Furthermore, we provide evidence that the capacity of deciduous tree species to preserve food may decline as temperatures increase, which could also have negative implications for Gray Jays inhabiting the southern edge of their range. Although a range shift has not yet been noted in this species, the fact that territories with low conifers are increasingly unoccupied in Algonquin indicates that the southern

range edge of these birds may be defined by the availability of winter food.

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