

**Demographic and Environmental Drivers of Canada Jay Population
Dynamics in Algonquin Provincial Park, ON**

by

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ABSTRACT

Demographic and Environmental Drivers of Canada Jay Population Dynamics in Algonquin
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Knowledge of the demographic and environmental drivers of population growth throughout the annual cycle is essential to understand ongoing population change and forecast future population trends. Resident species have developed a suite of behavioural and physiological adaptations that allow them to persist in seasonal environments. Food-caching is one widespread behavioural mechanism that involves the deferred consumption of a food item and special handling to conserve it for future use. However, once a food item is stored, it can be exposed to environmental conditions that can either degrade or preserve its quality. In this thesis, I combine a novel framework that identifies relevant environmental conditions that could cause cached food to degrade over time with detailed long-term demographic data collected for a food-caching passerine, the Canada jay (*Perisoreus canadensis*), in Algonquin Provincial Park, ON. In my first chapter, I develop a framework proposing that the degree of a caching species' susceptibility to climate change depends primarily on the duration of storage and the perishability of food stored. I then summarize information from the field of food science to identify relevant climatic variables that could cause cached food to degrade. In my second chapter, I used 40 years of Canada jay reproductive performance data to understand how environmental conditions during the food storage period can carry over to influence brood size, nest success and nestling

condition. I found evidence that fall freeze-thaw events, and, to a lesser degree, winter temperatures negatively influence all metrics of reproductive performance. In my third chapter, I investigated the effect of density and environmental conditions throughout the annual cycle on population growth. Fecundity was the primary vital rate driving variation in population growth and fall conditions had a strong indirect effect, acting primarily through fecundity, on population growth. In my fourth chapter, I investigated the mechanisms promoting density-dependent fecundity. I found evidence that site-dependent regulation is acting on fecundity, but only when environmental conditions are otherwise poor for breeding. Together my thesis highlights the importance of understanding how events throughout the annual cycle are connected and how such connections can, in turn, contribute to predicting population dynamics.

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1 General Introduction

The central challenge of population ecology is to understand the factors that drive changes in abundance over time (Murdoch 1994, Betini et al. 2015). At the most basic level, population growth can be considered a function of four primary vital rates: immigration, emigration, survival and fecundity (Murdoch 1994, Sibly and Hone 2002) and it is well documented that vital rates can vary in their relative contribution towards driving changes in abundance over time (Wisdom et al. 2000, Taylor et al. 2012, Wilson et al. 2016). In long-lived species, adult survival typically has the greatest influence on population growth (Doak et al. 1994, Franklin et al. 2000, Wisdom et al. 2000, Wilson et al. 2016), while the abundance of short-lived species tends to be driven by fecundity (Franco and Silvertown 1996, Heppell et al. 2000, Sæther and Bakke 2000). Though several studies have provided evidence that dominant vital rates can be, at least, partly explained by differences in species life-history, dominant vital rates are not always the same among similar species (Sæther and Bakke 2000) and may also change over time within a population (Villellas et al. 2013, 2015). Knowledge of the relative contribution of vital rates is therefore important because it can help guide research aimed at understanding the primary external (environmental) factors driving population growth. For example, while severe cold temperatures and increases in snow depth have a strong negative influence on the survival of neonatal elk (*Cervus elaphus*; Griffin et al. 2011), neonatal survival contributed relatively little to variation in population growth compared to the contribution of adult female survival (Eacker et al. 2017). Further, in Eurasian oystercatchers (*Haematopus ostralegus*) increasing mean winter temperatures negatively influence fecundity, but had a relatively small effect on population growth due to strong contribution of adult survival (Van De Pol et al. 2010).

The challenge for understanding the factors that influence population growth is further complicated by the fact that our understanding of the ecology of most organisms is limited to specific periods of the annual cycle (Hostetler et al. 2015, Rushing et al. 2016). While research may frequently be conducted during important periods of the year, such as breeding, it often fails to capture periods that may be critical for understanding population growth (Sillett et al. 2000, Calvert et al. 2009, Marra et al. 2015). For example, breeding populations of wandering albatross (*Diomedea exulans*) were monitored for 20 years and experienced dramatic declines for six years of the study (Weimerskirch and Jouventin 1987). However, as events outside of the breeding period were not monitored, the key vital rates and external conditions driving this decline could not be identified and rigorously tested, resulting only in speculation about potential mechanisms. Thus, without a full annual cycle approach towards determining what drives population dynamics, we may often fail to either estimate a key vital rate or fail to measure a key environmental variable linked to that vital rate (Adahl et al. 2006).

Examining the full annual cycle of an organism also provides the ability to examine how events in one period could carry over to influence individuals and potentially population growth in a subsequent period (Betini et al. 2013, Morrison et al. 2013, Marra et al. 2015). Such non-lethal carry-over effects have been documented in a number of taxa and, in some cases, have been shown to have an impact on fitness (reviewed by Harrison et al. 2011). Laboratory experiments have shown, in a few specific instances, that carry-over effects can also have important consequences at the population level, such as decreasing long-term stability (Betini et al. 2013, 2014) and increasing the probability of extinction (Elliot et al. 2017).

Climatic conditions, by acting on individual vital rates, regulate population dynamics through a number of different mechanisms (Coulson et al. 2001, Benton et al. 2006, Frederiksen et al. 2013, Kanno et al. 2015). Most often, climatic conditions act on vital rates such as fecundity and survival, by augmenting resource availability (e.g. food; Sillett et al. 2000, Nilsson et al. 2011, Townsend et al. 2016) or by exceeding the physiological tolerance of a species, which decreases survival (Beever et al. 2010, Cahill et al. 2012, Isaak and Rieman 2013). Multiple climate variables can also act additively to dampen effects of a single variable on population growth. For example, volcanic ashfall reduced survival in Montserrat orioles (*Icterus oberi*), but the negative effect of ashfall on population growth was dampened by the positive effect of pre-breeding rainfall on fecundity (Oppel et al. 2014). This relationship can be further complicated by the possibility that multiple vital rates could be influenced by a single climate variable, sometimes with counteracting effects (Zani 2008, Pfeifer-Meister et al. 2013). Temperature, for example, was found to increase growth and seed production of prairie plant species, but negatively influenced recruitment of those same species (Pfeifer-Meister et al. 2013). In order to develop a mechanistic understanding of population dynamics, it is imperative to consider the relative contribution of vital rates to population growth and the factors that contribute to their variation over time (Schaub et al. 2013).

One major gap in our understanding of how climate change is influencing species is that most studies do not identify or rigorously test proximate mechanisms linking climate to fitness and vital rates (Cahill et al. 2012). The identification of proximate mechanisms allow predictive models to be built, allowing for the estimation of future population declines under different climate scenarios and the development of conservation initiatives. For example, *Aloe dichotoma*,

a desert tree, is sensitive to reductions in precipitation, which cause desiccation (Foden et al. 2007). Building on climate models for the range of *A. dichotoma* (Hulme et al. 2001), Foden et al. (2007) were able to predict future range reductions and areas of the range that would be particularly susceptible to climate change due to decreases in precipitation. Further, there are relatively few examples of climate-induced population declines that show a straightforward relationship between population declines and a single climate variable (e.g. temperature; Cahill et al. 2012). Instead, abiotic conditions often influence the strength of biotic interactions (e.g. competition for resources; Pearce-Higgins et al. 2010). In these cases, it is imperative to identify the proximate causes driving the relationships between climate and population growth in order to predict future population trends. For instance, warmer winter temperatures promote increases in fecundity of white-throated dippers (*Cinclus cinclus*), leading to increased population growth (Gamelon et al. 2017). However, this increase in population abundance also increases the strength of competitive interactions and leads to density-dependent regulation of the population through limited access to breeding territories and food (Nilsson et al. 2011, Gamelon et al. 2017).

In this thesis, I address the question of how climate may influence individual vital rates and population dynamics of food caching species by developing a predictive framework and applying this framework to long-term population study of Canada jays (*Perisoreus canadensis*) in Algonquin Provincial Park, ON. I conducted four studies to contribute to our understanding of how food caching species may be influenced by climate change and the demographic and climatic drivers of an observed population decline of Canada jays at the southern edge of their range. In chapter 1, I conducted a literature review and synthesis exploring how knowledge from the field of food science can be applied to understand how climate may influence food quality in

food caching species. In doing so, I provide a general framework to predict the degree of susceptibility of all food caching species to climate change. In chapter 2, I apply this general framework to long-term records of Canada jay reproductive performance in Algonquin Provincial Park, ON (APP) to understand how environmental conditions acting on food cached in the late summer and fall can carry-over to negatively influence breeding success, brood size and nestling condition. In chapter 3, I use long-term demographic data of Canada jays in APP and an integrated population model to identify the relative influence of vital rates on population growth and the indirect effects of climate, acting through vital rates, on population growth. In chapter 4, I investigate the mechanisms promoting density-dependent fecundity of Canada jays in APP using long-term fecundity and territory occupancy data.

Collectively, my thesis research identifies the climatic and demographic drivers of an observed population decline of Canada jays at the southern edge of their range. My research also provides insight into the proximate mechanisms linking climate change and population vital rates and how climate change can modulate the strength of density-dependent relationships with implications for how wild populations are regulated.

Chapter publications and author contributions

Chapter 1 is published in *Climate Change Responses* (Sutton, A. O., Strickland, D., Norris, D. R. 2016. Food storage in a changing world: implications of climate change for food-caching species. *Climate Change Responses* 3:12) and was co-authored by Dan Strickland and D. Ryan Norris. AOS, DS and DRN conceived of the paper and contributed to drafting the manuscript.

Chapters 2 – 4 incorporate data from a long-term study of Canada jays in Algonquin Provincial Park, ON. Russ Rutter initiated the study in 1964 and, beginning in the early 1970's, Dan Strickland led the study and expanded the study area. Ryan Norris has co-led the project since 2009. Countless volunteers, field assistants, and several graduate students have contributed to data collection since the beginning of the study.

Chapter 2 is published in *Royal Society Open Science* and was co-authored by Dan Strickland, Nikole E. Freeman, Amy E. M. Newman and D. Ryan Norris. All authors contributed to data collection and drafting of the manuscript. AOS, DRN and DS conceived of the study and AOS carried out the statistical analyses.

Chapter 3 has been revised and resubmitted to *Proceedings of the Royal Society B* and was co-authored by Dan Strickland, Nikole E. Freeman, Marjorie C. Sorensen and D. Ryan Norris. AOS and DRN conceived of the study. AOS, NEF and MCS conducted the field caching experiment. AOS conducted statistical analyses and wrote the initial draft of the manuscript. All authors provided comments and feedback on the manuscript.

Chapter 4 is under review in *Ecology* and was co-authored by Dan Strickland, Nikole E. Freeman and D. Ryan Norris. AOS and DRN conceived of the study and AOS conducted all

statistical analyses. AOS wrote the manuscript with feedback from DRN and DS. All authors provided comments and feedback on the manuscript.

2 Chapter 1 - Food storage in a changing world: implications of climate change for food-caching species

2.1 Abstract

Food caching is a behavioural strategy used by a wide range of animals to store food for future use. When food is stored, it is susceptible to environmental conditions that can lead to spoilage via microbial proliferation or physical and chemical processes. Given that the nutrition gained from consuming cached food will almost always be less than consuming it immediately upon capture, the degree of degradation will play a central role in determining the ecological threshold at which caching is no longer profitable. Our framework proposes that the degree of susceptibility among caching species is based primarily on the duration of storage, and the perishability of stored food. We first summarize the degree of susceptibility of 203 vertebrate caching species. Thirty-eight percent (38%) of these species are long-term cachers (>10 days) but only 2% are both long-term cachers and store highly perishable food. We then integrate insights from the fields of applied food science and plant biology to outline potential mechanisms by which climate change may influence food-caching species. Four climatic factors (temperature, number of freeze-thaw events, deep-freeze events and humidity) have been shown to affect the degradation of food consumed by humans and are also expected to influence the quality of perishable food cached in the wild. Temperature and moisture are likely important factors influencing seemingly nonperishable seeds. Although we are able to provide broad classifications for caching species at risk of climate change, an improved understanding of how

environmental conditions affect the quality and persistence of cached food may allow us to better predict the impact of changing climatic conditions on the fitness of food-caching animals.

2.2 Introduction

Evidence suggests that climate change is influencing a wide range of biological phenomena, including species distributions (Easterling et al. 2000, Hughes 2000, McCarty 2001), population abundance (Gibbons et al. 2000, Grøtan et al. 2009), and rates of extinction (Carpenter et al. 2008, Keith et al. 2008). Such studies provide important documentation of the potentially serious impacts of climate change on natural systems but, with few exceptions (e.g. Both et al. 2006, Waite and Strickland 2006, Post and Forchammer 2008), fail to identify the proximate mechanisms by which climate change has influenced fitness and population growth rates (Cahill et al. 2012) and, by extension, community structure (Winder and Schindler 2004, Post et al. 2009, Walther 2010, Nakazawa and Doi 2012). Identifying proximate mechanisms is important for the development of predictive frameworks, permitting an evaluation of the susceptibility of different species to long-term changes in the environment (Both et al. 2009).

Here, we seek to develop such a framework for food-caching animals by integrating insights from the fields of food science and plant biology with knowledge of the food-caching behaviours and preferences. Food caching is a widespread behavioural adaptation used primarily by non-migratory species to store food for future use during periods of low resource availability or uncertainty (Vander Wall 1990). Once a food item is cached, it is exposed to environmental conditions that can either maintain or degrade its quality over time. Furthermore, the degree of degradation may also depend on a variety of factors, including food type, the duration of

exposure and the location where food is stored. Although well studied in the field of food science, this knowledge has not been applied to natural systems.

Our motivation for understanding the mechanisms behind environmental degradation of cached food stems from our long-term research on a declining population of Gray Jays (*Perisoreus canadensis*) at the southern edge of their range (Waite and Strickland 2006, Strickland et al. 2011, Norris et al. 2013, Derbyshire et al. 2015). Gray Jays cache a wide range of perishable food items during the late summer and fall and use this food for over-winter survival and late-winter breeding (Strickland and Ouellet 2011). Waite and Strickland (2006) proposed that warmer fall temperatures may be leading to the degradation of cached food, which then carries over to influence breeding success. They presented some correlational support for the ‘*hoard-rot hypothesis*’ but the effect of fall temperatures on reproductive success was relatively small compared to the steep population declines and there was only weak evidence that fall temperatures increased over the period in which Gray Jays declined. Additionally, a recent experiment using simulated caches did not find a consistent effect of warmer fall temperatures on food quality (Sechley et al. 2015). Sechley et al. (2015) did, however, show that temperature thresholds, such as the presence or absence of deep freeze events, could be driving observed differences in the degree of food preservation over a latitudinal gradient. These lines of evidence lead us to speculate that (a) the persistence of stored food may be influenced by more than a simple linear relationship with temperature and (b) that a deeper understanding of how climate influences food quality may be gained by drawing upon applied research related to the degradation of food stored by humans.

Our three primary goals in this paper are to (1) place the potential effects of climate change on cached food quality in a broader context of the costs and benefits of caching, (2) introduce a framework, based on variation in caching behaviour across species and in the types of food they store, for assessing their susceptibility to climate change and, (3) use insights from the fields of food science and plant biology to identify environmental conditions that could contribute to the degradation or preservation of cached food in the wild. We anticipate that these new perspectives will stimulate future research on a wider range of caching species and improve our ability to understand the potential effects that climate change may have on this subset of animals.

2.3 Relating the potential effects of climate change to the costs and benefits of caching

To put the potential effects of climate change into a broader context, we consider the simple cost-benefit equation outlined by Andersson and Krebs (1978). They proposed that the fitness (considered here as nutritional gain), F , of a caching species can be estimated by $F = Gp - C$, where G is the fitness (or nutrition) gained by eating a cached food item at a future date, p is the probability that that food item is retrieved, and C is the cost of deferring consumption of that food item (in other words, the nutrition lost from not consuming it upon capture). Andersson and Krebs (1978) argued that, if $Gp > C$, then caching would evolve. However, in theory this principle could also be used to assess how the costs and benefits of caching may change over ecological time and this will be particularly relevant under rapidly changing environmental conditions.

Of course, many species-specific factors will influence G , p , and C . Past studies have primarily focused on determining what drives p , for example, by quantifying the frequency of conspecific and heterospecific competitors pilfering cached food (Lahti et al. 1998, Leaver and Daly 2001, Vander Wall et al. 2006) and estimating the cognitive ability of a species to recover stored food at a future date (Moreno et al. 1981, Jacobs and Liman 1991, Pravosudov and Clayton 2001, 2002). In most cases (particularly for species that cache perishable food), the nutrition gained from consuming a cached item will almost always be less than consuming it immediately upon acquisition and that this is due, in large part, to the degradation of cached food over time. The rate at which a cached food item will degrade is dependent on duration for which it is stored and the type of food that is stored (see detailed discussion in section below).

We provide an example of how $F = Gp - C$ could be used to estimate the effect of different climatic conditions on caching in Gray Jays. To estimate G , we use data from Sechley et al. (2015) who determined the caloric value of mealworms experimentally cached over a typical storage-retrieval period (fall-winter) at two locations with different climatic conditions. In the middle of the range in Cochrane Ontario, where temperatures rarely go above freezing beginning in November, mealworms retrieved in March were an average of 0.977 kcal, whereas at the southern edge of their range in Algonquin Park, where temperatures are rarely below zero until November, the average caloric value of mealworms stored over the same period was 0.663 kcal. For p , we used estimates of cache retrieval from two nutcrackers (0.84; *Nucifraga columbiana* Tomback 1980, *Nucifraga caryocatactes* Balda and Conrads 1983). Similar to Gray Jays, both species rely on cached food for both over-winter survival and reproduction and, therefore, likely have relatively accurate spatial memories (Balda and Kamil 1998) The cost of

caching, C , can be estimated as the energy it takes an individual to find a food item that is of equal nutritional quality to the item that was cached. Because the energetic cost of foraging is not known for Gray Jays, we estimated C by taking an estimate of the daily energetic requirement of an individual Gray Jay (47 kcal; Shank 1986) and multiplying it by the proportion of the day an individual would take to find a food item (24 hrs/10 min = 0.007) resulting in $C = 0.33$ kcal. Using these values, the nutrition gained from caching food at the more southern site is estimated to be >50% lower (0.23 kcal) compared to the more northern site (0.50 kcal). Given temperatures in Algonquin were similar to the Cochrane as early as 1990 (Sechely et al. 2015), this suggests that Gray Jays in Algonquin park have experienced a significant decline in nutritional quality of cached food. Of course, these are crude estimates but they do serve as an example of how this equation can be used to assess the influence of environmental conditions on the nutritional benefits of caching.

2.4 Predicting the susceptibility of food-caching species to climate change

Caching behaviour is widely distributed across 30 families of mammals and 15 families of birds and is believed to have evolved independently numerous times within each taxa (Honacki et al. 1982, Smith and Reichman 1984, Vander Wall 1990, de Kort and Clayton 2006). Given the repeated, independent evolution of caching behaviour, it is perhaps no surprise that there is also a wide diversity of caching behaviours and types of food that are cached (Vander Wall 1990; Table 1). We believe that the degree to which cached food is influenced by climate change depends primarily on three major axes of variation that we discuss in detail below. In order of importance they are: 1) the duration of time that food is stored, 2) the type of food that is cached, and 3) the location where food is stored (Figure 1).

Duration of food storage

Caching species can generally be divided into two classes based on cache duration. The first is 'short-term cachers' that can be characterized by temporally overlapping and episodic caching and recovery events (Vander Wall 1990). These species are primarily motivated by present and/or imminent uncertainty in resource availability and will typically cache food for no longer than 10 days before retrieval. One type of caching species that falls into this class are single-item-surplus cachers that cannot consume all of a prey item in a single sitting and, therefore, attempt to protect the remaining portion of food for future feeding bouts (e.g. Tigers, *Panthera tigris*; Schaller 1967). A second type of short-term cacher stores food to protect it from heterospecific and conspecific competitors. For example, Leopards will bring carcasses into trees in order to protect their kills from Lions and Hyenas (Eisenberg and Lockhard 1972, Eltringham 1979). Barbados Green Monkeys (*Cercopithecus aethiops*) have been observed to cache food for short periods of time in order to prevent conspecific competitors from accessing their food (Baulu et al. 1980). A third type of short-term cacher are 'insurance' cachers, such as parids (Sherry 1989) and mustelids (Snead and Hendrickson 1942), who cache food items for hours or days as an apparent hedge against present or imminent uncertainty in the environment.

The second class of caching species is 'long-term cachers' that are characterized by distinct, non-overlapping storage and recovery periods that are > 10 days but are more typically separated by two or more seasons (Vander Wall 1990). Long-term cachers store food as a response to a certain lack of food in the future. Species in this class typically engage in intense periods of caching, usually in the late summer or fall (Jansson et al. 1981, DeGange et al. 1989, Vander Wall 1990, Strickland and Ouellet 2011) and are followed by intervals of limited

resources (e.g. winter) during which caches are retrieved. Food stored by long-term cachers will be more susceptible to environmental change simply because it is exposed to the environment for longer periods compared to food stored by short-term cachers. Long-term storage also increases the probability that food will be stored during transitional periods between seasons that are characterized by large fluctuations in environmental conditions that can negatively affect food quality. For example, late summer and fall storage exposes items to potentially damaging freeze-thaw cycles as the year transitions into winter.

Latitude plays an important role in determining the duration that food is stored, particularly for long-term cachers. At high latitudes, periods of limited resources are longer, which means more food must be cached over a comparatively shorter time period (Brodin et al. 1996, Pravosudov 2006). This could imply that populations at higher latitudes are more susceptible to changing climatic conditions because of the presumably higher reliance on cached food compared to populations at lower latitudes. Similarly, along elevational gradients, high elevation populations could be at greater risk due to an increased reliance on cached food (Varner et al. 2016). Climate warming could benefit caching species by prolonging food availability during the storage season or by reducing the length of low-resource periods in which cached food is relied upon. Both of these examples highlight how caching behaviour changes over temperature gradients, thus, it will be important to consider how changing climatic patterns influence not only food once it is cached, but also how it could influence caching decisions.

Type of food stored

A wide variety of food is cached by wild animals (Smith and Reichman 1984, Covich 1987, Vander Wall and Smith 1987, Vander Wall 1990). The type of food that a species stores will have an impact on how susceptible they may be to climate change. At the broadest level, the distinction can be made between perishable and non-perishable food items. Food perishability is a function primarily of its water content, which dictates not only how food will respond to freezing temperatures but also the growth rate of bacteria (McMeekin and Ross 1996, Isengard 2001, Mathlouthi 2001, Pham 2004). Although some species store exclusively perishable (e.g. carnivores, such as canids, felids and raptors; Chesemore 1975, McCord and Cardoza 1982, and Gray Jays; Strickland and Ouellet 2011) or non-perishable (e.g. tree squirrels *Sciurus spp.* and new world mice *Peromyscus spp.*); Moller 1982, Vander Wall 1990) food, many other species store both types of food. For example, herbivores, such as Collared Pikas (*Ochotona collaris*), and Agoutis (*Dasyprocta punctata*) have been documented to store both non-perishable nuts, and seeds, and perishable fruit (MacRoberts and MacRoberts 1976, Vander Wall and Balda 1977, Elliot 1978, Kawamichi 1980, Reichman et al. 1984).

Below, we discuss how the field of food science can be used to develop an understanding of conditions that maintain and degrade perishable food items. Although there are few studies in food science that examine the influence of the environment on seeds and nuts, we also discuss how the field of plant biology may offer some insight into how variation in climate could influence germination rates and reduce the functional quality of stored seeds.

Location of food storage

With the exception of Beavers (*Castor canadensis* and *Castor fiber*) and Spotted Hyenas (*Crocuta crocuta*) which cache food in water, caching species store food in two types of locations: in the ground or in trees (Vander Wall 1990). When food is stored below ground it will tend to be more buffered from environmental conditions compared to food that is stored above ground. For example, Arnold et al. (1991) found that when air temperatures were below zero, temperatures remained above freezing in underground burrows of Alpine Marmots (*Marmota marmot*). When food is stored during the temperate zone winter, snow accumulation of 30-40 cm can decouple soil and air temperature (Sturm et al. 1997). In contrast, when food is cached above ground, it is more likely to be directly exposed to environmental conditions. For example, White-breasted Nuthatches (*Sitta carolinensis*) store food caches in exposed bark crevices on the trunk and limbs of trees (Kilham 1974, Petit et al. 1989, Woodrey 1991), while Jays of the genus *Perisoreus* cache food under pieces of bark or lichen on branches (Ekman et al. 1996, Strickland and Ouellet 2011). Other species, such as Leopards, leave food items conspicuously on branches where it is difficult for competitors, such as Lions and Spotted Hyenas, to access them (Eisenberg and Lockhard 1972, Eltringham 1979). Other species, such as Boreal Owls (*Aegolius funereus*), store food in tree cavities (Korpimaki 1987), which likely offers greater protection from environmental conditions compared to food stored on the exterior of a tree.

Regardless of whether species store food above or below ground, some species may also exploit different microhabitats. For example, Banner-tailed Kangaroo Rats (*Diopdomys spectabilis*) store food in multiple chambers within their complex subterranean burrows (Reichman et al. 1985). Storage chambers can vary in both humidity and temperature, resulting in differential microbial activity between chambers (Reichman et al. 1986). Banner-tailed

Kangaroo Rats prefer seeds with intermediate levels of mould and, therefore, exploit differences in microhabitats by moving seeds with high mould levels to low humidity chambers, and seeds with low mould levels to high humidity chambers (Reichman et al. 1986). Differences in cache placement (subterranean burrows, ground surface, tree cavities and tree surfaces) mean that food items will be exposed to different climatic conditions, which could lead to variation in the degree of degradation. It is clear that additional research is required to better understand the extent to which exposure to environmental conditions differs between caching locations.

Summary of trends and susceptibility estimates

We compiled a list of 203 caching species for which there is information on both the duration of storage and perishability of cached food (Table 1). From this information, we developed a susceptibility score for each species using a hierarchical classification system. Species were first divided into three categories based on the duration of food storage (short, mixed or long) and then, within each of these three categories, further divided into three groups according to the degree of perishability of cached food (low, mixed or high). We termed what is typically considered ‘non-perishable’ food (nuts, seeds) as low perishability because climate may influence germination rates (see food science and plant biology discussions below). For both storage duration and perishability, species that were defined as ‘mixed’ when there was evidence in the literature for both ‘high’ and ‘low’ storage duration or perishability. This classification created nine possible categories ranging from the least susceptible (short-term cachers that store low perishable food, susceptibility score of 1) to the most susceptible (long-term cachers that store high perishable food, susceptibility score of 9). Storage location was not used to determine susceptibility scores because there is not yet enough empirical evidence about how food cached

at these different locations (e.g. subterranean vs. arboreal surface) is influenced by environmental conditions.

Because of the short-term nature of their caching behaviour, the largest proportion of caching species (44%) were assigned to the three lowest susceptibility scores (1-3). Of the 38% of species in the three highest susceptibility categories (score of 7-9), 91% relied on low-perishable food (score of 7). Seven percent (7%) stored both high and low perishable food and only 2% (four species: the Bull-headed Shrike *Lanius borealis*, Gray Jay, Siberian Jay *Perisoreus infaustus* and Wolverine *Gulo gulo*) were both long-term cachers and relied exclusively on perishable food (susceptibility score of 9). Population declines at the southern edge of ranges have already been documented for both Gray Jays (Waite and Strickland 2006) and Wolverines (Aubry et al. 2007) and studies on both of these species also suggest that climate change could be contributing to population declines (Waite and Strickland 2006, Inman et al. 2012, Sechley et al. 2014).

A smaller proportion of species (18%) were classified as mixed duration cachers (e.g. Artic Foxes, *Alopex lagopus* and Red Foxes, *Vulpes vulpes*, susceptibility scores of 6). The reason why some species are classified as mixed duration cachers may partly reflect geographic differences in caching behaviour within a species (Frank 1979, Macdonald et al. 1994, Varner et al. 2016). However, some species or populations may cache a variety of food items with different degrees of perishability (Figure 1). In such circumstances, food that is more perishable may also be of higher nutritional value (e.g. meat), which implies that species in this category may be more susceptible to climate change than we have estimated here. Nevertheless, it is clear that, for a number of species, more information is required to quantify how long food is stored, as well as

the proportion of specific food items that are stored and their degree of perishability. Such information will improve our estimates of susceptibility and will, therefore, be important for understanding how climate change could influence abundance.

2.5 Integrating concepts from food science to understand the susceptibility of perishable food to climate change

Understanding how environmental conditions influence food quality is a major focus of food science (Mossel et al. 1995, Potter and Hotchkiss 1998). A number of conditions have been identified that can degrade or preserve a wide range of perishable food consumed by humans (Mossel et al. 1995, Boonsumrej et al. 2007, Matos 2011, Leygonie et al. 2012). At the most general level, food can be degraded in three ways. First, even in the complete absence of bacteria or fungi, food may lose nutritional quality through a breakdown in structure due to a number of physical and chemical processes (Boonsumrej et al. 2007, Barrett and Lloyd 2012). Second, microbial proliferation in food leads to losses of the nutrients and energy originally available to non-microbial competitors (e.g., humans) as these resources are diverted into the growth of indigestible bacteria (Hughey and Johnson 1987, Huis in't Veld 1996, Gram et al. 2002). Third, even when food still contains energy and nutrients potentially useful to non microbes, these resources may be rendered inaccessible as many bacteria (e.g., *Staphylococcus aureus* and *Clostridium botulinum*) produce toxins or noxious substances that induce vomiting, diarrhea or otherwise render food inedible for humans (Gram and Huss 1996, Gram et al. 2002). Although spoilage is fundamentally different from the physical or microbial degradation of a food item, in nature the three processes can be considered tightly linked. For example, the physical

degradation of a food item (e.g. through freeze-thaw cycles) may accelerate microbial proliferation, which could then enhance the production of toxins that render food inedible. Thus, when examining how environmental conditions influence cached food, these processes will likely have to be considered together as they will be difficult to separate in the wild. Here, we focus on four classes of environmental factors that are recognized to influence perishable food stored by humans and that we believe are relevant to natural systems.

Temperature

Temperature has long been the subject of study in the field of food science because it influences microbial growth, with different temperature thresholds responsible for facilitating or inhibiting microbial growth depending on the food item and species of bacteria (Mossel et al. 1995).

Generally, warm temperatures act to facilitate microbial growth, whereas cold temperatures inhibit growth (Brackett 1994). Humans have manipulated temperature for centuries to extend the duration for which food can be stored (Stannard et al. 1985, Mossel et al. 1995). Lowering temperature is extremely effective because it acts to retard microbial growth across a range of food groups, such as meat, fruit and vegetative matter (Brackett 1987, Brackett 1994, Ragaert et al. 2007).

Many studies have investigated the relationship between temperature and microbial growth (e.g. Gibson et al. 1988, Zwietering et al. 1991, Baranyi et al. 1995, Bovill et al. 2000, Bovill et al. 2001). Zwietering et al. (1991) focused on modelling the relationship between temperature and bacterial growth rate. Simple models, including a linear relationship between temperature and growth rate and constant growth at all temperatures were not supported. Instead,

the best fitting models were derived from a square root model originally proposed by Ratowsky et al. (1982). Part of the reason why simpler models show a lack of fit is that asymptotes exist to bacterial growth, particularly at extreme temperatures (Zwietering et al. 1991). These studies also highlight the importance of both bacterial species and the food substrate in determining rates of bacterial growth at different temperatures. For example, Bovill et al. (2000) demonstrated that the proliferation of *Listeria monocytogenes* and *Salmonella* spp. at the same temperature depended on substrate (milk vs. broth vs. meat) and bacteria species. This dependence is likely the result of competition between the existing bacterial flora of a food item and novel bacteria (Pin et al. 1999). Naturally occurring bacteria could prevent additional harmful bacteria from colonizing a food item, preventing food spoilage due to the accumulation of noxious substances. This is especially pertinent to wild systems as food items would likely host a variety of bacteria or other microbes, which could prevent additional colonization by bacterial species.

The majority of studies on the effects of climate change in wild animal populations have focused on the effect of temperature (e.g. Erb et al. 2011, Klamt et al. 2011) and temperature is certainly the most common environmental predictor variable used in studies of caching species as well (e.g. Morrison and Hik 2007, Waite and Strickland 2006). The advantage is that temperature is the most commonly recorded long-term environmental variable and, where it is not recorded, several models are available to estimate past temperature values on either a monthly or annual basis (Mann et al. 1998). Using mean temperature values over a specific time period is clearly convenient, but we argue, perhaps not always the only ecologically relevant factor for caching animals because it may not capture specific temperature values or other

environmental conditions that are associated with different mechanisms known to influence the quality of stored food.

Deep freezing

It may be useful to separate deep freeze from the general effects of temperature because it represents a specific threshold below which microbial growth is halted rather than simply retarded. The specific temperature associated with a deep freeze event will depend on the microbe in question as cold tolerance varies across species (Kaale et al. 2011). As microbial activity is a major cause of food spoilage, stopping this process to preserve food over long time periods has been a major focus in the field of food science (Borch et al. 1996, Fernandez et al. 2010). One study suggested that temperatures as low as -55°C represent ideal storage conditions for meat (Hansen et al. 2004) because enzymatic reactions and oxidative rancidity cease completely, removing most of the key processes that would degrade food quality (Zhou et al. 2010). However, temperatures do not necessarily need to be this extreme to halt microbial activity over time. A number of studies have found that bacteria and fungi on frozen food generally cease growth at -8°C (Geiges 1996) and other research has provided evidence that the growth of some microbes halts at around -12°C (Mazur 1980, Finegold 1996).

Perhaps more importantly, deep freeze events can also cause cell death or injury to microbial cells (Oliver 2005). If microbes are killed when exposed to deep freeze temperatures, it means that subsequent degradation will occur at a slower rate, as fewer bacteria will be present to deplete nutritional resources or render a food item inedible through spoilage when temperatures increase (Mackey 1984, Wesche et al. 2009). However, if not all bacteria are killed,

deep freeze events can also act as a selection agent to promote cold tolerance (Wesche et al. 2009). Many bacterial species can also enter a 'viable but nonculturable' (VBNC) state, characterized by a large reduction in metabolic activity in response to extreme temperatures and other environmental stressors (Kell et al. 1998, Oliver 2005). Once in the VBNC state, bacteria remain dormant until conditions facilitate resuscitation. Some studies suggest that an increase in temperature can result in resuscitation of cells in the VBNC state (Wolf and Oliver 1992, Oliver and Bockian 1995, Oliver et al. 1995). This highlights the importance of understanding the relationship between temperature and the activity of microbes present on cached food. In particular, understanding relevant thresholds that inhibit bacterial growth or kill bacteria will be key to interpreting the influence of climatic variables on food quality over time.

For caching species, deep freeze events could play a significant role in preserving the quality of stored food, in particular for species that store food for use over the winter. For example, in a study of the caloric content of simulated Gray Jay caches at three different latitudes in Ontario, Canada, Sechley et al. (2015) found that the mass loss and caloric content of cached food (mealworms and raisins) was similar between low- and mid-latitude sites even though these sites differed in mean fall temperatures. However, food caches from the high-latitude site lost less weight and caloric content leading Sechley et al. (2015) to speculate that 'deep freeze' events may be driving this pattern as the high-latitude site was the only site that reached an average of -16°C during the winter. In Finland, bacterial activity was halted in two different decomposer communities in soil at -16°C , suggesting that this may be an important threshold in natural systems (Sulkava and Huhta 2003). Nevertheless, there have been no studies

that have experimentally examined whether deep freeze events contribute to the preservation of perishable cached food of a wild animal.

Humidity

Another influence on microbial growth is the amount of water in the surrounding environment (Abdullah 2000, Ayala-Zavala et al. 2008). Humidity, a measure of the moisture content of air, influences the transfer of moisture between the air and surface of adjacent substrates (Kimball et al. 1997). It is well known that increases in moisture around a food item leads to increased microbial growth and proliferation (Tournas 2005). For example, lower environmental moisture content has been found to decrease microbial growth on rice and flour and, consequently, increase the length of time these food items can be stored (Abdullah 2000, Genkawa et al. 2008).

Since high ambient humidity facilitates microbial degradation and spoilage (Abdullah 2000), pronounced seasonal fluctuations in rainfall and ambient humidity may mean that during large portions of the year it is likely not profitable to store perishable food, particularly at low latitudes. In contrast, high-latitude ecosystems have lower ambient humidity levels, punctuated by increases in moisture in the form of rain and snow. This reduction in humidity favours long-term storage and could also allow species to store at multiple time points throughout the year.

At high latitudes, humidity is likely to influence food caches primarily in the spring, summer, and fall because warm air can hold a larger quantity of water vapour (Trenberth et al. 2005) and this means that more water is available to microbes (Lawrence 2005). Conversely, in winter, much of the moisture is present as a solid (i.e. ice), which means that it cannot be easily accessed by microbes, thus inhibiting growth.

Freeze-thaw events

Freeze-thaw events cause phase changes of bound water within a cell (e.g. ice crystal formation) and the associated rapid expansion and contraction of water can result in damage to cellular structures (Wagner and Anon 1985, Li and Sun 2002, Barrett and Lloyd 2012, Leygonie et al. 2012). As a result of the degradation of cellular structures, freeze-thaw events can affect multiple aspects of food quality and several studies in applied food science have been conducted to understand the mechanisms behind these processes.

Microstructure is one major component of food quality that is heavily influenced by freeze-thaw events (Alizadeh et al. 2007, Barrett and Lloyd 2012). The denaturation of proteins, particularly within meat and fish products, has been linked to changes to the microstructure of a food item (Alizadeh et al. 2007, Boonsumrej et al. 2007). Associated with these changes in microstructure is a process known as ‘drip loss’ (Pham 2004, Zhou et al. 2010). As a food item undergoes a freeze-thaw cycle, damaged cells leak an exudate containing soluble nutrients, vitamins, minerals and protein (Pham 2004, Barrett and Lloyd 2012, Leygonie et al. 2012). In addition to siphoning nutritional content away from the cell, this exudate also produces favourable conditions for microbial growth by increasing nutrient and moisture available around a food item (Leygonie et al. 2012).

The number of freeze-thaw events that a food item experiences can also influence the amount of damage that is caused. Multiple freeze-thaw events can have strong additive effects that can cause food to degrade more rapidly (Srinivasan et al. 1997, Jeong et al. 2011, Boonsumrej et al. 2007, Sriket et al. 2007, Xia et al. 2010, Qi et al. 2012). Srinivason et al.

(1997) documented an increase in mechanical damage sustained by freshwater prawns (*Macrobrachium rosenbergii*) exposed to repeated freeze-thaw events and this damage was caused by repeated melting and reformation of ice-crystals within a cell. Boonsumrej et al. (2007) found similar mechanical damage to Tiger Shrimp (*Penaeus monodon*) characterized by torn muscle fibres, an increase in distance between adjacent muscle fibres, and a breakdown of the subcuticular membrane surrounding muscle fibres. This mechanical damage was associated with increased thawing loss (the weight lost by a sample when comparing frozen and thawed weight), a decrease in protein concentrations and an increase in thiobarbituric acid, a compound associated with food decomposition (Boonsumrej et al. 2007).

In the field of food science, studies have typically examined the effect of up to five consecutive freeze-thaw events on food quality (e.g. Sriket et al. 2007, Xia et al. 2009, Xia et al. 2010, Jeong et al. 2011). However, one study demonstrated that meat might continue to degrade after 15 freeze-thaw cycles (Qi et al. 2012). Further studies are needed to determine if various food types have different threshold numbers of freeze-thaw cycles beyond which no further damage can be inflicted. Such studies would be important in order to determine if possible increases in the number of freeze-thaw events resulting from long-term changes in climate could decrease survival of food caches in the wild.

2.6 Integrating concepts from plant biology to understand the susceptibility of non-perishable food to climate change

Although cached seeds are generally considered non-perishable, seed germination will result in seeds being inedible. The field of plant biology has identified a number of regulatory processes

and environmental conditions that influence the likelihood of germination (Baskin and Baskin 1998). To understand how environmental conditions regulate germination, it is necessary to understand seed dormancy and how environmental conditions can break dormancy. Dormancy is the failure of a seed to germinate when conditions are otherwise favourable to promote germination (Eira and Caldas 2000, Geneve 2005). Dormancy ensures that seeds will only germinate when conditions are favourable for the growth (Vleeshouwers et al. 1995, Eira and Caldas 2000). Temperature and moisture are two key environmental parameters that can break dormancy and promote germination.

Temperature

The effect of temperature is generally related to the life history of the plant species (Baskin and Baskin 1998). Winter annuals require periods of warm temperatures preceding cold temperatures in order for their seeds to germinate (Baskin and Baskin 1982a), whereas summer annuals require periods of cold weather followed by warm temperatures in order to germinate. This temperature cycle corresponds to seeds being deposited in the ground in the fall and germinating in the spring, after remaining dormant over the winter (Baskin and Baskin 1983, Baskin et al. 1993). Patterns of temperature fluctuations can also be important to stimulate germination, with many species responding favourably to alternating temperatures (Nishimoto and McCarty 1997, Leskovar et al. 1999, Soltani et al. 2005, Shin et al. 2006).

Freeze-thaw cycles may also influence the germination of seeds that are stored by many food-caching species. Soil temperature regimes, which can be influenced by freeze-thaw events, have a strong bearing on the occurrence and timing of germination (Pritchard et al. 1988, Probert

2000). The influence of low soil temperatures is highly variable across plant species (Baskin et al. 2000). Several studies indicate that exposure to low soil temperatures is necessary for germination to occur (Körner 2003, Shimono and Kudo 2005) and other studies have shown that freeze-thaw cycles can lead to scarification, a necessary precondition for germination in some plant species (Zuur-Isler 1982). Van Assche et al. (2003) proposed that freeze-thaw cycles could interact with cold winter temperatures in a two-step process to promote germination. First, low winter temperatures make seeds sensitive to freeze-thaw cycles. Second, freeze-thaw cycles cause seeds to become water permeable, facilitating germination. For such species, warming winter temperatures could lead, in the short term, to prolonged availability of food caches, as seeds would fail to germinate and, in the long term, to eventual local extinction of the trees/plants producing the seeds favoured by food-caching species. On the other hand, for plant species whose seeds germinate independently of exposure to cold temperatures or freeze-thaw cycles, warmer and shorter winters could shorten the availability of seeds to any animals that cached them (Makoto et al. 2013).

Moisture

In general, some moisture is required to facilitate germination but the optimum water content varies across species (O'Reilly and De Atrip 2007). Soaking seeds is a common commercial method used to “prime” seeds for germination, leading to a higher percentage of germination for many species (Pill et al. 2000, Abro et al. 2009). Similar to temperature, variability in moisture is necessary for many species to promote germination. However, for some species, variability in moisture levels can result in a decreased germination rate or have no effect at all (Lush et al. 1981, Baskin and Baskin 1982b, Taylorsen 1986). There may also be strong interactive effects

between moisture and temperature. For example, in seeds without sufficient water content, dormancy will not be broken by temperature alone (Baskin and Baskin 1998).

Additional factors influencing germination

It is important to note, however, that the consequences of climate change on germination are not consistent across species (Baskin et al. 2002), with responses depending on a number of factors, including species geographic and evolutionary origin (Milbau et al. 2009) and life history (Wesche et al. 2006). Furthermore, different habitats may exert distinct selective pressures on plant life histories and seed germination strategies (Humphrey and Schupp 1999, Merrett et al. 2002, Wang and Kimball 2005). Baskin and Baskin (1998) provide a review of species germination and dormancy traits by habitat type. Nevertheless, if changes in climate influence germination rates of cached seeds, then they should not strictly be considered ‘non-perishable’ food items.

2.7 Linking food-degrading environmental conditions with climate change

The environmental variables outlined above are particularly relevant to natural systems as they are rapidly shifting due to climate change (IPCC 2014). Already mean temperatures across the globe have increased (Wang et al. 2011, IPCC 2014), precipitation patterns have shifted resulting in altered moisture regimes (Stocks et al. 1998, Soja et al. 2006) and an increase in unpredictable weather patterns, such as mid-winter thaws and late frosts, have been documented (ACIA 2005, Wang et al. 2011, IPCC 2014). The shift in these environmental variables suggests that the relationship between caching species and their environment is changing and potentially altering

the benefits of caching food. However, it is important to note that not all of these environmental variables will necessarily shift in the same way or with similar magnitudes.

2.8 Extracting climatic variables from historical weather data

Historical weather records are valuable for quantifying how climatic variables may influence long-term changes in abundance of caching species. Even when data are sparse, minimum, maximum and mean temperatures can be used to estimate other climatic variables, such as freeze-thaw events and the duration of deep freeze events. Natural history characteristics, such as when a species begins caching food and when it retrieves cached food, should be used to determine relevant time points to extract data from historical records.

Freeze-thaw events

Extracting information on freeze-thaw events from historical records requires knowledge of food-specific initial freezing point (Miles et al. 1997). Initial freezing points are directly related to the concentration of solutes in a food item and its water content (Rahman et al. 2009) and are known for a variety of food items. Many of these estimates could be used as surrogates for food items cached by wild species. Missing from the existing literature, however, are estimates of arthropod initial freezing points, which are relevant to a number of food-caching species that regularly store these taxa. Once initial freezing points have been determined by experiments or estimated from the literature, the numbers of freeze-thaw events can then be extracted from historical weather records by determining the point when the temperature drops below and then rises above the initial freezing point.

Deep-freeze Events

Although deep-freeze events can be easily extracted from historical temperature records, the use of minimum, mean or maximum daily temperatures has an important bearing on how deep-freeze events are interpreted. For example, extracting deep-freeze events based on minimum daily temperature implies, in most cases, that temperatures will drop below the deep-freeze threshold for only part of the day. Alternatively, using maximum daily temperatures implies that temperatures will remain below the given deep freeze threshold for the entire day. Maximum daily temperatures allow for the estimation of deep-freeze days, which is the number of complete days that microbial activity is inhibited. Incorporating multiple estimates of deep-freeze events (i.e. maximum, minimum and mean daily temperature) into an analysis would likely provide a more accurate estimate of the amount of time that temperatures inhibit microbial activity. However, it is important to note that without hourly weather records it is difficult to estimate exactly how long deep freeze events would inhibit microbial growth. To better predict deep-freeze thresholds, it is also important to understand the species or groups of microbes that are present in a food caching system. An understanding of the microbial diversity present on a food item could better predict the temperature at which microbial activity is halted, rather than relying on estimates obtained from the literature.

Humidity

Estimates of humidity from historical records can be difficult to obtain, as many weather stations have not recorded daily humidity (Friend 1996). In spite of this, proxies can be used to provide estimates of humidity or moisture levels in the environment. Rainfall and snowfall are climatic variables that are commonly found in in historical weather records and can be used to provide a crude estimate of moisture in the environment. Predictive models based on precipitation in

combination with minimum daily temperature have been shown to provide better estimates of humidity in multiple regions of the globe, such as North America and Europe. However, in more arid environments, such as parts of Africa, this relationship is not as accurate (Friend 1996) and it is necessary to use more complex models proposed by Kimball et al. (1997) to increase the reliability of humidity estimates.

2.9 Characteristics of caching species that could mitigate the impact of climate change

Behavioural strategies

Caching species have developed a number of behavioural strategies that retard cache degradation (Martin 1981, Elgmork 1982, Rich and Trentlage 1983, Sulkava and Nyholm 1987, Jenkins and Davenport 2014) and, therefore, may mitigate the effects of changing climate. These strategies include handling techniques, exploitation of chemical properties in the environment, and exploitation of certain climatic factors to decrease food perishability.

Several species have been documented to use specific handling techniques that lessen degradation of a cached food item. For example, some species incapacitate prey at the time of capture. Presumably, the selective advantage of such behaviour is to inhibit spoilage or reduce the rate of degradation. Burrowing Owls (*Athene cunicularis*) have been shown to incapacitate long-horned beetles to facilitate storage (Rich and Trentlage 1983), while Elf Owls (*Micrathene whitneyi*) have been observed to damage the thorax and remove the legs from live sphinx moths (Ligon 1968). Other animals, such as the Short-tailed Shrew (*Blarina brevicauda*), produce

toxins in their saliva that immobilize prey by rendering them comatose (Martin 1981). Once in this state, prey can remain alive for several days after capture.

Some species may exploit antimicrobial compounds in the environment to preserve cached food. Elgmork (1982) suggested that Brown Bears (*Ursus arctos*) cover carcasses with *Sphagnum* moss to aid in long-term preservation because *Sphagnum* is known to contain phenolic compounds that have antimicrobial properties. Arboreal caching species may exploit similar antimicrobial compounds of coniferous trees (e.g. spruce *Picea spp.*), which have been proposed to preserve cached food better than deciduous trees. In Gray Jays, evidence suggests that territory quality at the southern edge of their range is related to the percentage of conifers on their territories (Strickland et al. 2011, Norris et al. 2013), which appears to be partly due to the superior ability of conifers to preserve food (Strickland et al. 2011). Willow Tits (*Parus montanus*) have also been observed to preferentially cache food on conifers rather than deciduous trees (Lahti et al. 1997), which could also be related to the antimicrobial properties of conifers.

A third method that caching species use to retard microbial degradation over time is to exploit microhabitats and climatic conditions. Tigers have been documented to cache prey in areas with increased brush and cover prey items in debris. Schaller (1967) suggested that these techniques were used to lower the temperature experienced by a food item to reduce microbial activity. Many rodents dry grass and berries (Smith and Reichman 1984) and Red Squirrels hang mushrooms in trees (Hardy 1949). This drying process likely produces a similar outcome as freeze-drying, which numerous studies have noted increases the length of time a food item can be stored (Roos and Karel 1990, Ratti 2001). Cones, however, are susceptible to disintegration

through drying which may explain why squirrels place cones in terrestrial middens, where moisture levels are higher than above the ground or snow (Sulkava and Nyholm 1987).

Species that have developed behavioural strategies to mitigate the influence of exposure to the environment may be less susceptible to the effects of climate change. For example, dried food will likely be less influenced by an increase in freeze-thaw cycles, as damage due to the phase change of water will be reduced. However, it is important to note that examples of species exploiting the environment to enhance preservation are largely anecdotal and, therefore, require more rigorous study.

Physiological adaptations

To our knowledge, no studies have explicitly investigated potential physiological adaptations of caching species to cope with microbial proliferation on cached food items but studies of scavengers could help to inform future research on this subject. Recently, Roggenbuck et al. (2014) characterized a variety of adaptations in the digestive tracts of two New World vultures, *Coragyps aratus* and *Cathartes aura*. Both species were found to have low pH in their digestive systems that destroyed most bacterial species before they could reach the hindgut. Additionally, the intestinal microbiome of both species had a high prevalence of both Clostridia and Fusobacteria (Roggenbuck et al. 2014), which are commonly found on carrion. Their abundance in the hindgut likely benefits vultures by further breaking down carrion, allowing for the more complete digestion of food (Roggenbuck et al. 2014). Both Clostridia and Fusobacteria have been demonstrated to cause a variety of negative effects in both wildlife and humans (Immerseel et al. 2004, Grass et al. 2013, Kostic et al. 2013). Their presence in vulture intestinal tracts

suggests that they tolerate bacterial toxins, a finding also documented in other scavenging birds (Ohishi et al. 1979). It is possible that food-caching species also possess similar physiological adaptations to eliminate harmful microbes that colonize stored food.

Specialized oral or gut microbiomes could also allow caching species to cope with microbial colonization of a cache or digest rotting food. These adaptations could be particularly important for species that cache perishable food items, which are more likely to be colonized by bacteria. Such adaptations could buffer the impact of increased degradation arising from climate change. Investigations of oral and gut microbiomes have been undertaken for a diverse range of species, including amphibians, reptiles and mammals (e.g. Ley et al. 2008, McKenzie et al 2012, Keenan et al. 2013), including one caching species (Red Squirrel; Stothart et al. 2016).

2.10 Conclusions and future directions

Developing an understanding of the mechanisms by which environmental variables presently affect species is necessary to predict how a species will respond to future changes in climate. We outline a novel approach to address these mechanisms in food-caching species by synthesizing information from the fields of food science and plant germination ecology to understand how climate change may affect stored food and then classifying the vulnerability of species based on caching behaviour. As caching species rely on stored food for survival during periods of limited food availability and, in some cases, for reproduction, factors that influence food quality could have major downstream effects on fitness and population dynamics.

Studies on both the Gray Jays (Waite and Strickland 2006) and Wolverines (Aubry et al 2007, Inman et al. 2012) highlight how climate could be influencing population abundance but

detailed demographic studies on caching species remain limited. It will also be important to consider what cached food is being used for during periods of low resource availability. For example, both Gray Jays and Wolverines use cached food not just for survival but also for reproduction (Inman et al. 2010, Strickland and Ouellet 2011), meaning that multiple demographic vital rates may be linked to changes in cached food quality over time. Identifying the vital rates driving population dynamics will help to identify how the downstream effects of climate change on cached food quality may influence population growth rates.

In addition to demographic studies, understanding the influence of climate change on caching species will require experimental work on how environmental variables may influence cached food. Such studies could take place in the field (e.g. Sechley et al. 2015) or in the laboratory by borrowing many of the approaches used in the field of food science (e.g. Gormley et al. 2002, Boonsumrej et al. 2007, Phimolsiripol et al. 2008). Ultimately, a combination of experimental and demographic studies will be the most rigorous approach for identifying specific mechanisms by which climate change could influence this fascinating group of animals.

2.11 Tables

2.11.1 Summary of vertebrate caching species

The caching behaviour of 203 species is outlined in this table. All species for which information on the duration a food item was cached for, the perishability and type of food cached, and the location where food is stored are included within the table. In many cases, information on each of these three axes of caching behaviour represents a 'best estimate', as much of the literature on caching behaviour relies on anecdotal reports or natural history observations. All species were assigned a susceptibility score from one to nine based on variation in two major aspects of caching behaviour: duration and food perishability (see text for details on classification). Susceptibility to climate change was predicted to be lowest for short-term cachers of low perishable food item (1) and highest for long-term cachers of perishable food items (9). Information on the location where food is stored is included in the table as it could dictate what environmental conditions a food item experiences once it is cached. However, more study is necessary to determine if the conditions experienced in different microhabitats are significantly different and how these microhabitats contribute to food degradation.

Species	Duration	Perishability	Food Cached	Placement	Susceptibility
Jackdaw <i>Corvus monedula</i>	S	Low	E, N, Mi, SM	Arboreal Cavity	1
Red tree vole <i>Arborimus longicaudus</i>	S	Low	WV	Arboreal Cavity	1
Black-capped chickadee <i>Parus atricapillus</i>	S	Low	I, N, S	Arboreal Surface	1
Boreal chickadee <i>Parus hudsonicus</i>	S	Low	N, S	Arboreal Surface	1
Brown-headed nuthatch <i>Sitta pusilla</i>	S	Low	I, S	Arboreal Surface	1
Coal tit <i>Parus ater</i>	S	Low	I	Arboreal Surface	1
Eurasian nuthatch <i>Sitta europaea</i>	S	Low	N, S	Arboreal Surface	1
Marsh tit <i>Parus palustris</i>	S	Low	S	Arboreal Surface	1
Pygmy nuthatch <i>Sitta pygmaea</i>	S	Low	I, S	Arboreal Surface	1
Red-breasted nuthatch <i>Sitta canadensis</i>	S	Low	N, S	Arboreal Surface	1
Siberian tit <i>Parus cinctus</i>	S	Low	S	Arboreal Surface	1
Tufted titmouse <i>Parus bicolor</i>	S	Low	N, S	Arboreal Surface	1
White-breasted nuthatch <i>Sitta carolinensis</i>	S	Low	N, S	Arboreal Surface	1
Large Japanese field mouse <i>Apodemus speciosus</i>	S	Low	N, S	Subterranean Ground	1
Mexican spiny pocket mouse <i>Liomys irroratus</i>	S	Low	S	Subterranean Ground	1

Small Japanese field mouse	S	Low	N, S	Subterranean Ground	1
<i>Apodemus argenteus</i>					
Wood mouse	S	Low	N, S	Subterranean Ground	1
<i>Apodemus sylvaticus</i>					
Yellow-necked mouse	S	Low	N, S	Subterranean Ground	1
<i>Apodemus flavicollis</i>					
Fish crow	S	Mixed	Mi	Arboreal Surface	2
<i>Corvus ossifragus</i>					
African striped weasel	S	High	Ca, SM	Arboreal Cavity	3
Barn owl	S	High	SM	Arboreal Cavity	3
<i>Tyto alba</i>					
Elf owl	S	High	I	Arboreal Cavity	3
<i>Micrathene whitneyi</i>					
	S	High	SM	Arboreal Cavity	3
Schreech owl					
<i>Otus asio</i>					
American kestrel	S	High	Bi, Re, SM	Arboreal Surface	3
<i>Falco sparverius</i>					
Barred owl	S	High	SM	Arboreal Surface	3
<i>Strix varia</i>					
Bat falcon	S	High	Ba, Bi	Arboreal Surface	3
<i>Falco rufigulais</i>					
Boreal owl	S	High	SM	Arboreal Surface	3
Aegolius funereus					
Broad-winged hawk	S	High	Bi	Arboreal Surface	3
<i>Buteo platypterus</i>					
Buzzard	S	High	SM	Arboreal Surface	3
<i>Buteo buteo</i>					
Crowned eagle	S	High	MM	Arboreal Surface	3
<i>Stephanoaetus coronatus</i>					
Eagle owl	S	High	Bi	Arboreal Surface	3
<i>Bubo bubo</i>					
Eleonora's falcon	S	High	Bi		3

<i>Falco eleonarae</i>				Arboreal Surface	
Eurasian pygmy owl	S	High	Bi, SM	Arboreal Surface	3
<i>Glaucidium passerinum</i>					
European kestrel	S	High	SM	Arboreal Surface	3
<i>Falco tinnunculus</i>					
Goshawk	S	High	Bi, SM	Arboreal Surface	3
<i>Accipiter gentilis</i>					
Great horned owl	S	High	SM, MM	Arboreal Surface	3
<i>Bubo virginianus</i>					
Leopard	S	High	LM, MM	Arboreal Surface	3
<i>Panthera pardus</i>					
Little owl	S	High	Bi, SM	Arboreal Surface	3
<i>Athene noctua</i>					
Merlin	S	High	Bi, SM	Arboreal Surface	3
<i>Falco columbarius</i>					
New Zealand falcon	S	High	Bi	Arboreal Surface	3
<i>Falco novaehollandiae</i>					
Northern hawk owl	S	High	SM	Arboreal Surface	3
<i>Surnia ulula</i>					
Northern pygmy owl	S	High	SM	Arboreal Surface	3
<i>Glaucidium gnoma</i>					
Northern shrike	S	High	Bi, SM	Arboreal Surface	3
<i>Lanius excubitor</i>					
Orange-breasted falcon	S	High	Ba	Arboreal Surface	3
<i>Falco deiroleucus</i>					
	S	High	Bi	Arboreal Surface	3
Peregrine falcon					
<i>Falco peregrinus</i>					
Prairie falcon	S	High	Bi	Arboreal Surface	3
<i>Falco mexicanus</i>					
Prevost's squirrel	S	High	Fr	Arboreal Surface	3
<i>Callosciurus prevosti</i>					
Saw-whet owl	S	High	SM	Arboreal Surface	3
<i>Aegolius acadicus</i>					

South island robin <i>Petroica australis</i>	S	High	I	Arboreal Surface	3
Sparrowhawk <i>Accipiter nisus</i>	S	High	Bi, SM	Arboreal Surface	3
Tawny owl <i>Strix aluco</i>	S	High	SM	Arboreal Surface	3
African wild dog <i>Lycaon pictus</i>	S	High	LM, MM	Ground Surface	3
Barbados green monkey <i>Cercopithecus aethiops</i>	S	High	Fr	Ground Surface	3
Black bear <i>Ursus americanus</i>	S	High	Ca, MM, SM	Ground Surface	3
Black-backed jackal <i>Canis mesomelus</i>	S	High	LM, SM, MM	Ground Surface	3
Black-billed magpie <i>Pica pica</i>	S	High	Ca, E, N, Mi	Ground Surface	3
Bobcat <i>Lynx rufus</i>	S	High	MM, SM	Ground Surface	3
Brown bear <i>Ursus arctos</i>	S	High	Ca, LM, MM	Ground Surface	3
Canadian lynx <i>Lynx canadensis</i>	S	High	MM, SM	Ground Surface	3
Carrion crow <i>Corvus corone</i>	S	High	Ca	Ground Surface	3
Common crow <i>Corvus brachyrhynchos</i>	S	High	A, E, Fi, N, SM	Ground Surface	3
Common raven <i>Corvus corax</i>	S	High	Ca, E, Mi, SM	Ground Surface	3
Coyote <i>Canis latrans</i>	S	High	LM, SM, MM	Ground Surface	3
European lynx <i>Lynx lynx</i>	S	High	MM, SM	Ground Surface	3
Fennec fox <i>Vulpes zerda</i>	S	High	E, MM, SM	Ground Surface	3

Fisher	S	High	Bi, MM, SM	Ground Surface	3
<i>Martes pennanti</i>					
Golden jackal	S	High	LM, SM, MM	Ground Surface	3
<i>Canis aureus</i>					
Lion	S	High	LM, MM	Ground Surface	3
<i>Panthera leo</i>					
MacGregor's bowerbird	S	High	Fr	Ground Surface	3
<i>Amblyornis macgregoriae</i>					
Mink	S	High	Bi, MM, SM	Ground Surface	3
<i>Mustela vison</i>					
Mountain lion	S	High	LM, MM	Ground Surface	3
<i>Felis concolor</i>					
Northwestern crow	S	High	Fi, I	Ground Surface	3
<i>Corvus caurinus</i>					
Pine marten	S	High	Bi, Ca, MM, SM	Ground Surface	3
<i>Martes martes</i>					
Polar bear	S	High	LM, MM	Ground Surface	3
<i>Ursus maritimus</i>					
Snowy owl	S	High	MM, SM	Ground Surface	3
<i>Nyctea scandiaca</i>					
Tiger	S	High	LM, MM	Ground Surface	3
<i>Panthera tigris</i>					
Wolf	S	High	LM, SM, MM	Ground Surface	3
<i>Canis lupus</i>					
Arctic shrew	S	High	I	Subterranean Ground	3
<i>Sorex arcticus</i>					
Badger	S	High	Ca, MM, SM	Subterranean Ground	3
<i>Taxidea taxus</i>					
Burrowing owl	S	High	I, R	Subterranean Ground	3
<i>Athene cunicularia</i>					
European mole	S	High	I	Subterranean Ground	3
<i>Talpa europaea</i>					
Least weasel	S	High	SM	Subterranean Ground	3
<i>Mustela nivalis</i>					

Long-tailed weasel <i>Mustela frenata</i>	S	High	SM	Subterranean Ground	3
Masked shrew <i>Sorex cinereus</i>	S	High	I	Subterranean Ground	3
Mole-rat <i>Spalax leucodon</i>	S	High	B, V	Subterranean Ground	3
Pygmy shrew <i>Microsorex hoyi</i>	S	High	I	Subterranean Ground	3
Short-tailed weasel <i>Mustela erminea</i>	S	High	SM	Subterranean Ground	3
Siberian mole <i>Talpa altaica</i>	S	High	I	Subterranean Ground	3
Water shrew <i>Sorex palustris</i>	S	High	A, I, SM	Subterranean Ground	3
Spotted hyena <i>Crocuta crocuta</i>	S	High	LM, MM	Water	3
Heather vole <i>Phenacomys intermedius</i>	Mixed	Low	WV	Arboreal Surface	4
Eastern gray squirrel <i>Sciurus carolinensis</i>	Mixed	Low	N, S, Mi	Ground Surface	4
Eurasian red squirrel <i>Sciurus vulgaris</i>	Mixed	Low	Co, N, S	Ground Surface	4
Fox squirrel <i>Sciurus niger</i>	Mixed	Low	N, S	Ground Surface	4
Great basin pocket mouse <i>Perognathus parvus</i>	Mixed	Low	S	Ground Surface	4
Hispid pocket mouse <i>Perognathus hispidus</i>	Mixed	Low	S	Ground Surface	4
Japanese squirrel <i>Sciurus lis</i>	Mixed	Low	Co	Ground Surface	4
Little pocket mouse <i>Perognathus longimembris</i>	Mixed	Low	S	Ground Surface	4
Long-tailed pocket mouse <i>Perognathus formosus</i>	Mixed	Low	S	Ground Surface	4

Plains pocket mouse <i>Perognathus flavescens</i>	Mixed	Low	S	Ground Surface	4
Red-tailed squirrel <i>Sciurus granatensis</i>	Mixed	Low	N	Ground Surface	4
Rock pocket mouse <i>Perognathus intermedius</i>	Mixed	Low	S	Ground Surface	4
Tassel-eared squirrel <i>Sciurus aberti</i>	Mixed	Low	N, S, Mu	Ground Surface/Arbo real Surface	4
Alaska ground squirrel <i>Spermophilus undulatus</i>	Mixed	Low	S, V	Subterranean Ground	4
Arctic ground squirrel <i>Spermophilus parryii</i>	Mixed	Low	S, V	Subterranean Ground	4
Botta's pocket gopher <i>Thomomys bottae</i>	Mixed	Low	S	Subterranean Ground	4
Djungarian hamster <i>Phodopus sungorus</i>	Mixed	Low	N, S	Subterranean Ground	4
Golden-mantled ground squirrel <i>Spermophilus lateralis</i>	Mixed	Low	N, S	Subterranean Ground	4
Lesser bandicoot rat <i>Bandicota bengalensis</i>	Mixed	Low	N, S, T	Subterranean Ground	4
Mountain pocket gopher <i>Thomomys monticola</i>	Mixed	Low	V	Subterranean Ground	4
Muskrat <i>Ondatra zibethicus</i>	Mixed	Low	B, R, T, V	Subterranean Ground	4
Northern pocket gopher <i>Thomomys talpoides</i>	Mixed	Low	R, T	Subterranean Ground	4
Pouched mouse <i>Saccostomus campestris</i>	Mixed	Low	N, S	Subterranean Ground	4
Richardson ground squirrel <i>Spermophilus richardsonii</i>	Mixed	Low	S, V	Subterranean Ground	4
Rock squirrel <i>Spermophilus variegatus</i>	Mixed	Low	N, S	Subterranean Ground	4

Syrian golden hamster <i>Mesocricetus auratus</i>	Mixed	Low	S, R, T	Subterranean Ground	4
Thirteen-lined ground squirrel <i>Spermophilus tridecemlineatus</i>	Mixed	Low	S, V	Subterranean Ground	4
Desert woodrat <i>Neotoma lepida</i>	Mixed	Mixed	V	Ground Surface	5
Eastern woodrat <i>Neotoma floridana</i>	Mixed	Mixed	V	Ground Surface	5
White-throated woodrat <i>Neotoma albigula</i>	Mixed	Mixed	V	Ground Surface	5
Bushy-tailed woodrat <i>Neotoma cinerea</i>	Mixed	Mixed	V	Subterranean Ground	5
Mexican woodrat <i>Neotoma mexicana</i>	Mixed	Mixed	S, V	Subterranean Ground	5
Mountain beaver <i>Aplodontia rufa</i>	Mixed	High	V	Subterranean Ground	6
Arctic fox <i>Alopex lagopus</i>	Mixed	High	E, MM, SM	Ground Surface	6
Red fox <i>Vulpes vulpes</i>	Mixed	High	Bi, E, MM, SM	Ground Surface	6
Short-tailed shrew <i>Blarina brevicauda</i>	Mixed	High	A, Fi, I, SM	Subterranean Ground	6
Agouti <i>Dasyprocta punctata</i>	L	Low	N, S	Ground Surface	7
Alipne chipmunk <i>Tamias alpinus</i>	L	Low	N, S	Ground Surface	7
Blue jay <i>Cyanocitta cristata</i>	L	Low	N, Mi, S	Ground Surface	7
Clark's nutcracker <i>Nucifraga columbiana</i>	L	Low	S	Ground Surface	7
Cliff chipmunk <i>Tamias dorsalis</i>	L	Low	N, S	Ground Surface	7
Eastern chipmunk	L	Low	I, N, S		7

<i>Tamias striatus</i>				Ground Surface	
Eurasian jay	L	Low	Co, N, S	Ground Surface	7
<i>Garrulus glandarius</i>				Ground Surface	
Eurasian nutcracker	L	Low	S	Ground Surface	7
<i>Nucifraga caryocatactes</i>				Ground Surface	
Flat-headed vole	L	Low	V	Ground Surface	7
<i>Alticola strelzowi</i>				Ground Surface	
Green achouti	L	Low	N, S	Ground Surface	7
<i>Myoprocta acouchi</i>				Ground Surface	
Least chipmunk	L	Low	N, S	Ground Surface	7
<i>Tamias minimus</i>				Ground Surface	
Lodgepole pine chipmunk	L	Low	N, S	Ground Surface	7
<i>Tamias speciosus</i>				Ground Surface	
North American pika	L	Low	V	Ground Surface	7
<i>Ochotona princeps</i>				Ground Surface	
Pinyon jay	L	Low	N, S	Ground Surface	7
<i>Gymnorhinus cyanocephalus</i>				Ground Surface	
Red achouchi	L	Low	N, S	Ground Surface	7
<i>Myoprocta exilis</i>				Ground Surface	
Red-tailed chipmunk	L	Low	N, S	Ground Surface	7
<i>Tamias ruficaudus</i>				Ground Surface	
Western scrub jay	L	Low	N, S	Ground Surface	7
<i>Aphelocoma coerulescens</i>				Ground Surface	
Siberian chipmunk	L	Low	N, S	Ground Surface	7
<i>Tamias sibiricus</i>				Ground Surface	
Siberian pika	L	Low	V	Ground Surface	7
<i>Ochotona alpina</i>				Ground Surface	
Steller's jay	L	Low	N, Mi, S	Ground Surface	7
<i>Cyanocitta stelleri</i>				Ground Surface	
Yellow pine chipmunk	L	Low	N, S	Ground Surface	7
<i>Tamias amoenus</i>				Ground Surface	
Douglas' squirrel	L	Low	Co, Mu, S	Ground Surface/Arbo	7
<i>Tamiasciurus douglasii</i>				real Surface	

Red squirrel <i>Tamiascurus hudsonicus</i>	L	Low	Co, Mu, S	Ground Surface/Arbo real Surface	7
African giant rat <i>Cricetomys gambianus</i>	L	Low	N, S, T	Subterranean Ground	7
Alaska vole <i>Microtus miurus</i>	L	Low	V	Subterranean Ground	7
Bank vole <i>Clethrionomys glareolus</i>	L	High	V (Lichen)	Arboreal Cavity/Surfa ce	7
Banner-tailed kangaroo rat <i>Dipodomys spectabilis</i>	L	Low	S	Subterranean Ground	7
Black-bellied hamster <i>Cricetus cricetus</i>	L	Low	T, V	Subterranean Ground	7
Brandt's vole <i>Microtus brandti</i>	L	Low	V, WV	Subterranean Ground	7
California ground squirrel <i>Spermophilus beecheyi</i>	L	Low	S, V	Subterranean Ground	7
Cape mole-rat <i>Georychus capensis</i>	L	Low	B, R, T	Subterranean Ground	7
Cape dune mole-rat <i>Bathyergus suillus</i>	L	Low	T	Subterranean Ground	7
Common mole-rat <i>Cryptomys hottentotus</i>	L	Low	B	Subterranean Ground	7
Common vole <i>Microtus arvalis</i>	L	Low	B	Subterranean Ground	7
Coruro <i>Spalacopus cyanus</i>	L	Low	B, T	Subterranean Ground	7
Daurian pika <i>Ochotona daurica</i>	L	Low	V	Subterranean Ground	7
Deer mouse <i>Peromyscus maniculatus</i>	L	Low	S	Subterranean Ground	7
Desert kangaroo rat <i>Dipodomys deserti</i>	L	Low	S	Subterranean Ground	7
Diurnal sand rat	L	Low	S, V		7

<i>Psammomys obesus</i>				Subterranean Ground	
Edible doormouse	L	Low	B, N, S	Subterranean Ground	7
<i>Myoxus glis</i>				Subterranean Ground	
Forest dormouse	L	Low	Co, S	Subterranean Ground	7
<i>Dryomys nitedula</i>				Subterranean Ground	
Giant kangaroo rat	L	Low	S	Subterranean Ground	7
<i>Dipodomys ingens</i>				Subterranean Ground	
Great basin kangaroo rat	L	Low	S	Subterranean Ground	7
<i>Dipodomys microps</i>				Subterranean Ground	
Greater long-tailed hamster	L	Low	V	Subterranean Ground	7
<i>Cricetulus triton</i>				Subterranean Ground	
Hazel doormouse	L	Low	Co, N, S	Subterranean Ground	7
<i>Muscardinus avellanarius</i>				Subterranean Ground	
Heermann's kangaroo rat	L	Low	S	Subterranean Ground	7
<i>Dipodomys heermanni</i>				Subterranean Ground	
Indian gerbil	L	Low	S, V	Subterranean Ground	7
<i>Tatera indica</i>				Subterranean Ground	
Meadow vole	L	Low	R	Subterranean Ground	7
<i>Microtus pennsylvanicus</i>				Subterranean Ground	
Merriam's kangaroo rat	L	Low	S	Subterranean Ground	7
<i>Dipodomys merriami</i>				Subterranean Ground	
Mexican jay	L	Low	N, S	Ground Surface	7
<i>Aphelocoma ultramarina</i>				Ground Surface	
Mid-day gerbil	L	Low	N, S, T, V	Subterranean Ground	7
<i>Meriones meridianus</i>				Subterranean Ground	
Mole-rat	L	Low	B, R, T, V	Subterranean Ground	7
<i>Spalax microphthalmus</i>				Subterranean Ground	
Mole vole	L	Low	B, T	Subterranean Ground	7
<i>Ellobius talpinus</i>				Subterranean Ground	
Mountain pygmy possum	L	Low	N, S	Subterranean Ground	7
<i>Burramys parvus</i>				Subterranean Ground	
Namaqua gerbil	L	Low	S	Subterranean Ground	7
<i>Desmodillus auricularis</i>				Subterranean Ground	

Nothern grasshopper mouse	L	Low	S	Subterranean Ground	7
<i>Onychomys leucogaster</i>					
Pale kangaroo mouse	L	Low	S	Subterranean Ground	7
<i>Microdipodops pallidus</i>					
Pallas' pika	L	Low	V	Subterranean Ground	7
<i>Ochotona pallasi</i>					
Plains pocket gopher	L	Low	B, T	Subterranean Ground	7
<i>Geomys bursarius</i>					
Prairie vole	L	Low	S	Subterranean Ground	7
<i>Pitmys ochrogaster</i>					
Reddish-gray vole	L	Low	V	Subterranean Ground	7
<i>Clethrionomys rufocanus</i>					
Rook	L	Low	Co, N, S	Ground Surface	7
<i>Corvus frugilegus</i>					
Santa Cruz kangaroo rat	L	Low	S	Subterranean Ground	7
<i>Dipodomys venustus</i>					
Social vole	L	Low	B, R	Subterranean Ground	7
<i>Microtus socialis</i>					
Southeastern pocket gopher	L	Low	B, T	Subterranean Ground	7
<i>Geomys pinetis</i>					
Spiny pocket mouse	L	Low	Fr, N, S	Subterranean Ground	7
<i>Heteromys desmarestianus</i>					
Taiga vole	L	Low	V	Subterranean Ground	7
<i>Microtus xanthognathus</i>					
Tamarisk gerbil	L	Low	N, S, T,	Subterranean Ground	7
<i>Meriones tamariscinus</i>					
Tree mouse	L	Low	S, N	Subterranean Ground	7
<i>Beomys major</i>					
White-footed mouse	L	Low	N, S	Subterranean Ground	7
<i>Peromyscus leucopus</i>					
American beaver	L	Mixed	V, WV	Water	8
<i>Castor canadensis</i>					

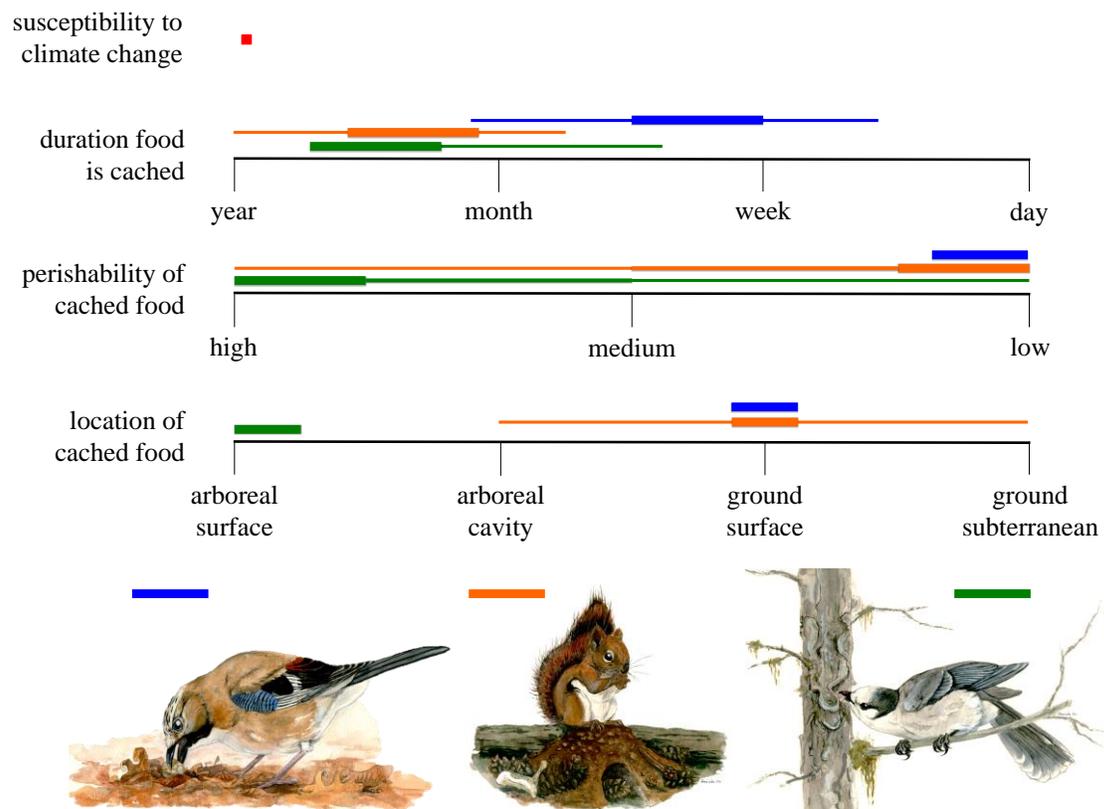
Dusky-footed woodrat <i>Neotoma fuscipes</i>	L	Mixed	N, S, V	Subterranean Ground	8
Eurasian beaver <i>Castor fiber</i>	L	Mixed	V, WV	Water	8
Bull-headed shrike <i>Lanius bucephalus</i>	L	High	Bi, I, SM	Arboreal Surface	9
Gray jay <i>Perisoreus canadensis</i>	L	High	Ca, Fr, I, Mi	Arboreal Surface	9
Siberian jay <i>Perisoreus infaustus</i>	L	High	Ca, Fr, I	Arboreal Surface	9
Wolverine <i>Gulo gulo</i>	L	High	LM, MM	Ground Surface	9

Legend: A-amphibian, B-bulb, Ba-bat, Bi-bird, Ca-carrion, Co-cone, E-eggs, Fi-fish, Fr-fruit, I-invertebrates, LM-large mammal, N-nuts, Mi-miscellaneous human foods, MM-medium mammal, Mu-mushroom, R-roots, Re-reptiles, S-seeds, SM-small mammal, T-tuber, V-vegetation, WV-woody vegetation. Note that mammal classifications are based off of Vander Wall (1990).

2.12 Figures

2.12.1 Predicted susceptibility of food-caching species to climate change

Major axes predicted to influence the susceptibility of caching species to climate change with three examples of species plotted along each axis (drawings below depict each species displaying their typical caching behaviour). Duration indicates the length of time that a food item is stored. Perishability indicates how susceptible a food item is to microbial degradation. The location where food is stored falls under four categories ranging from high (arboreal) to low (ground) susceptibility. On each axis, being placed towards the left side of the continuum means that a species is predicted to be most susceptible to climate change. Each line represent the variation within a species on a particular axes with the thickness of a line increasing with the more characteristic location, duration and perishability of caches for each focal species. For example, Gray Jays store a variety of perishable food items ranging from meat to mushrooms and store food for durations ranging from weeks to months. The line is thickest for highly perishable food as this is their primary food source. Green represents Gray Jays, blue represents Eurasian Jays and orange represents Red Squirrels. All illustrations by A. Gubbe.



3 Chapter 2 - Fall freeze-thaw events carry over to depress late-winter reproductive performance in Canada jays

3.1 Abstract

Evidence suggests that range-edge populations are highly vulnerable to the impacts of climate change but few studies have examined the specific mechanisms that are driving observed declines. Species that store perishable food for extended periods of time may be particularly susceptible to environmental change because shifts in climatic conditions could accelerate the natural degradation of their cached food. Here, we use 40 years of breeding data from a marked population of Canada jays (*Perisoreus canadensis*) located at the southern edge of their range in Algonquin Provincial Park, Ontario, to examine whether climatic conditions prior to breeding carry over to influence reproductive performance. We found that the number of fall freeze-thaw events was negatively correlated with reproductive performance (brood size, nest success, and nestling condition) in the subsequent late-winter breeding season of the Canada jay. Our results suggest that freeze-thaw events have a significant negative impact on the quality and/or quantity of cached food available to Canada jays. Future increases in such events, caused by climate change, could pose a serious threat to Canada jays and other food caching species that store perishable foods for long periods of time.

3.2 Introduction

There is strong evidence to suggest that long-term changes in climate have affected a wide range of species around the world (Easterling et al. 2000, Hughes 2000, Cahill et al. 2012). A major consequence of climate change is a poleward shift in the distribution of species (Walther et al. 2002, Poloczanska et al. 2013), whereby populations living at lower latitudes of a species' distribution decline, and are eventually extirpated, because they are most susceptible to warming temperatures (Cahill et al. 2014). However, documentation of such range-edge population declines is rare (Pinsky et al. 2013, Burrows et al. 2014) and even fewer specific mechanisms have been proposed to explain how changes in climate could be causing declines (Cahill et al. 2012, 2014).

One group of animals that may be vulnerable to climate change are those that cache food, especially perishable food (Sutton et al. 2016). Food caching is a behavioural strategy in which an animal defers consumption of a food item and handles it in a way that deters other organisms from accessing stored food so that it can be retrieved during a period when demand for resources outweighs supply (Vander Wall 1990). Once food is cached, it is exposed to environmental conditions that may reduce its quality over time (Sutton et al. 2016, Neuschulz et al. 2015). The degree to which food degrades depends on both the type of food that is stored, as well as where and how long it is stored (Sutton et al. 2016). For example, foods such as nuts and seeds are likely more resistant to changes in environmental conditions compared to perishable foods such as meat, berries, and fleshy fungi (Sutton et al. 2016, Vander Wall 1990).

Canada jays (*Perisoreus canadensis*) are year-round residents of the boreal forest that cache a wide variety of perishable foods including arthropods, mushrooms, berries and vertebrate flesh (both carrion and prey) in the late summer and fall (Strickland and Ouellet 2011). Canada jays are arboreal scatter-hoarders and distribute food caches widely across their territories (Strickland and Ouellet 2011). Foraging for food is not a conspicuous activity in winter, however, and Canada jays do not exploit boreal tree seed crops or have regular access to animal carcasses in otherwise seemingly foodless boreal winter conditions (Strickland and Ouellet 2011). In contrast, food caching is very prominent in the summer and fall (e.g. individuals can make as many as 1000 caches a day in Alaska; T. Waite *unpublished data*). This evidence strongly implies that large quantities of food are stored throughout a typical jay territory and almost certainly account for their observed high territorial fidelity and winter survival (Strickland and Ouellet 2011, Norris et al. 2013). Cached food also supports female increases in body mass prior to clutch initiation (Sechlet et al. 2014) and some evidence suggests that breeding pairs also use stored food to feed nestlings, at least occasionally (Derbyshire et al. 2019). Critically, however, and notwithstanding the high perishability of food cached by Canada jays, food must survive in sufficient quantity or quality from the time of storage in summer or fall to the following breeding season if it is to explain the high winter survival and late-winter breeding performance in this species.

Until the onset of consistent sub-freezing winter temperatures, the temperature dependent degradation of perishable food items stored in the fall is expected to be an important determinant of food quality (Sechlet et al. 2015). Waite and Strickland (2006) documented a decline in our southern range-edge population of Canada Jays and proposed that warmer fall temperatures

might be accelerating declines in the quality of cached perishable food items, which then carry over to influence reproductive success. Using 26 years of data from Algonquin Provincial Park, Ontario (APP), they provided some support for their ‘hoard-rot’ hypothesis by showing that both clutch size and the timing of breeding were negatively correlated with mean fall temperatures. However, the support for both models was relatively weak and there was no evidence that fall temperature influenced brood size, one of the key indicators of reproductive performance.

One possible explanation for this relative lack of support is that other changing features of our study area’s warming climate (i.e., beyond higher temperatures) may be contributing to declines in the quality or quantity of stored food, ostensibly resulting in the observed decline of our study population. Food scientists have identified a number of environmental variables, including temperature, and freeze-thaw events, that influence food quality and which may be relevant to wild populations (Sutton et al. 2016). Temperature affects the quality of perishable food primarily through its influence on microbial growth rates (Mossel and Ingram 1955). In contrast, freeze-thaw events act in three distinct ways to degrade perishable food. First, freezing and thawing of a food item causes the denaturation of proteins, which can have downstream consequences on nutritional quality (Kidmose and Martens 1999, Boonsumrej et al. 2007, Ali et al. 2015). Second, as water undergoes phase changes (i.e. liquid to solid and vice versa) it causes cell membranes to rupture and this breakage allows enhanced physical leakage during subsequent thaw periods. This process of the soluble contents of the cell leaving is known as ‘drip-loss’ (Castrillón et al. 1996, 1997, Matos et al. 2011). Finally, ‘drip-loss’ also causes enhanced microbial degradation during thaw periods as nutrients are easily accessed by microbes both within a cell and in the area surrounding the damaged food item (Li and Sun 2002). By

extension, perishable food cached by Canada jays could be susceptible to degradation caused by freeze-thaw events and thus they should be considered when evaluating the ‘hoard-rot’ hypothesis.

Our goal was to examine how climate variables linked to specific food degradation mechanisms might influence Canada jay reproductive performance. Using data on reproductive performance from an individually marked population of Canada jays in APP, we examined two hypotheses. The first, “Warmer-Temperatures” hypothesis was that increasing mean temperatures during the fall and pre-breeding periods lead to greater microbial degradation of perishable food caches that are used by jays during their late-winter breeding period. The second, “Number of Freeze-Thaw Events” hypothesis was that the number of freeze-thaw events that occurred during the fall and pre-breeding periods would damage perishable cached food through both physical and microbial degradation, limiting the amount of food available during the late-winter breeding period. We tested predictions arising from these hypotheses by measuring brood size, nest success and nestling condition from 718 nests monitored between 1977 and 2016.

3.3 Methods

3.3.1 Study area and species

We conducted our study in Algonquin Provincial Park, Ontario, Canada (Figure 1; APP; 45° N, 78° W), where Canada jays have been marked and monitored since 1964 (Rutter 1969, Strickland 1991, Whelan et al. 2016). Individuals within the study area maintain ~130 ha year-round territories and store food items under tree bark and arboreal lichens beginning in the late summer and early fall (Strickland et al. 2011). In this analysis, we use data beginning in 1977

because few nests were found prior to this year and it also allowed us to include a higher proportion of known-age birds.

Each year (N = 40; 1977 - 2016) up to 24 nests (mean = 18, range 9 – 25) in the study area were found and monitored throughout the breeding season (February-May). Nests were accessed approximately 11 d after the nestlings hatched to take morphometric measurements of young and determine brood size. All young were given a unique combination of coloured leg bands and a Canadian Wildlife Service aluminum band. Unmarked individuals that disperse into the study site, typically as juveniles, were captured during the fall population census conducted in October and uniquely marked in the same way as nestlings.

3.3.2 *Reproductive performance*

We considered three metrics of reproductive success: (1) '*brood size*': the total number of nestlings in a nest at the time of banding (excluding nests that failed prior to nestling being banded and measured), (2) '*nest success*': whether the first nest attempt of the year had young in the nest at banding, and (3) '*nestling condition*': mass given body size of a nestling at the time it was banded in the nest (typically ~ 11 d after hatching). Nestling condition was calculated following Derbyshire et al. (2015) by first estimating body size using a principal component analysis (PCA; Dunteman 1989, Rising and Somers 1989) on a correlation matrix of tarsus, seventh primary and bill length measurements. This estimate was then regressed against mass using an asymptotic exponential model and residuals from this model were considered to be an estimate of body condition (Derbyshire et al. 2015). Negative residuals represent individuals that weighed less than expected for a given body size and therefore were assumed to be in below-average condition, while individuals with positive residuals weighed more than expected for a

given body size and were assumed to be in above-average condition. In total, 1263 nestlings from 718 nests were used in the analysis.

3.3.3 Historical weather data

Historical weather records (maximum, minimum and mean temperatures) for two periods of the annual cycle ('fall': Oct. - Dec. and 'pre-breeding': Jan. - Feb.) were available from two weather stations. Weather data from 1977 - 2005 were collected from the Dwight weather station (45°23' N 78°54' W; http://climate.weather.gc.ca/historical_data/search_historic_data_e.html), 15 km outside Algonquin's western boundary and data from 2004-2017 were collected at its East Gate (45°32' N 78°16' W; https://weather.gc.ca/city/pages/on-29_metric_e.html), located in the south-eastern section of our study area. For the time period of overlap between the two weather stations (Sept. 2004 – Dec. 2005), we compared temperatures from the two stations using reduced major axis regression (RMA). RMA regression was used because there is potential measurement error associated with temperature (i.e. at each station; Schulte-Hostedde et al. 2005). The regression equations generated were then used to transform data from the Dwight weather station. The relationship of all three temperature variables between the two weather stations appeared to vary seasonally, so we used two season-specific ('seasons' determined by the equinoxes) equations to adjust the data from the Dwight station (East Gate fall temperature: $-0.949 + 0.997 \cdot \text{Dwight fall temperature}$, $R^2 = 0.96$, $p < 0.001$ and East Gate winter temperature: $-0.989 + 1.023 \cdot \text{Dwight winter temperature}$, $R^2 = 0.91$, $p < 0.001$) were applied to the Dwight data.

3.3.4 *Quantifying weather variables*

Freeze-thaw events were calculated by estimating the ‘*initial freezing point*’ (IFP) of food types (meat, mushrooms and berries) that emulated food items consumed by Canada jays (Strickland and Ouellet 2011; see Table S1). IFP, the point at which ice crystal formation begins, is required to predict both physical and microbial properties of food (Miles et al. 1997). We decided to use the mean of the initial freezing point of meat (-1.9°C) as the value to calculate freeze-thaw events from the historical climate records because this was the lowest value among the food types we surveyed from the literature (Table S2) and, therefore, a conservative representation of the initial freezing point for food consumed by jays (i.e. produced the fewest freeze-thaw events). We considered a freeze-thaw event to occur when daily maximum temperatures and daily minimum temperature fluctuated above and below the IFP. For example, if minimum temperatures were below the IFP on consecutive days and maximum temperature rose above IFP on one of these days, then we considered this to be a freeze-thaw event (Figure 1). The total number of freeze-thaw events was then summed for both fall (Oct. – Dec.) and pre-breeding (Jan. – Feb.) periods. Mean daily temperatures were averaged during the fall and pre-breeding periods to calculate a mean temperature for each period.

3.3.5 *Statistical analysis*

To understand how the frequency of freeze-thaw events and mean temperature during the fall and pre-breeding periods influenced reproductive performance, we constructed a series of generalized mixed effect models for each response variable (brood size: Poisson distribution; nest success: binomial distribution; nestling condition: Gaussian distribution). For each model series, we considered four climate variables: the frequency of freeze-thaw events during the fall

(‘Freeze-Fall’), the frequency of freeze-thaw events during the pre-breeding period (‘Freeze-Pre’), mean temperature during the fall (‘Temp-Fall’), and mean temperature during the pre-breeding period (‘Temp-Pre’). Each series of models, including the base model without climate variables, included the following fixed effects: supplementation (whether individuals on specific territories were regularly fed by park visitors; see Derbyshire et al. (2015)), male age, female age and first egg date (the date at which females began incubating). Each fixed effect was included based on previous evidence suggesting that it influences reproductive performance (supplementation: Derbyshire et al. 2015, male age: Whelan et al. 2016, female age: Strickland et al. 2011, Whelan et al. 2017, lay date: Whelan et al. 2017). For the nestling condition model, brood size was also included as a fixed effect. All models also included year and male and female identity as random effects because many individuals bred in multiple years. For each response variable, we constructed models with single climate variables as well as all possible combination of climate variables in addition to the fixed effects in the base model. We also included an interaction between first egg date and freeze-thaw events or temperature because we were interested in examining whether the possible negative effects of these climate variables were stronger for pairs that nested later in the season given that (a) there is evidence that later nesting birds have lower reproductive success (Whelan et al. 2016, 2017) and (b) later nesting birds would retrieve caches that have been stored for longer periods of time to feed their young compared to earlier nesting birds.

Akaike’s Information Criterion corrected for small sample sizes (AICc) was then used to rank competing models (Burnham and Anderson 2002). All models within $\Delta AICc \leq 2$ were considered as competing to describe variation in reproductive performance (Burnham and

Anderson 2002) and Akaike weights provided the cumulative support for a model given all competing models. All statistical tests and calculations were performed in R v. 3.3.2 (R Core Team 2017) using the lme4 (Bates et al. 2015) and AICcmodavg (Mazorelle 2017) packages. Visreg (Breheny and Burchett 2017) was used to visualize regression lines and confidence intervals for each regression line were estimated using bootpredictlme4 (Duursma 2017).

Fixed effects in each model predicting either brood size, nest success or nestling condition were not highly correlated ($r < 0.3$).

3.4 Results

3.4.1 Description of climate variables and reproductive performance

Both mean temperature and frequency of freeze-thaw events varied considerably over the course of the study. Mean temperature in the fall ranged from -4.4°C to 2.4°C (mean \pm S.D; $-0.6^{\circ}\text{C} \pm 1.5$), while mean pre-breeding temperature varied from -16.4°C to -6.2°C ($-10.7^{\circ}\text{C} \pm 2.3$). The frequency of freeze-thaw events in the fall ranged from 20 to 57 (40 ± 11) and between 1 and 32 (15 ± 7) in the pre-breeding period.

Brood size ranged from 0 nestlings (failed nests) to a maximum of 5 nestlings (1.7 ± 1.4 nestlings). Thirty-five percent (252 of 718) of nests failed before banding at day 11 and nestling condition varied widely across nests, with residuals from the mass-body size regression ranging from -18.80 to 13.44 (0.18 ± 4.1).

3.4.2 Brood size

Four top models ($\Delta\text{AICc} \leq 2$) best predicted brood size (Table 1) but each model included the frequency of fall freeze-thaw events and mean pre-breeding temperature, both of which were

negatively correlated with brood size (Figure 2a and b; Table S3). As expected, female age was positively correlated with brood size (Figure 2d; Table S3) and lay date showed a strong negative correlation with brood size (Figure 2c; Table S3).

3.4.3 Nest Success

There was only one top model to predict variation in nest success (whether a nest contained nestlings at the time of banding) and, similar to brood size models, it included both the frequency of fall freeze-thaw events and mean pre-breeding temperatures (Table 3). However, the top model also included an interaction between lay date and the frequency of fall freeze-thaw events, suggesting that the negative effect of freeze-thaw events on nest success was more pronounced for late nests compared to early nests (estimate and 95% confidence interval; -0.26 (-0.275 - -0.225); Figure 3a). There was a negative correlation between mean pre-breeding temperatures and nest success (-0.22 (-0.255 - -0.185); Figure 3b). As expected, female age was positively correlated with nest success (0.24 (-0.22 – 0.7); Figure 3c).

3.4.4 Nestling condition

The top model to explain variation in nestling condition only included climate variables from the fall: the frequency of freeze-thaw events and mean temperature. Consistent with both the brood size and nest success models, the frequency of fall freeze-thaw events was negatively correlated with nestling condition (-0.70 (-1.08 - -0.33); Figure 4a). Mean fall temperature, however, was positively correlated with nestling condition (0.32 (0.091 – 0.54); Figure 4b). As expected, there was evidence for a negative correlation between lay date and nestling condition (-0.47 (-0.77 - -0.17); Figure 4c). Nestling condition was also negatively correlated with brood size, suggesting

that lower nestling condition was also associated with a higher number of siblings in the nest (-0.74 (-1.08 - -0.41); Figure 4d).

3.5 Discussion

Our study provides evidence that the number of freeze-thaw events during the fall caching period and, to a lesser extent, mean temperature in the winter pre-breeding period carry over to influence several measures of reproductive performance in Canada jays during their subsequent late-winter breeding season. These results support the general idea of the hoard-rot hypothesis (Waite and Strickland 2006) but our analysis provides stronger support for an effect of freeze-thaw events that can cause physical degradation and may exacerbate the microbial degradation of perishable food associated with above-freezing temperatures.

Experimental studies on food consumed by humans have demonstrated consistent negative effects of freeze-thaw events on food quality (Kidmose and Martens 1999, Boonsumrej et al. 2007, Castrillón et al. 1996, Castrillón et al. 1997, Miles et al. 1997, Matos et al. 2011) and it is likely that similar effects occur with perishable food items cached by Canada jays. We provide support for this hypothesis but it is important to note that we have not directly tested the effect of freeze-thaw events on cached food. Further, our results permit few firm conclusions about the relative importance of the mechanisms by which freeze-thaw events are known to degrade food quality. It seems unlikely that the denaturation of proteins alone could be responsible for a majority of the degradation of food caches, as protein within a food item is likely not being degraded to the point where it is no longer usable by Canada jays (Boonsumrej et al. 2007, Li and Sun 2002). It is difficult to differentiate between the degradation caused by the two remaining processes associated with freeze-thaw events as they are directly related. Both

drip loss and enhanced microbial degradation during thaw periods stem from the prior physical damage to cell membranes caused by freezing and thawing (Castrillón et al. 1996, Castrillón et al. 1997, Boonsumrej et al. 2007). The primary differences between these processes are that degradation due to drip-loss could, in principle, occur in a completely sterile environment and would be dependent on the duration of post-freezing thaws (i.e. longer thaws allow more liquid to leave the cell), whereas food quality degradation attributable to enhanced of microbial growth will depend on the intensity (warmth), as well as the duration of post-freezing thaws. These distinctions aside, our finding of an important effect of freeze-thaw events in the fall, as opposed to those occurring in the pre-breeding period, is equally consistent with degradation due to both drip loss and microbial growth, making it difficult to distinguish between them. A fall freeze-thaw event is expected to have a more negative impact on subsequent reproductive performance simply because the total duration of subsequent thaws, between storage and the eventual breeding-season consumption of a cached food item, will be longer after a fall freezing event than after a late-winter, pre-breeding event.

Our finding that the total number of fall freeze-thaw events is negatively correlated with reproductive performance also suggests that continued freezing and thawing is an important determinant of food quality. Above we outlined the processes by which a single freeze-thaw event may influence food quality, but there is evidence that the negative effects become compounded with each freeze-thaw event that occurs (Boonsumrej et al. 2007, Ali et al. 2015). Previous experiments have demonstrated this over the course of relatively few cycles (e.g. 4 to 6), but it remains to be seen if the negative effects of freeze-thaw events would continue to

accumulate over a typical fall/late winter in APP, or if there is a point where food quality deteriorates to a point where it is no longer influenced by additional freeze-thaw events.

Individual metrics of reproductive success are correlated with fall and pre-breeding climatic conditions via different mechanisms that link food degradation and the use of a cached food item. Both brood size and nest success are directly related to decisions that a breeding pair makes, in particular how much energy to allocate to reproduction instead of maintaining individual condition (Norris et al. 2013). Cached food is used to support pre-breeding weight gain in females (Sechley et al. 2014) and, therefore, if food has degraded prior to clutch initiation, females may choose to invest less energy towards the number of eggs laid and divert it instead towards maintaining their over-winter condition. This is supported by previous work on Canada jays that has demonstrated an effect of fall climatic conditions on reproduction, but not on over-winter survival (Norris et al. 2013, Waite and Strickland 2006). Similarly, nest success could be influenced by food available to a female because this would dictate the amount of energy that can be invested in reproduction and when a female should abandon a nest to devote more energy to survival. In contrast to both brood size and nest success, nestling condition is directly influenced by the quality of food that is being fed to young as they develop (Magrath 1991). Therefore, when food is degraded by environmental conditions, less energy can be derived from each cached food item and nestling condition would be expected to suffer.

Our analysis also points to an intriguing interaction between events in two different periods of the annual cycle. In terms of nest success, Canada jays nesting later in the season, perhaps due to inexperience or lower food reserves, appear to be more susceptible to variation in the frequency of fall freeze-thaw events compared to individuals nesting early in the season.

Individuals nesting later in the season may be raising nestlings at times when temperatures have warmed sufficiently to degrade cached food stores and when there is still little fresh food available in the environment. Thus, late nesting pairs could be more heavily impacted by poor fall conditions, while early nesting pairs may still have sufficient cached food stores to raise young, even under poor fall conditions. The importance of early nesting for reproductive performance has been reported previously (Derbyshire et al. 2015, Whelan et al. 2017) and, collectively, our work highlights an interesting, potentially opposing effect of long-term changes in climate: warmer falls, which could lead to an increased number of freeze-thaw events, appear to have a negative effect on reproductive performance (Waite and Strickland 2006), whereas warmer late winters appear to have a positive effect because a higher proportion of birds nest earlier in the season and, therefore, have higher reproductive success. How these opposing effects of climate may influence long-term population trends remains to be investigated.

In addition to the observed effects on reproductive performance, climate variables in the fall and pre-breeding periods could carry-over to influence other vital rates, such as survival. Nestling condition is a key determinant of post-fledging survival and, in many passerine species including European blackbirds (*Turdus merula*), great tits (*Parus major*), and coal tits (*P. ater*), there is a positive relationship between nestling condition and survival (Magrath 1991, Naef-Daenzer et al. 2001, Mitchell et al. 2011). The negative relationship we observed between fall climate and nestling condition suggests that conditions during the fall caching period could influence more than just fecundity. Future studies are needed to quantify potential effects of climatic phenomena across critical life stages, which could have a significant downstream impact on population growth rate.

Contrary to the predictions of the hoard-rot hypothesis, we found a positive correlation between fall temperature and nestling condition. This surprising effect is challenging to explain but one possibility is that warmer temperatures could have a positive influence on the over-winter survival of prey items that become available in the spring during the nestling period. Warmer fall conditions generally translate to more benign over-wintering conditions that increase arthropod survival (Turnock and Fields 2005). Higher fall temperatures could, therefore, produce larger or earlier emergence events in the spring and more opportunity for adults to collect greater volumes of food to feed nestlings.

Although we provide evidence that Canada jay reproductive performance is influenced by climate during the fall and, to a lesser extent, the winter pre-breeding period, we do not yet know if these factors are driving the observed decline of Canada jays in APP. Neither freeze-thaw events nor mean temperature in either the fall or pre-breeding period showed a significant linear increase over time (mean temperature: $t = 1.3$, $p > 0.05$, freeze-thaw events: $t = -2.6$, $p = 0.02$). Thus, while variation in fall and winter climate may play important roles in determining fecundity, it is possible that fecundity may not be the primary vital rate driving population growth. Consistent with this, observed declines in fecundity in our study population do not match steeper declines in population abundance. There is also no evidence for a corresponding decline in adult survival over the same time period (Norris et al. 2013). The primary demographic vital rate driving declines may be juvenile (first year) survival and subsequent lack of recruitment into the population. What is required is an understanding of how environmental factors throughout the annual cycle influence all vital rates, as well as the relative contribution of those vital rates to population growth (Woodworth et al. 2017).

Identifying mechanisms that link climate change and fitness is important in order to predict future population responses to climate change (Cahill et al. 2014). Our results suggest that Canada jay populations in areas experiencing increases in the number of freeze-thaw events and warmer winter temperatures could be particularly susceptible to climate change.

Environments at both high elevations and northern latitudes, which include much of the Canada jay's range, are predicted to experience more pronounced climatic changes over time than other regions in North America (Plummer et al. 2006). These predicted changes in climate across North America could lead to widespread population declines that may not be restricted to the current southern edge of the Canada jay's range.

Our study presents evidence of freeze-thaw events influencing reproductive performance in a single food-caching species, but several other food-caching species could be similarly affected by carry-over effects of environmental phenomena. Following the framework proposed by Sutton et al. (9), species that store perishable foods for long periods of time, similar to Canada jays, are predicted to be most susceptible to environmental conditions that influence food quality over time. One species in this high-risk category is the wolverine (*Gulo gulo*), which is declining at the southern edge of its range (Inman et al. 2012). However, few other species in this category have sufficient demographic data necessary to evaluate how degradation of cached food could influence either survival or reproduction. Long-term demographic studies are needed to assess how climatic events throughout the year, and in particular the events that occur between storage and retrieval of a food item, could influence either survival or reproduction in these species.

3.6 Tables

3.6.1 Table 1 Model comparison to explain variation in brood size of Canada jays using Akaike's Information Criterion for small sample sizes (AICc).

The base model included level of supplementation, male age, female age and lay date but no climate variables. All other models also included these fixed effects. Climate variables added in each model are listed in addition to the total number of parameters in a model (K), AICc and Δ AICc scores and AICc weight.

Model predicting brood size	K	AICc	ΔAICc	AICc Weight
Freeze-Fall + Temp-Pre + Freeze-Fall*Lay Date	11	2178.66	0	0.23
Freeze-Fall + Temp-Pre	10	2178.76	0.10	0.22
Freeze-Fall + Temp-Pre + Freeze-Pre	11	2178.86	1.20	0.13
Freeze-Fall + Temp-Fall + Temp-Pre	11	2180.35	1.69	0.10
Freeze-Fall	8	2180.78	2.11	0.08
Freeze-Fall + Temp-Fall	9	2181.52	2.85	0.06
Freeze-Fall + Temp-Fall + Temp-Pre + Freeze-Pre	12	2181.58	2.92	0.05
Temp-Pre	9	2181.85	3.19	0.05
Temp-Fall	8	2182.43	3.77	0.04
Temp-Pre + Freeze-Pre	10	2183.21	4.55	0.02
Base Model	7	2183.78	5.12	0.02

Freeze = frequency of freeze-thaw events, Temp = mean temperature, Fall = fall caching period (October – November), Pre = Pre-breeding period (January – February)

3.6.2 Table 2 Model comparison to explain variation in nest success of Canada jays using Akaike's Information Criterion for small sample sizes (AICc).

The base model included level of supplementation, male age, female age and lay date but no climate variables. All other models also included these fixed effects. Climate variables added in each model are listed in addition to the total number of parameters in a model (K), AICc and Δ AICc scores and AICc weight.

Model predicting nest success	K	AICc	ΔAICc	AICc Weight
Freeze-Fall + Temp-Pre + Freeze-Fall*Lay Date	11	767.34	0	0.58
Freeze-Fall + Temp-Pre	10	770.24	2.90	0.15
Freeze-Fall + Temp-Fall + Temp-Pre	11	771.73	4.39	0.07
Freeze-Fall + Temp-Pre + Freeze-Pre	11	772.26	4.92	0.05
Temp-Pre	9	773.29	5.95	0.03
Freeze-Fall	9	773.55	6.21	0.03
Freeze-Fall + Temp-Fall + Temp-Pre + Freeze-Pre	12	773.71	6.37	0.03
Freeze-Fall + Temp-Fall	10	773.87	6.60	0.02
Freeze-Pre	9	774.61	7.27	0.02
Temp-Pre + Freeze-Pre	10	775.25	7.91	0.01
Base Model	8	775.90	8.56	<0.01

Freeze = frequency of freeze-thaw events, Temp = mean temperature, Fall = fall caching period (October – November), Pre = Pre-breeding period (January – February)

3.6.3 Table 3 Model comparison to explain variation in nestling condition of Canada jays using Akaike's Information Criterion for small sample sizes (AICc).

The base model included level of supplementation, male age, female age and lay date but no climate variables. All other models also included these fixed effects. Climate variables added in each model are listed in addition to the total number of parameters in a model (K), AICc and Δ AICc scores and AICc weight.

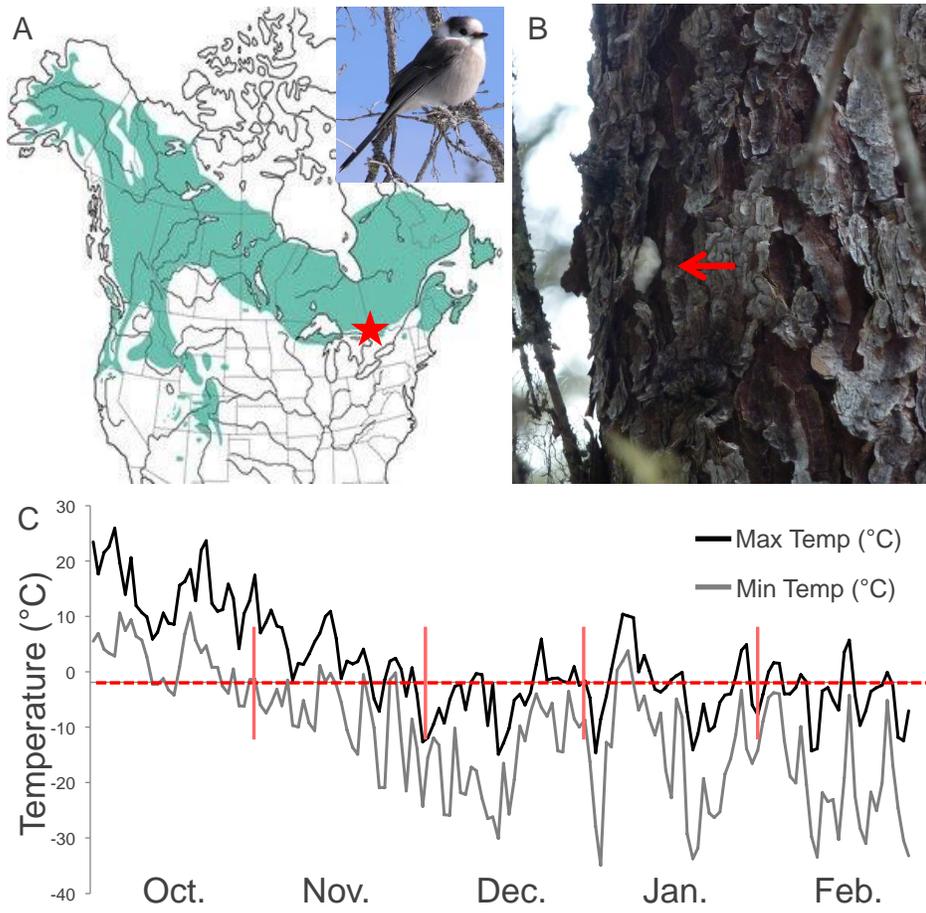
Model predicting nestling condition	K	AICc	ΔAICc	AICc Weight
Freeze-Fall + Temp-Fall	11	6624.6	0	0.65
Freeze-Fall + Temp-Fall + Freeze-Fall*Lay Date	12	6627.4	2.8	0.16
Freeze-Fall + Temp-Fall + Freeze-Pre	12	6628.9	4.3	0.08
Freeze-Fall + Temp-Pre + Temp-Pre	12	6629.0	4.4	0.07
Freeze-Fall	10	6631.6	7.0	0.02
Freeze-Fall + Temp-Fall + Temp-Pre + Freeze-Pre	13	6632.1	7.5	0.02
Freeze-Fall + Temp-Pre	11	6634.5	9.9	<0.01
Freeze-Fall + Temp-Pre + Freeze-Pre	12	6637.7	13.1	<0.01
Base Model	9	6641.3	16.7	<0.01
Temp-Pre	10	6643.3	18.7	<0.01
Temp-Fall	10	6643.4	18.8	<0.01
Freeze-Pre	10	6646.3	19.8	<0.01

Freeze = frequency of freeze-thaw events, Temp = mean temperature, Fall = fall caching period (October – November), Pre = Pre-breeding period (January – February)

3.7 Figures

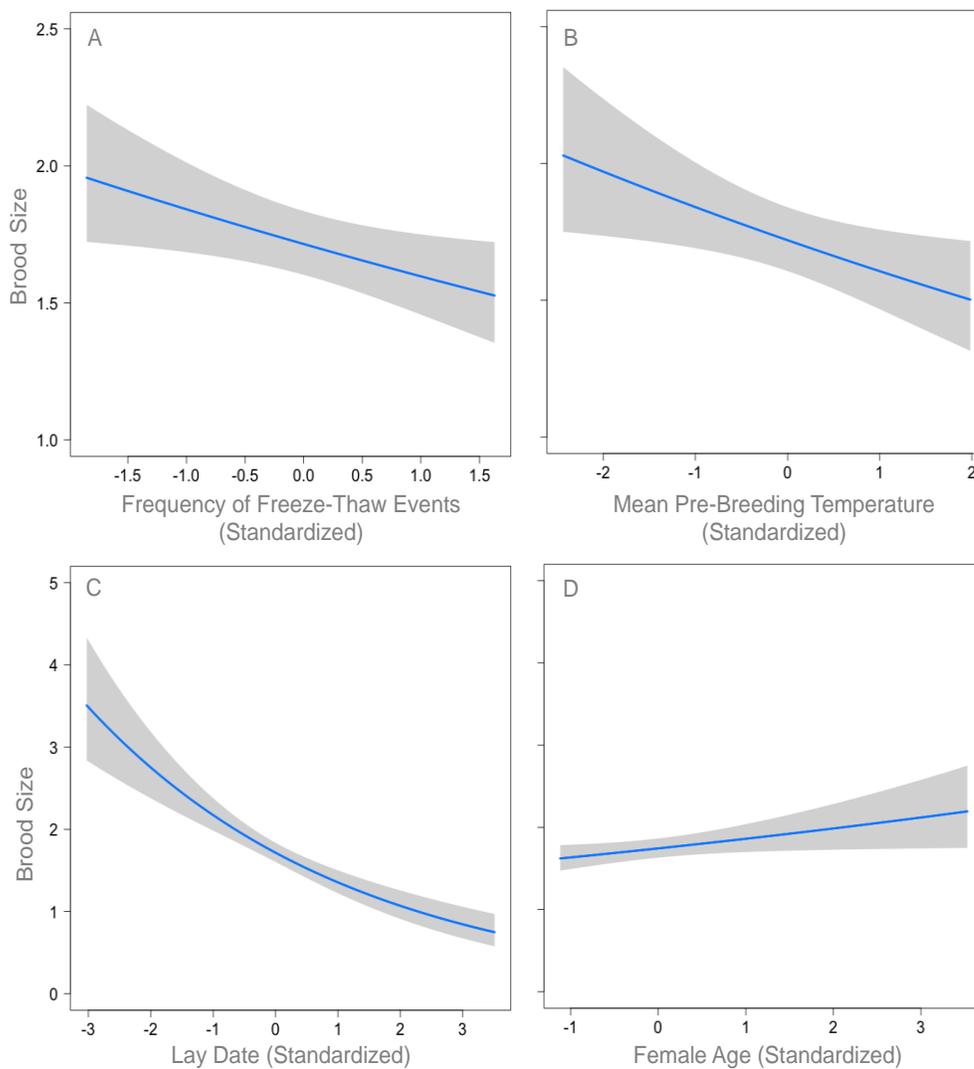
3.7.1 *Figure 1 Canada jay range, cached food item and example of a fall temperature profile*

A) range of Canada jays (*Perisoreus canadensis*) across North America. The red star denotes the study area in Algonquin Provincial Park, Ontario. Inset is a Canada jay. B) A Canada jay food cache in the fall. The red arrow indicates the food bolus placed under a bark flake on a black spruce (*Picea mariana*). C) An example of a temperature profile throughout the fall caching period (Oct. – Dec.) and the pre-breeding period (Jan. – Feb.) from 2003. The dashed red line represents the initial freezing point (-1.9°C), which was used to calculate freeze-thaw events (see methods). When maximum daily temperatures exceeded the initial freezing point and minimum temperatures were below the initial freezing point a freeze-thaw event was determined to have occurred.



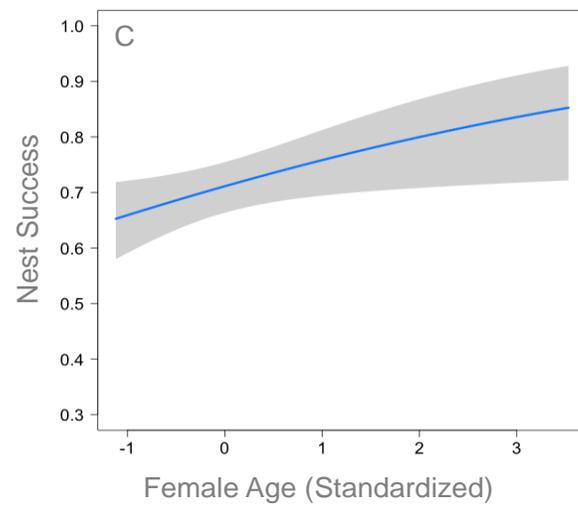
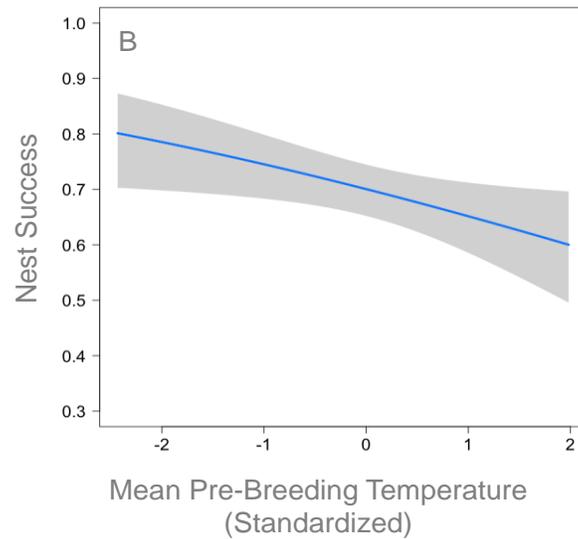
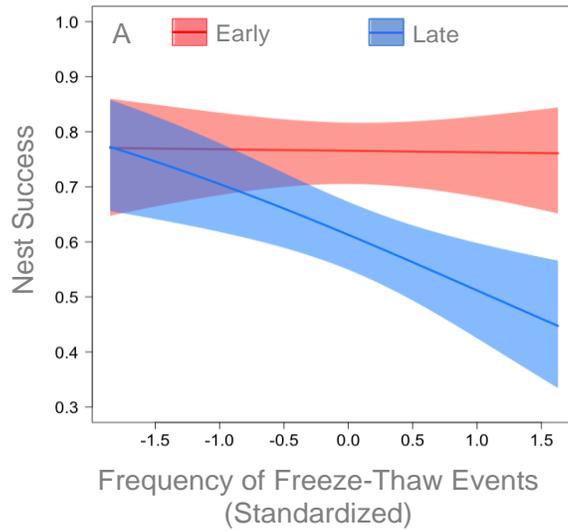
3.7.2 Figure 2 Climatic and non-climatic predictors of brood size in Canada jays

The frequency of freeze-thaw events (A), mean pre-breeding temperature (B) and lay date (C) were all negatively correlated with brood size. Female age was positively correlated with brood size (D). The shaded area on each graph represents a 95% confidence interval. Each line represents the average parameter estimate taken a model average of all top models ($\Delta AIC_c < 2$).



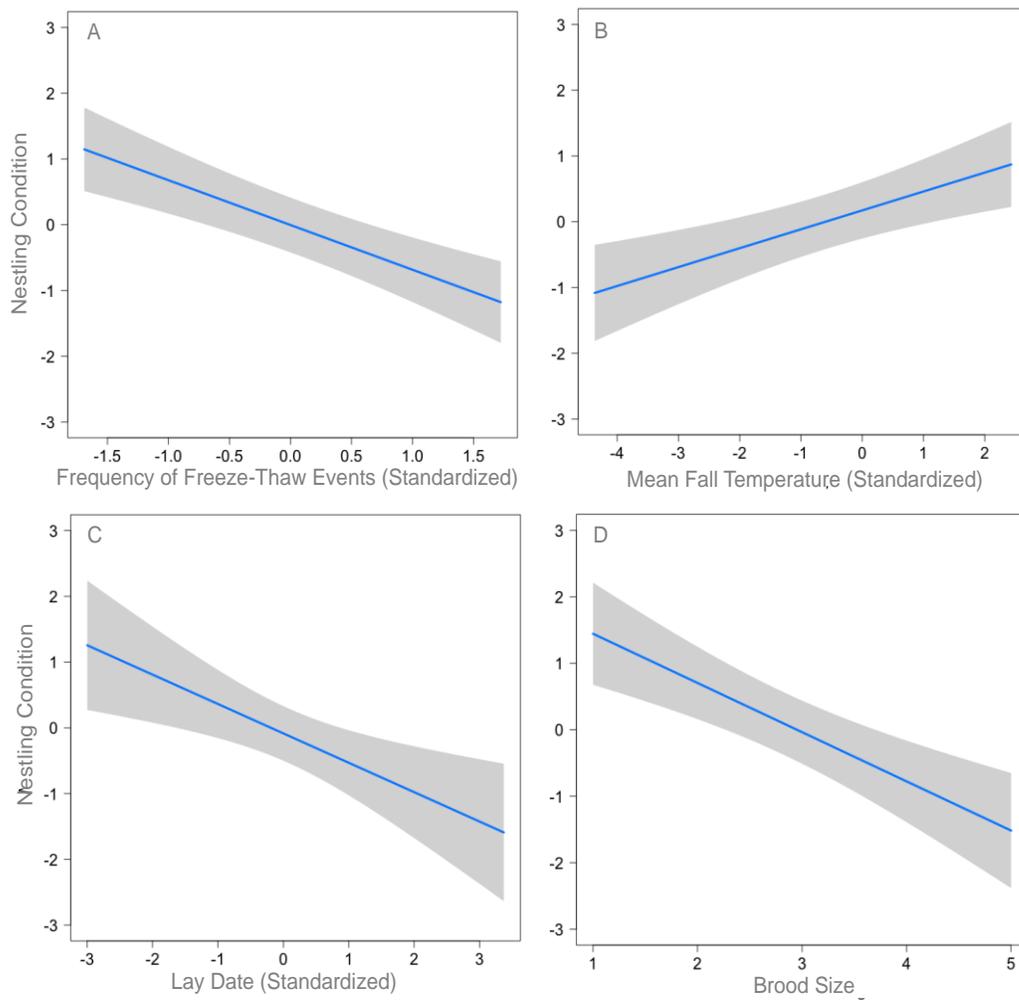
3.7.3 Figure 3 Climatic and non-climatic predictors of nest success in Canada jays

A) There was a significant interaction between lay date and the frequency of fall freeze-thaw events, whereby early nesting pairs (red) were less influenced by freeze-thaw events than late nesting pairs (blue). B) Mean pre-breeding temperatures were negatively correlated with nest success. C) Female age was positively correlated with nest success. The shaded area around each line represents a 95% confidence interval. Each line is taken from the top model as determined through model selection using AICc.



3.7.4 Figure 4 Climatic and non-climatic predictors of nestling condition in Canada jays

Nestling condition of Canada jays was negatively correlated with the frequency of fall freeze-thaw events (A), lay date (C) and brood size (D). Nestling condition was positively correlated with mean fall temperature (B). The shaded area around each line represents a 95% confidence interval. Each line is taken from the top model as determined through model selection using AICc.



4 Chapter 3 - Climate-driven carry-over effects negatively influence population growth rate in a food-caching boreal passerine

4.1 Abstract

Understanding how events throughout the annual cycle are linked is important for predicting variation in individual fitness, but whether and how carry-over effects scale up to influence population dynamics is poorly understood. Using 38 years of demographic data from Algonquin Provincial Park, ON and a year-round integrated population model, we examined the influence of environmental conditions and density throughout the annual cycle on the population growth rate of Canada jays (*Perisoreus canadensis*), a resident boreal passerine that relies on cached food for over-winter survival and late-winter breeding. Our results demonstrate that fall environmental variables, most notably the number of freeze-thaw events, carried over to influence late-winter fecundity, which, in turn, was the main vital rate driving population growth. These results are consistent with the hypothesis that warmer and more variable fall conditions accelerate the degradation of perishable stored food that is relied upon for successful reproduction. Additional support for this hypothesis came from a simulated food cache experiment showing that the number of freeze-thaw events was the best environmental predictor of weight loss in meat and berries, two food types commonly consumed by Canada jays. Our study not only provides experimental evidence of a climatic mechanism linking events across the annual cycle but also demonstrates how carry-over effects can impact long-term population dynamics.

4.2 Introduction

Understanding how events throughout the annual cycle are linked is critical for predicting variation in fitness of animals living in seasonal environments (Harrison et al. 2011, Hostetler et al. 2015). Carry-over effects occur when an individual's previous history or experience contributes to explaining their current performance (O'Connor et al. 2014). In seasonal environments, studies on a variety of taxa have provided evidence that non-lethal events in one period of the annual cycle can have lasting consequences on individual success in subsequent periods of the year (Harrison et al. 2011, O'Connor et al. 2014). One common type of carry over effect that has been demonstrated in birds, fish and mammals is the influence of conditions during the non-breeding period on subsequent reproductive performance (Perryman et al. 2002, Cook et al. 2004, Kennedy et al. 2008). In some species, non-breeding conditions can explain 7-40% of variation in annual breeding success (Norris et al. 2004, Morrissette et al. 2010, Rockwell et al. 2012). Under laboratory conditions, there is evidence that carry-over effects can scale to influence population growth and stability (Betini et al. 2013), but there has been little evidence of whether or how carry-over effects could influence population growth rates of wild animals (Morissette et al. 2010).

Climate often plays an important role in modulating the strength of seasonal carry-over effects (Dickey et al. 2008, Juillet et al. 2012, Harrison et al. 2013). Variation in climatic conditions can alter the abundance, availability, or timing of resource pulses (Fogden 1972, Durant et al. 2007, Parmesan and Hanley 2015), which can impact individual condition and then carry over to influence success the following season (Perryman et al. 2002, Cook et al. 2004, Sorensen et al. 2009). In food-caching species that are year-round residents of highly seasonal

environments, stored food acts to buffer individuals from temporary or seasonal unavailability of fresh food (Wall 1990). Depending on the location, duration of storage and type of food cached, post-storage variation in climate could act to mitigate or accelerate declines in food quality (Sutton et al. 2016) and carry over to influence individual success during ensuing periods of the annual cycle (Sutton et al. 2019).

The Canada jay (*Perisoreus canadensis*), a widespread sedentary resident of the boreal and subalpine forests of North America, relies on perishable food (arthropods, vertebrate flesh, berries and mushrooms) cached in the summer and fall on year-round territories for its subsequent winter survival and breeding season (Strickland and Ouellet 2018). Our study population in Algonquin Provincial Park, Ontario, at the southern edge of their range, has declined by over 50% since the 1980's (Waite and Strickland 2006) (Figure 1c) and one hypothesis for this decline is that warmer fall temperatures increase the spoilage rate of cached food, which then carries over to impact reproduction (Waite and Strickland 2006, Sechley et al. 2015). Although there is some evidence to support the effect of fall temperature on brood size (Waite and Strickland 2006), fall freeze-thaw events appear to have wider ranging effects on reproductive performance through simultaneous, negative effects on brood size, nesting success and nestling condition (Sutton et al. 2019). Despite this, there has been no experimental evidence that freeze-thaw events affect cached food or that their apparent carry-over effect on fecundity scales up to impact population growth rate. In this study, using 38 years of detailed demographic data from Algonquin Provincial Park and a simulated food cache experiment, we sought to: (1) identify the relative contribution of season-specific vital rates to population growth rate, (2) assess the indirect contribution of population density and environmental conditions, including

fall freeze-thaw events, on population growth rate through each of the vital rates, and (3) experimentally test the impact of freeze-thaw events on the mass lost by simulated food caches.

4.3 Methods

4.3.1 Study population and field methods

Canada jays are a resident passerine of North American boreal and subalpine forests, ranging from Arizona to the tree line (Strickland and Ouellet 2018) (Figure 1a). Although abundant throughout their northern range, local extirpations or declines have been observed along the southern edge of their range (Menebroeker et al. 2016, Waite and Strickland 2006). Canada jays in Algonquin Provincial Park, Ontario, Canada (45.590°, -78.517°) have been studied since 1964 along the park's highway 60 corridor and have experienced a long-term decline in abundance since the late 1970s (Waite and Strickland 2006) (Figure 1c).

Annual monitoring has occurred during two periods of the year. From 1980 to 2018, nests were found and monitored on up to 22 territories beginning in mid-February and monitored until the end of the breeding season in May. Once a nest was found, it was checked regularly every 2-4 days until nests were accessed when nestlings were approximately 11 d old. At this time, young were individually marked with three colour bands and one aluminum USFWS/CWS band. During the breeding period, all juveniles and adults in the study area were observed and individuals were identified by their unique colour band combinations. Each October (1980 – 2018), a second population count was conducted to determine which territories were occupied within the study area and the total number of individuals present. Throughout this second population count, we used suet placed at 'bait stations' on territories to attract and re-sight marked individuals. During both population counts, all banded individuals were re-sighted and

unbanded individuals were captured and given a unique combination of bands. We assumed that all unbanded individuals observed during either population count were born outside the study area because we found all nests on the territories we monitored. Collectively, this monitoring resulted in 39 years of data on reproductive success, capture-re-capture/re-sighting and total counts for the study population. Additionally, the annual cycle could be divided into two distinct periods (spring/summer; Mar. – Oct. and fall/winter; Nov. – Feb.) because of the two population counts per year.

4.3.2 Environmental variable extraction

Historical weather records were collected from an Environment Canada weather station in the study area (“Algonquin Park East Gate”) and from another station nearby (“Dwight”). Values taken from the latter weather station located outside the study area were corrected so that they would reflect temperatures within the park (see Sutton et al. 2019). Mean daily temperature and cumulative precipitation were calculated for four distinct periods of the annual cycle based on the life-history of the Canada jay: fall caching (Oct. – Dec.), pre-breeding (Jan. – Feb.), breeding (Mar. – May) and post-breeding (Jun. – Aug.). Mean daily temperature was calculated by taking the average of all mean daily temperatures through each period. Cumulative precipitation was calculated by taking the sum of all precipitation that had fallen in each of these periods. For both fall caching and pre-breeding periods, we also calculated the cumulative number of freeze-thaw events that occurred following the methods in Sutton et al. (2019).

4.3.3 Integrated Population Model

We estimated vital rates and population growth rate from reproductive success, population counts, and capture-recapture/resighting data using a modified version of an integrated

population model (IPM) developed by Schaub et al. (2013) and similar to that described by Woodworth et al. (2017). Both productivity and population count data were restricted to 22 territories that have been continuously monitored since 1980. These two datasets do not include territories that were added after 1980 as the Algonquin Provincial Park study area continued to grow (Whelan et al. 2017, Sutton et al. 2019). In total, 40 territories were monitored in 1988, 48 in 1998, 49 in 2009, and 61 territories in 2018. The entire study area was used for the mark-recapture dataset to produce a more robust estimate of survival by accounting for movement outside the originally monitored territories.

Central to the IPM is a state-space model, which describes the likelihood of the population count data. The state process represents a population projection model that consisted of three stages, two sexes (s denotes sex, which could be either female, f , or male, m) and two periods of the annual cycle (t denotes period of the annual cycle, which could be either fall/winter or spring/summer). The three stages included local recruits R (individuals that were born in the study area the previous year; <1 yr), surviving adults S (≥ 2 year-olds that bred in the study area in the previous year) and immigrants I (unbanded individuals that were recorded during either population count). We assumed all unbanded immigrants originated from outside the study area and that these individuals had not previously bred or been born in the study area because all nests were found within the study area and almost all individuals were counted that were present on a territory during both population counts.

We projected stage-specific abundances as either binomial or Poisson processes to account for demographic stochasticity. The sex-specific number of local recruits in the model

was described by a binomial model $R_{s,t+1} \sim \text{Binomial}(F_{s,\text{spring/summer}}, \phi_{j,s,t})$, where $F_{s,\text{spring/summer}}$ is the number of fledglings of both sexes in a given year and $\phi_{j,s,t}$ is sex- and period-specific estimate of juvenile apparent survival. We were unable to determine the sex of young that did not recruit into our study population and assumed a 1:1 ratio of male:female young in the nest. Therefore, the number of female fledglings was estimated using a binomial model $F_{f,t} \sim \text{Binomial}(F_{s,\text{spring/summer}}, 0.5)$, and the number of male fledglings were estimated as $F_{m,t} = F_{s,\text{spring/summer}} - F_{f,t}$, where $F_{s,\text{spring/summer}}$ is the total number of fledglings produced in a given breeding season. The total number of fledglings produced in a given breeding season, $F_{s,\text{spring/summer}}$, was projected using a Poisson model, $F_t \sim \text{Poisson}(J_t \cdot B_{f,t})$, where J_t is the number of young produced in breeding season t per female and $B_{f,t}$ is the number of breeding females in breeding season t . J_t was estimated using a Poisson model, $J_t \sim \text{Poisson}(\rho_t \cdot C_{f,t})$, where ρ_t was the number of young produced in a given breeding season and $C_{f,t}$ is the number of females counted in the population. Due to logistical constraints, we could only access each nest once during the nestling period and, as a result, brood size was used to estimate the number of fledglings and fecundity. Sex-specific numbers of surviving adults in the subsequent period of the annual cycle were projected as $S_{s,t+1} \sim \text{Binomial}(B_{s,t}, \phi_{ad,s,t})$, where $B_{s,t}$ is the sex-specific number of breeding adults in period t and $\phi_{ad,s,t}$ is the sex-specific adult apparent survival probability from period t to $t+1$. Finally, the sex-specific number of immigrants in each season was estimated using a Poisson model, $I_{s,t+1} \sim \text{Poisson}(i_{s,t+1})$, where $i_{s,t+1}$ is the sex-specific expected number of immigrants. Immigration into our study population could happen during either period of the annual cycle and as a result, we estimated immigration during each period. Once the model was fitted, population growth

rate, λ_t , from spring at time t to spring $t+1$ was calculated using the equation $\lambda_t = (B_{f,t+1} + B_{m,t+1}) / (B_{f,t} + B_{m,t})$, with $B_{s,t} = R_{s,t} + S_{s,t} + I_{s,t}$.

The observation component of the state-space model was used to link population count data for each sex to our estimate of sex-specific population size for each season, $\log(C_{s,t}) \sim \text{Normal}(\log(B_{s,t}), \sigma_t)$. We are able to accurately count most individuals within our study area due to our extensive monitoring of territories throughout the annual cycle. Although individuals may not be seen on each visit to a territory, multiple visits provide the opportunity to develop robust re-sight/re-capture database to estimate population abundance. However, some individuals may still not have been seen during a given count and, for this reason, we used a state-space model.

Per capita brood size was modeled with a Poisson regression using productivity data from our study, $J_t \sim \text{Poisson}(\rho_t \cdot C_{f,t})$, where J_t was the number of young produced and $C_{f,t}$ is the number of females counted in the population. Due to logistical constraints, we could only access each nest once during the nestling period and, as a result, brood size was used to estimate the number of fledglings and fecundity.

Loss of an individual in the population could be due to either mortality or permanent emigration from our study area and therefore our survival estimates are ‘apparent’ survival, which represents a combination of both processes. We included two age classes in our capture-recapture model, juveniles (j ; <1 yr) and adults (a ; ≥ 2 yrs) and estimated sex- (s), age- (j or a) and period-specific (*fall/winter* or *spring/summer*) apparent survival and recapture probabilities using a Cormack-Jolly-Seber model (Kery and Schaub 2011). Therefore, $\phi_{j,s,t}$ represents juvenile

sex-specific survival from one period of the annual cycle to the next and $\phi_{ad,s,t}$ represents adult sex-specific survival from one period to the annual cycle to the next.

The IPM was implemented using JAGS in R with the jagsUI package (Plummer 2003) (R Core Team 2019). The model was run for 2,000,000 iterations with 3 independent chains, a burn-in period of 1,000,000 iterations and every hundredth sample was kept, resulting in 30,000 posterior samples. Convergence of model chains was assessed visually and using the Gelman-Rubin diagnostic statistic and was reached for all parameters ($R < 1.1$).

4.3.4 Environmental and density variable selection

The total number of variables included in the final path model was reduced by assembling a series of univariable models regressing a given season-specific vital rate against environmental and density covariates (Woodworth et al. 2017). This variable selection process was conducted in order to avoid including extraneous linkages in the final path model with effect sizes that were not different from zero. We included all covariates in the final path model whose 90% credible interval did not overlap zero. If all credible intervals overlapped zero for a given vital rate, we included the variable that overlapped zero the least in the final path model.

4.3.5 Direct and indirect effects on population growth rate

We applied a path model approach (Shiple 2016) by Woodworth et al. (2017) that used estimates of season-specific vital rates and population growth derived from the IPM and key environmental and density variables to estimate the relative contribution of both environmental variables and density throughout the annual cycle on population growth acting through all of the vital rates. The main advantage of this approach is that it allows for uncertainty in model inputs

to be accounted for by fitting every component model to each sample of their posterior distribution (Woodworth et al. 2017). It also allows for the use of common regression techniques to estimate the direct effects of environmental covariates and density on vital rates and the indirect effects of these covariates, acting through the vital rates, on population growth. The path model consisted of 14 linear models, relating season-, sex- and age-specific vital rates to population growth (1) and environmental variables and density to these vital rates (2 – 14):

- (1) $\lambda_t \sim \phi_{j,f,t,s} + \phi_{ad,f,t,s} + \phi_{j,m,t,s} + \phi_{ad,m,t,s} + \rho_t + I_{f,t} + I_{m,t}$
- (2) $\phi_{j,f,fall/winter} \sim \text{breeding mean temp}$
- (3) $\phi_{j,f,spring/summer} \sim \text{post-breeding precip}$
- (4) $\phi_{ad,f,t,fall/winter} \sim \text{breeding mean temp}$
- (5) $\phi_{ad,f,t,spring/summer} \sim \text{breeding mean temp}_{(t-1)}$
- (6) $\phi_{j,m,t,fall/winter} \sim \text{pre-breeding mean temp}$
- (7) $\phi_{j,m,t,spring/summer} \sim \text{density}$
- (8) $\phi_{ad,m,t,fall/winter} \sim \text{pre-breeding precip}$
- (9) $\phi_{ad,m,t,spring/summer} \sim \text{post-breeding precip}$
- (10) $\rho_t \sim \text{fall freeze-thaw}_{(t-1)} + \text{fall mean temp}_{(t-1)} + \text{pre-breeding freeze-thaw}_{(t-1)} + \text{pre-breeding precip}_{(t-1)} + \text{density}$
- (11) $I_{f,fall/winter} \sim \text{fall mean temp}$
- (12) $I_{f,spring/summer} \sim \text{pre-breeding precip}_{(t-1)} + \text{pre-breeding precip}_{(t-1)} + \text{density}$
- (13) $I_{m,fall/winter} \sim \text{fall mean temp}$
- (14) $I_{m,spring/summer} \sim \text{fall precip}$

In each of the component models and for each iteration, vital rates, environmental variables, density and population growth were scaled by subtracting the mean from each estimate and dividing by the standard deviation. Indirect effects of environmental variables and density on population growth were calculated as the product of the direct effect of a covariate (environmental or density) on a given vital rate and the direct effect of that vital rate on population growth. Indirect effects were then summed across all vital rates for a given environmental or density covariate. We also summed all covariates from a given period of the annual cycle to assess how periods of the annual cycle contribute to variation in population growth. For example, the effects of fall freeze-thaw events, fall mean temperature and fall precipitation were summed to calculate the cumulative indirect effect of fall conditions on population growth.

4.3.6 *Artificial food caching experiment*

To assess the effects of fall weather on food quality, we conducted an experiment in Algonquin Provincial Park (45.590°, -78.517°) using artificial caches (Strickland et al. 2011, Sechley et al. 2015) to simulate food caches made by Canada jays. Food items were individually weighed and placed in plastic caching chambers (Strickland et al. 2011) which were then affixed to the north side of a black spruce (*Picea mariana*) trunk to ensure that each cache was exposed to similar environmental conditions (Figure 6b). Two food types, commercial blueberries (mean mass per cache = 1.39 ± 0.27 , n = 240) and ground chicken (mean mass per cache = 1.00 ± 0.13 , n = 240), were used as surrogates for natural food items that Canada jays are known to consume and store (Strickland and Ouellet 2018). The artificial caches were deployed on October 19, 2018 and retrieved every 3-5 days until January 5, 2019. On each retrieval date, we collected 15 caches of

each food type and immediately weighed each item to the nearest 0.001 g using a Scout Pro Precision Balance (model SPX123, OHAUS, USA).

We used hourly weather data from the Algonquin Park East Gate weather station to calculate mean temperature and the number of freeze-thaw events that a food item was exposed to. Mean temperature was calculated as an average of all hourly mean temperature estimates from cache deployment to retrieval. Freeze-thaw events were calculated using the same methods outlined above for the long-term data (Sutton et al. 2019) and separately for each food type because initial freezing points differ for blueberries and ground chicken.

We constructed a series of linear models to predict the percentage of weight lost by a food item, which we considered to be a proxy for its nutritional quality (Sechley et al. 2015). We evaluated three hypotheses for why a food item may decline in quality:

- 1) ***Length of Storage Period***: The length of the storage period dictates the environmental conditions a food item is exposed to while it was stored. We predicted that there would be a positive correlation between the length of the storage period and the amount of weight lost by food items.
- 2) ***Mean Temperature***: Mean temperature determines microbial activity levels, with greater microbial activity and therefore, degradation, at higher temperatures. We predicted that there would be a positive correlation between mean temperature and weight loss.
- 3) ***Cumulative Freeze-thaw***: Freeze-thaw events cause physical degradation of food and nutritional declines due to drip loss in addition to positively influencing microbial growth

in food. We predicted that there would be a positive correlation between the cumulative number of freeze-thaw events a food item experiences and weight loss.

Each of the three variables were included in separate models because they were highly correlated. Food type was included as a fixed effect in each model to account for potential differences in weight loss between ground chicken and blueberries. To account for potential differences rates of weight loss over time between food types, we produced a second set of models that included an interaction between food type and given environmental variable. All competing models (with and without the interaction term) were ranked using Akaike's Information Criterion (AIC). All models within $\Delta AIC \leq 2$ were considered to be the top models. All statistical calculations were performed using R version 3.3.3 (R Core Team 2019).

4.4 Results

4.4.1 Demographic contributors to population growth rate

The population size within our study area of territories consistently monitored since 1980 in Algonquin Provincial Park declined sharply from a high of 55 individuals, including both juveniles and adults, in 1980 to a low of 14 individuals in 2003 (Figure 1c). Since 2003, the population has fluctuated between 14 and 25 individuals. Over the course of our 38-year study, population growth rates (λ) ranged from 0.6 to 1.53, with the population increasing ($\lambda > 1$) in only 12 of these years ($\lambda < 1$, $n = 19$ and $\lambda = 1$, $n = 7$; Figure 2a).

Based on the integrated population model, fecundity had the largest effect on λ , followed by fall/winter and spring/summer female immigration, spring/summer male immigration and

then spring/summer juvenile male apparent survival (Figure 3). All other season-specific vital rates had credible intervals that substantially overlapped with zero and none of the vital rates showed directional change over the course of the study (Figure 2b-h). Fecundity remained below the level of replacement for most of the study, especially during the period of most rapid decline in the 1980s (Figure 2b). Immigration was highly variable, but spring/summer immigration in both sexes was consistently higher than fall/winter immigration (Figure 2c,d). Mean adult apparent survival in both sexes was higher in the fall/winter than spring/summer, but there was a high amount of overlap of the credible intervals in both seasons (Figure 2e,f). Juvenile apparent survival for both sexes was lower during the spring/summer period (Figure 2g,h).

4.4.2 Direct effects of environmental conditions and density on vital rates

With the exception of spring/summer juvenile male apparent survival, which was influenced by spring/summer density (mean = -0.27, 95% CI = -0.50, -0.036; Figure 4), no other sex- or season-specific estimates of apparent survival were strongly correlated with density or environmental variables. Neither fall/winter and spring/summer male immigration, nor fall/winter female immigration were strongly correlated with any environmental variables. In contrast, spring/summer female immigration was negatively correlated with mean winter temperature (-0.24, 95% CI = -0.47, -0.062) and positively correlated with winter precipitation (0.13, 95% CI = 0.023, 0.23) and spring/summer density (0.24, 95% CI = 0.12, 0.45).

Unlike survival and immigration rates, fecundity was strongly correlated with both fall/winter density and several environmental variables (Figure 4). Both the number of fall freeze-thaw events (-0.25, 95% CI = -0.42, -0.096) and mean fall temperature (-0.17, 95% CI = -0.32, -0.024) were negatively correlated with fecundity in the subsequent breeding season.

Further, fecundity was negatively correlated with the number of winter freeze-thaw events (-0.21, 95% CI = -0.37, -0.052), winter precipitation (-0.21, 95% CI -0.38, -0.032), and fall/winter density (-0.18, 95% CI = -0.32, -0.034).

4.4.3 Indirect effects on population growth rate

By combining the direct effects of vital rates on population growth and the direct effects of density and environmental variables on season-specific vital rates, we found evidence for a strong effect of fall and, to a lesser-degree, pre-breeding weather on population growth rate (Figure 5). A higher frequency of freeze-thaw events in the fall and pre-breeding periods, and increased mean fall temperature and pre-breeding precipitation, resulted in a decrease in population growth, primarily through their negative effect on fecundity. Because density had a negative effect on fecundity but a positive effect on female immigration, there was no strong net directional effect of density throughout the annual cycle on population growth rate.

4.4.4 Food caching experiment

We conducted an experiment in which simulated food caches were retrieved every 3 – 5 days through the late fall and early winter in Algonquin Provincial Park (n = 240 for each food type). The interaction between cumulative number of freeze-thaw events and food type was the best predictor of overall weight loss in simulated caches (Table S1). Overall, the top model predicted 58% of the variation in weight loss over the course of our experiment ($F_{4,473} = 1197$, $p < 0.0001$), with blueberries predicted to lose 1.8% and chicken 3.6% of their mass with each additional freeze-thaw event experienced.

4.5 Discussion

Our study is the first to demonstrate that carry-over effects can affect long-term population growth in a wild population. We observed a strong effect of fall weather, and to a lesser degree pre-breeding weather, on fecundity, which, in turn, was the primary vital rate influencing population growth. Furthermore, our simulated cache experiment provides evidence of the potential mechanism driving this relationship: the number of freeze-thaw events experienced by a food item was the best predictor of weight loss by a perishable food item, likely because of the rupture of cell membranes caused by freezing and, consequently, the enhanced microbial access to cellular contents during the thaw portion of each freeze-thaw event (Boonsumrej et al. 2007, Ali et al. 2015, Raji et al. 2016). Taken together, our results strongly suggest that a more variable and warmer fall climate likely result in greater food limitation for Canada jays during the late-winter breeding period.

The observed population decline in Algonquin Provincial Park can be separated into two distinct periods, a period of rapid decline between 1980-1996 and then a period of stabilization from 1997 - 2018. During the period of rapid decline, 10 of the 16 years had a greater number of freeze-thaw events than average across the study period whereas only 8 of 22 later years had an above average number of freeze-thaw events (Figure S1). Canada jays are constrained by low clutch sizes that are typically just above replacement levels (modal clutch size of 3 in our study area and a maximum of 5; Strickland and Ouellet 2018). Therefore, even years of above average reproductive success are unlikely to result in sufficient recruitment for the population to rebound and sustained periods of low reproductive output could contribute to declines in abundance.

Our work also demonstrates how trade-offs between allocating resources to either self-maintenance or reproduction are likely important for understanding how organisms respond to a changing environment. While Canada jay fecundity was strongly influenced by a number of environmental variables, adult and juvenile survival were relatively resilient to variation in environmental conditions. This resiliency suggests that, similar to other long-lived species (Cox et al. 2010, Robinson et al. 2012, Colchero et al. 2018), Canada jays favour self-maintenance over reproduction in a resource-limited environment. However, this potential trade-off also means that, because of their low annual productivity, and in spite of their high adult survival, Canada jay populations could decline and take years to rebound (Rushing et al. 2017, Imlay et al. 2018, Bonnot et al. 2018). Examining potential trade-offs in resource allocation between and within species could further highlight the implications of climate on demography and its role in species declines (Mantyka-pringle et al. 2012, Selwood et al. 2015).

Seasonal differences in a number of vital rates are likely a result of differential predation risk and timing of dispersal of Canada jays in Algonquin Park. Mean apparent survival estimates of both adults and juveniles were lower in the spring/summer than in the fall/winter. In the case of adults, this pattern is largely attributable to the predominantly summer-only presence of Sharp-shinned Hawks (*Accipiter striatus*) and Merlins (*Falco columbarius*) (Tozer 2012). Lower apparent spring/summer survival of juveniles is likely similarly attributable to predation, but also due in part to a partial dispersal event, during which a single brood member expels its siblings from their natal territory (Strickland 1991). Some of the forced dispersers succeed in joining unrelated pairs on neighbouring territories (Strickland 1991), but most leave the study area, leading to a low-biased estimate of juvenile survival. Increased rates of immigration into the

study area during the spring/summer are also in part attributable to the partial dispersal of juveniles because juveniles ejected from territories outside the study area sometimes disperse into the study area. Further, adults are more likely to move in the spring/summer to fill predation-induced vacancies and settle on a territory early enough to amass sufficient cached food stores to survive the subsequent winter.

Weak density-dependence may be precluding an increase in this population even though it has been at a low density for the past two decades. The reasons for weak density-dependence, despite evidence of density-dependent effects on both fecundity and juvenile survival, remain unclear, but may be due to several factors. Contrasting effects of density on multiple vital rates that contribute strongly to population growth, such as fecundity and immigration, limits the positive compensatory effects of density on population growth (Herrando-Pérez et al. 2012). Fecundity, which is the most important vital rate driving population growth, is likely regulated by site-dependence (Sutton et al. *in review*). However, environmental conditions may be modulating the strength of density-dependence and this could further limit positive compensatory effects of density (Sutton et al. *in review*). Environmental conditions could also act to simultaneously reduce the quality of all territories and, therefore, the capacity of breeding pairs to contribute to higher recruitment even at low densities.

The diet of Canada jays consists of four main food types (Strickland and Ouellet 2018) and some may be more strongly affected by climatic conditions than others. Of the two food types used in our experiment, ground chicken declined more quickly in weight than blueberries (Figure 6b), providing support for the differential degradation of food items (Leygonie et al. 2012, Sutton et al. 2016). Therefore, quantifying the relative contribution of various food items

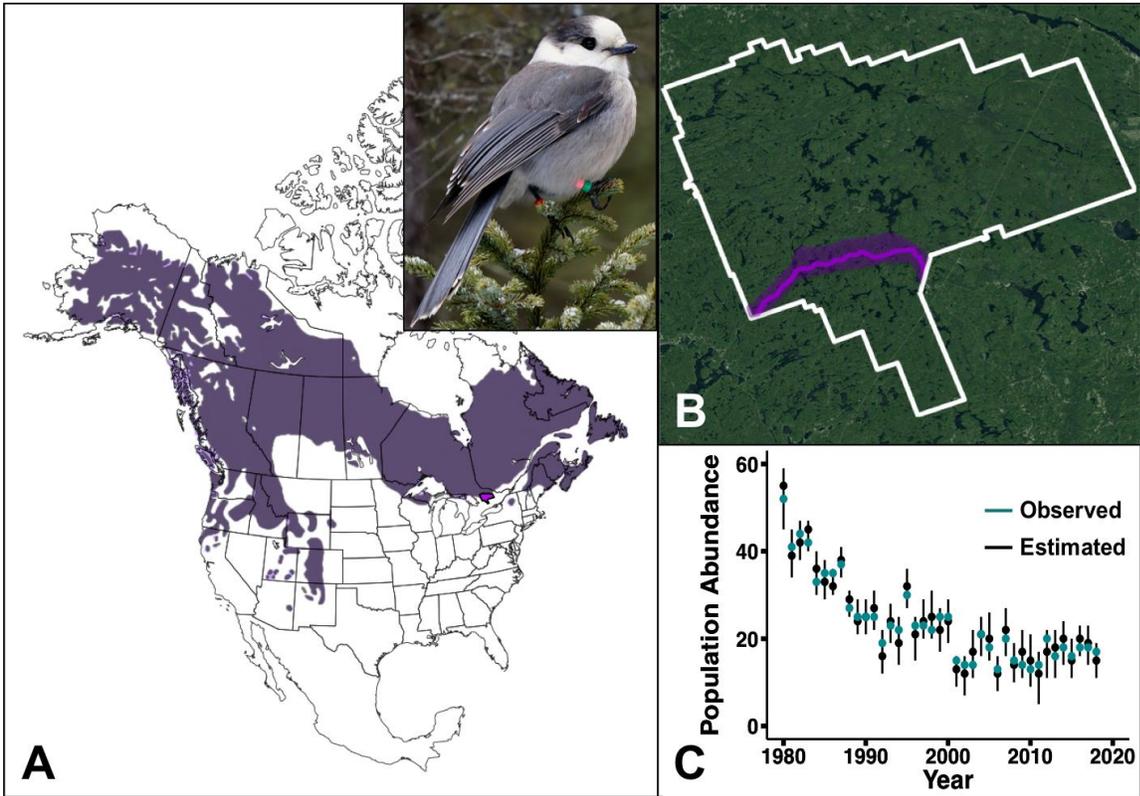
to the winter diet of Canada jays and their young may be important in order to better understand how climate change may be affecting food limitation in breeding Canada jays and the development of their young. Additionally, it will be important to quantify inter-annual variation in over-winter diet, which in turn could augment the susceptibility of Canada jays to changing fall climatic conditions.

High-latitude areas, such as the boreal forest, are predicted to experience the greatest changes in temperature, precipitation and climatic variability (Serreze and Francis 2006, Li et al. 2018). Fecundity may, therefore, continue to decline or remain below replacement levels throughout a portion of the Canada jay range. Several studies have already reported declines or local extirpations along the southern edge of the Canada jay range (e.g. Menebroeker et al. 2016, Waite and Strickland 2006) and under future warming scenarios (Ridgway et al. 2019), it is more likely that we will see the local extirpation of Canada jays from Algonquin Provincial Park and other southern range-edge populations. However, our ability to predict future declines of northern populations remains limited due to insufficient data. Citizen science databases, such as Christmas bird counts, could help to fill this gap in our knowledge and be used to estimate population trends at more northern latitudes (Soykan et al. 2016). Our results could be used to predict possible declines at other locations across the Canada jay range and provides a framework to test whether northern populations respond similarly to changes in climatic conditions (Cayuela et al. 2016).

4.6 Figures

4.6.1 *Figure 1 Canada jay distribution, study area in Algonquin Provincial Park, ON, and population decline*

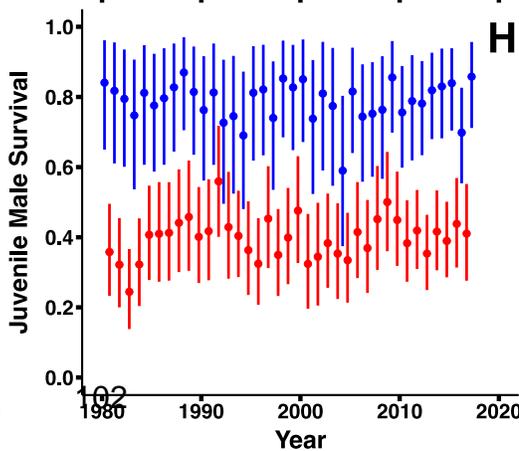
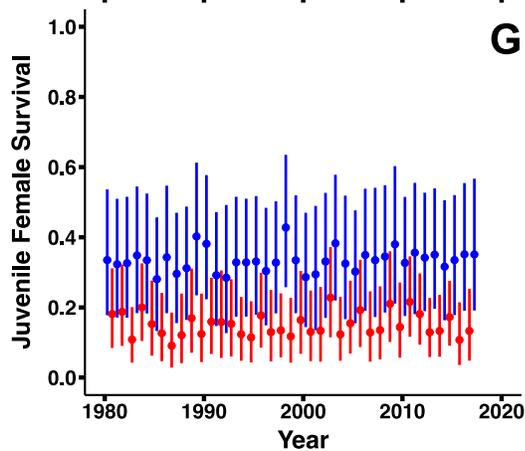
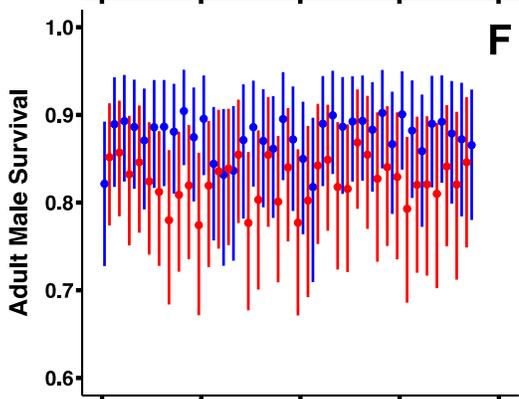
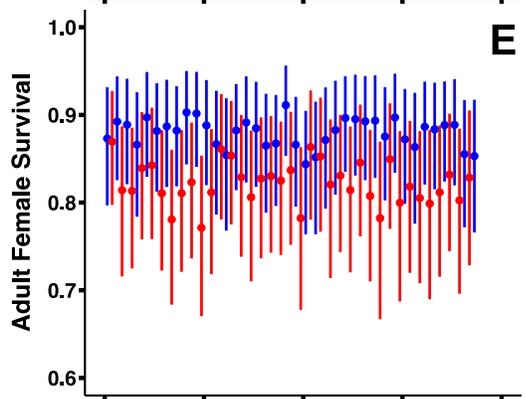
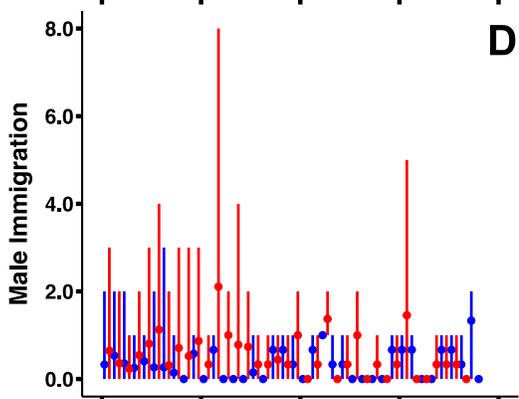
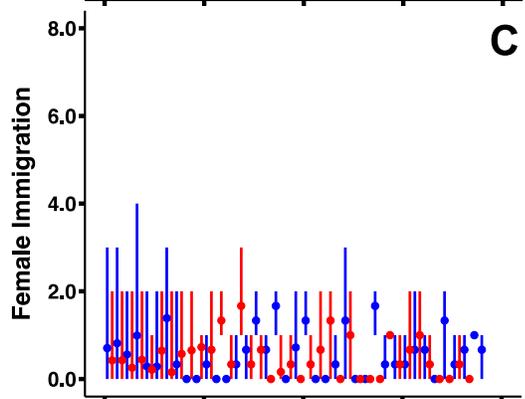
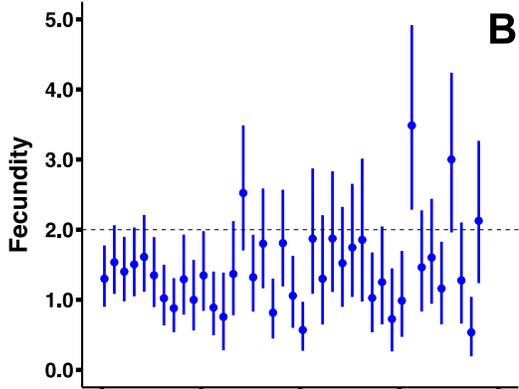
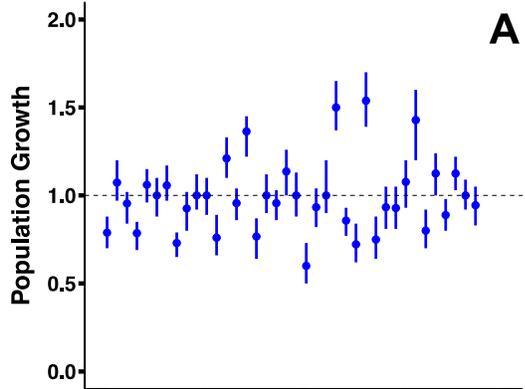
A) Range map outlining the distribution of Canada jays (*Perisoreus canadensis*) in purple with Algonquin Provincial Park, ON highlighted in violet. Inset: A colour banded Canada jay from the Algonquin study area. All individuals in the study area received a unique colour band combination consisting of three coloured bands and one aluminum USFWS/CWS band. B) The study area (highlighted in purple) is located along the highway 60 corridor in the southern portion of Algonquin Provincial Park. C) Long-term population decline within the study area. Black points represent estimated values from the integrated population model, with associated 95% credible intervals and teal points represent observed population counts.



4.6.2 Figure 2 Temporal trends of population growth and season-specific vital rates

A) population growth, B) fecundity, C) female immigration, D) male immigration, E) adult female apparent survival, F) adult male apparent survival, G) juvenile female apparent survival and H) juvenile male apparent survival. All points represent means and lines represent 95% credible intervals. Colours represent season-specific estimates of vital rates.

— Fall/Winter — Spring/Summer

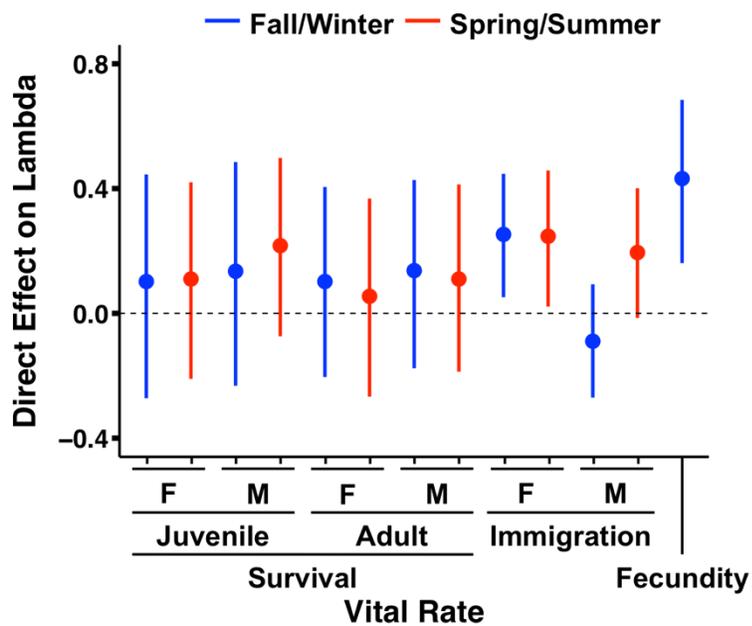


1980 1990 2000 2010 2020
Year

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Year

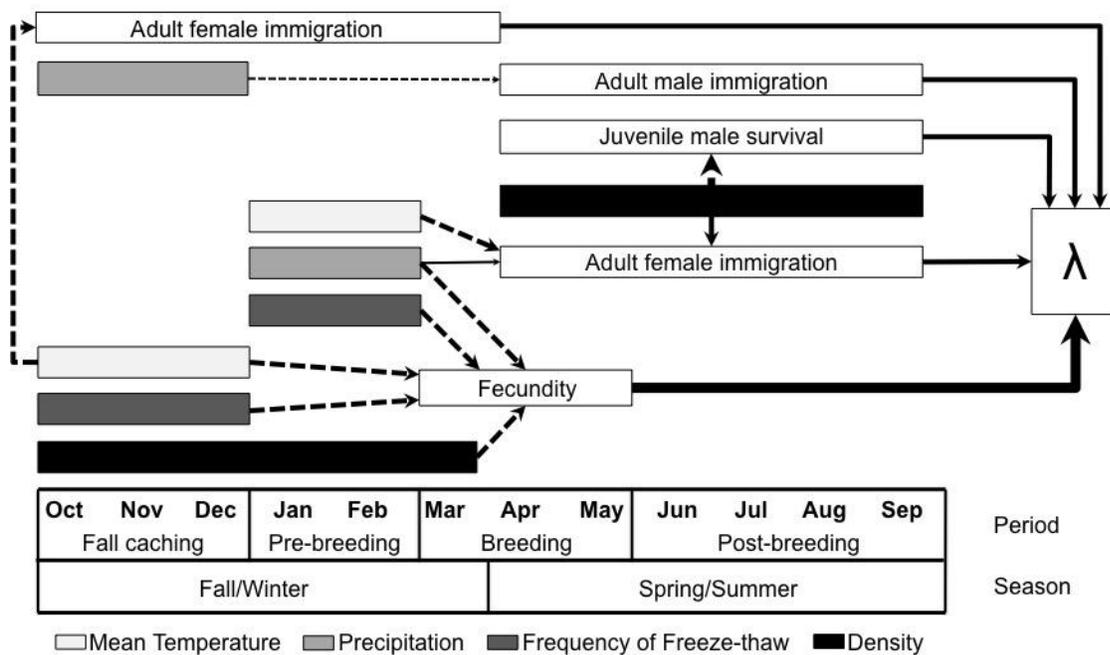
4.6.3 Figure 3 Direct effects of vital rates on population growth

Each point represents the mean and the line 95% credible intervals. All vital rates contributed positively to population growth, except over-winter male immigration. Vital rates were considered to contribute strongly to variation in population growth rate if the credible interval did not overlap zero.



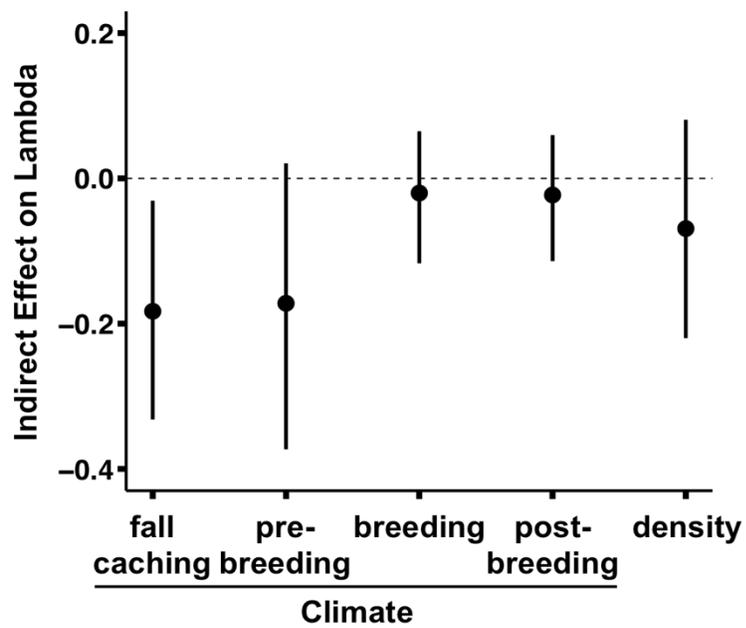
4.6.4 Figure 4 Path diagram outlining direct effects of vital rates of lambda and climate variables on vital rates

Only vital rates that had the largest direct effect on population growth were included in the path analysis. Solid lines indicate a positive relationship between variables and dashed lines represent a negative relationship. The width of each line indicates the strength of the relationship (thickest: 0.4 – 0.45, medium thickness: 0.2 – 0.25, thinnest: 0.1 – 0.15). Vital rates and environmental and density variables are arranged according to periods of the annual cycle, listed at the bottom of the diagram.



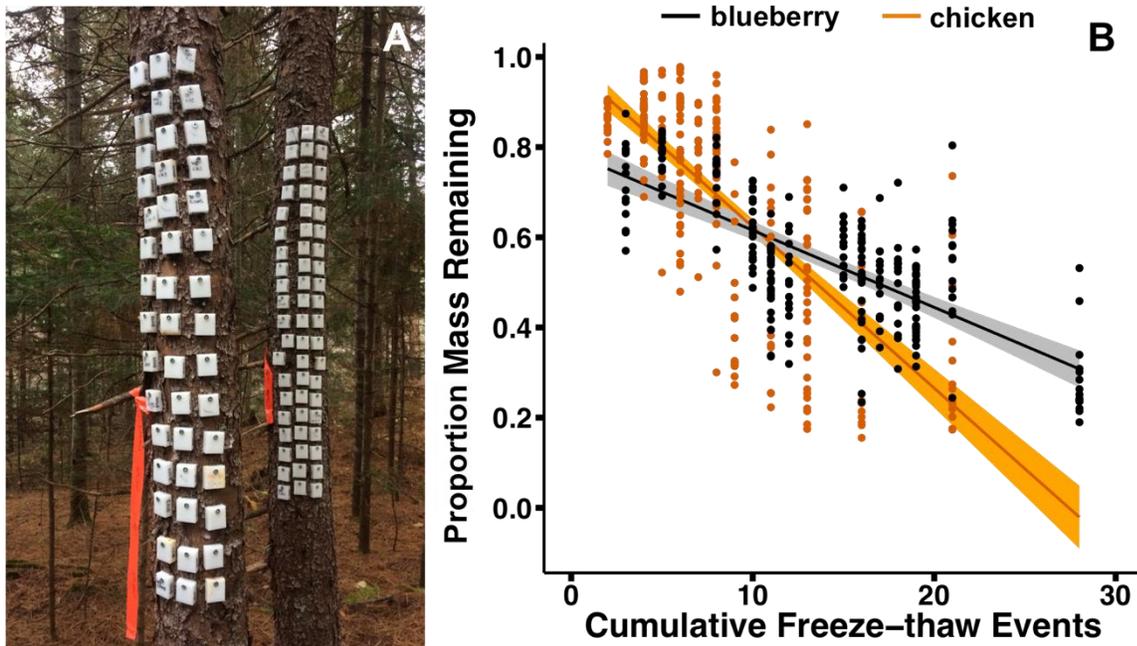
4.6.5 *Figure 5 Cumulative indirect effects of seasonal climate and density on population growth*

Variables were considered to have strong indirect effects if their credible interval did not overlap zero (represented by the dotted line). Each period and density estimate represents the sum of all period-specific climate variables that were included in the path model.



4.6.6 Figure 6 The effect of freeze-thaw events on the weight loss of simulated caches

A) Simulated caches were placed on black spruce (*Picea mariana*) trees within the Algonquin Provincial Park study area. Each simulated cache contained one food item. B) Proportion of mass remaining per freeze-thaw event experienced. Artificial caches were retrieved every 3-5 days between Oct. 19, 2018 and Jan. 5, 2019 and immediately weighed. The best predictor of weight lost over time was the cumulative number of freeze-thaw events experienced by the cached food item. A significant interaction between food type and the number of freeze-thaw events experienced suggested that, compared to the blueberry samples, ground chicken lost a greater proportion of weight with each freeze-thaw event experienced.



4.7 Supplemental Material

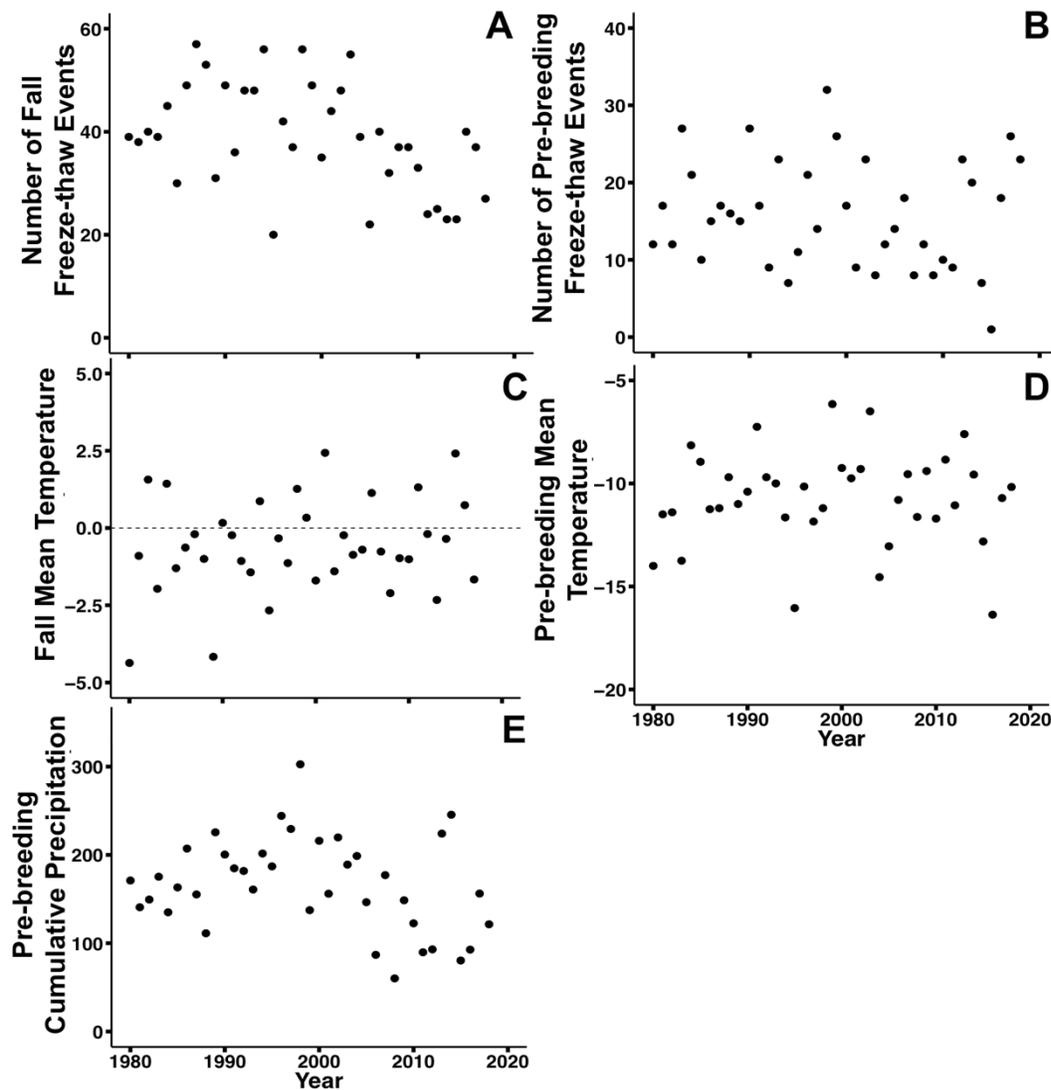
4.7.1 Table S1 Model selection table for food caching experiment

Competing models predicting the proportion of weight lost by a simulated food cache were ranked using Akaike's Information Criterion (AIC). All models within $\Delta\text{AIC} \leq 2$ were considered to be competing and Akaike weights provided the cumulative support for a model given all competing models.

Model predicting weight lost by simulated food caches	K	AIC	ΔAIC	AIC weight
food type*cumulative freeze-thaw events	5	-556.7	0	1
food type*date removed	5	-541.3	15.4	<0.001
food type*mean temperature	5	-512.0	44.8	0
food type + date removed	4	-511.0	45.8	0
food type + cumulative freeze-thaw events	4	-495.4	61.3	0
food type + mean temperature	4	-473.1	83.6	0
food type	3	-195.2	361.5	0

4.7.2 *Figure S1 Temporal trends in key climate variables associated with population growth and individual vital rates*

A) Number of fall freeze-thaw events, B) Number of pre-breeding freeze-thaw events, C) Fall mean temperature, D) Pre-breeding mean temperature, E) Pre-breeding cumulative precipitation.



5 Chapter 4 - Environmental conditions modulate compensatory effects of site-dependent regulation in a food-caching passerine

5.1 Abstract

Although density regulates the abundance of most wild animal populations, the mechanisms responsible for generating negative density-dependence are unclear for many species. Site-dependent regulation occurs when there is preferential filling of high-quality territories, which results in higher *per capita* vital rates at low densities because a larger proportion of occupied territories are of high quality. Using 41 years of territory occupancy and demographic data, we investigated whether site-dependent regulation was a mechanism acting to regulate a population of Canada jays in Algonquin Provincial Park, ON. As predicted by site-dependent regulation, the proportion of occupied territories that were of high quality was negatively correlated with population density and periods of vacancy were shorter for high-quality territories than for low-quality territories. We also found evidence that *per capita* fecundity was positively related to the proportion of occupied territories that were of high quality, but only when environmental conditions, which influence the entire population, were otherwise poor for breeding. Our results suggest that site-dependence likely plays a role in regulating this population but that environmental conditions can modulate the strength of density-dependence.

5.2 Introduction

Density-dependence, a common process regulating most wild animal populations (Lack 1966, Sinclair 1989, Ferrer and Donazar 1996, Rodenhouse et al. 1997), is characterized by a negative relationship between abundance and population growth, or individual vital rates, such as survival or fecundity (Sibly and Hone 2002). The strength of density-dependence can vary between vital rates of a single population (Herrando-Pérez et al. 2012, Sutton et al. *in review*), between conspecific populations at different locations (Forchhammer et al. 1998, Johnson 2006, Thorson et al. 2015), and between species (Saitoh et al. 1999, Chen et al. 2019). It is, therefore, important to understand the mechanisms that promote density-dependent relationships and how additional variables, such as environmental conditions, may modulate the strength of density-dependent relationships (Coulson et al. 2001, Hansen et al. 2019).

One mechanism that can produce density-dependence in wild populations is site-dependent regulation (Ferrer and Donazar 1996, Rodenhouse et al. 1997). Site-dependent regulation occurs when organisms preferentially fill territories that vary in suitability, such that *per capita* fecundity and/or survival is negatively related to population density (because a lower proportion of individuals occupy high-quality territories; Rodenhouse et al. 1997). Thus, for site-dependent regulation to act on a population there must be habitat heterogeneity and individuals must be territorial (Brown 1969, Pulliam and Danielson 1991). Site-dependent regulation predicts that high-quality territories will be occupied at a faster rate than low-quality territories, *per capita* fecundity will be negatively correlated with density, and fecundity within a territory class will not be negatively influenced by density (Brown 1969, Ferrer and Donazar 1996, Ferrer et al. 2006, 2008, Grünkorn et al. 2014). However, despite the fact that territoriality and variation

in habitat quality are common features of natural systems, there is only limited evidence for site-dependent regulation acting on wild populations, with most work focusing on birds (Rodenhouse et al. 1997, Kokko et al. 2004, Nevoux et al. 2011, Ferrer et al. 2014), in particular birds of prey (Sergio and Newton 2003). Many studies investigating site-dependent regulation have reported preferential occupation of high-quality sites (Kokko et al. 2004, Flesch et al. 2015, Zuberogoitia et al. 2019) and that site-dependence regulates fecundity (Krüger and Lindström 2001, Kokko et al. 2004, Nevoux et al. 2011, Zuberogoitia et al. 2019). Additionally, when site-dependent regulation is acting on a population, high-quality territories can contribute a disproportionate amount of the overall number of young produced in a given year (Ferrer and Donazar 1996, Zuberogoitia et al. 2019). A relatively small number of studies have investigated how extrinsic conditions, such as weather, can interact with territory quality and modulate the effects of density on fecundity, and results are equivocal, with some studies suggesting that high-quality territories may buffer individuals from severe weather events (Franklin et al. 2000, Ferrer et al. 2014, Zuberogoitia et al. 2019), while others suggest that weather events may influence all territories equally (Flesch et al. 2015, Reynolds et al. 2017).

The Canada jay (*Perisoreus canadensis*) is a year-round territorial passerine whose range includes all of North America's boreal forest north to the tree-line and subalpine forests of the Rocky Mountains as far south as Arizona (Strickland and Ouellet 2018). During the summer and fall, Canada jays cache a variety of perishable food items, including mushrooms, berries, arthropods and vertebrate flesh, in the bark and branches of trees (Strickland and Ouellet 2018), and later depend on those caches for their over-winter survival and late-winter reproduction (Sechley et al. 2014, Derbyshire et al. 2018). Given this critical dependence on perishable cached

food items, two factors have been proposed as being especially important for Canada jay survival and reproductive success. The first is a consistent, below-freezing winter temperature regime, which is supported by evidence indicating that Canada jay reproductive performance is *greater* following falls and winters of *lower* than normal temperatures and/or numbers of fall freeze-thaw events (Waite and Strickland 2006, Sutton et al. 2019, Sutton et al. *in review*). The second is the availability and quality of storage sites that preserve cached food over time. Algonquin Provincial Park, lying in a transition zone between southern, mainly broadleaf forests and northern, mainly coniferous forests has a highly heterogeneous patchwork of differing habitats (Fig. 1c, d; Strickland 2015). Using simulated caches, Strickland et al. (2011) provided evidence that, compared to deciduous trees, conifers were better able to preserve perishable food items and they speculated that this was because of the antimicrobial properties of conifer resins. A higher proportion of conifers on Canada jay territories in Algonquin Provincial Park, ON is also associated with higher rates of occupancy (Strickland et al. 2011), a greater likelihood of successfully fledging young (Strickland et al. 2011, Whelan et al. 2016), and a higher probability of both adults and juveniles dispersing onto these territories (Norris et al. 2013).

We examined whether site-dependent regulation of fecundity was acting on a population of Canada jays in Algonquin Provincial Park. To do this, we used 41 years of occupancy and demographic data to examine the effect of density and territory quality on territory occupancy, the effect of territory quality on the time that a territory remained vacant, and the effect of density and the proportion of occupied territories that were of high quality on *per capita* fecundity, estimated by brood size. We focused on fecundity rather than survival because fecundity is the major vital rate driving population growth rate and is also negatively density-

dependent (Sutton et al. *in review*). The regulation of fecundity is, therefore, likely to contribute strongly to population regulation. We predicted that site-dependent regulation would result in an interaction between density and territory occupancy, such that density would have the strongest effect on the probability of occupancy of low-quality territories. The slope of the relationship between density and territory occupancy would be steepest for low-quality territories and shallowest for high-quality territories. We also predicted that high-quality territories would remain vacant for shorter periods of time compared to lower quality territories. Finally, we predicted that the proportion of occupied territories in a given year that were of high quality would influence *per capita* fecundity and also be a better predictor than overall density of the population.

Due to the strong influence of environmental conditions on reproductive performance (Waite and Strickland 2006, Sutton et al. 2019, Sutton et al. *in review*), we also investigated two competing hypotheses of how weather could influence the strength of site-dependent regulation. The first hypothesis was that high-quality territories would buffer breeders from the negative effects of freeze-thaw events by limiting degradation of cached food. Because breeding pairs on high-quality territories would have more cached food supplies that could be used to support reproduction, we predicted that there would be an interaction between the proportion of occupied territories that are of high quality and the number of freeze-thaw events on *per capita* fecundity. In years with a higher than average number of fall freeze-thaw events (poor breeding conditions), we expected a positive relationship between the proportion of occupied territories that were of high quality and *per capita* fecundity. However, in years with a low number of freeze-thaw events (good breeding conditions), we expected the proportion of occupied territories that were

of high quality to have no effect on *per capita* fecundity because environmental conditions would not have pronounced effects on cached food quality (i.e. caches are being preserved by environmental conditions) and all territories would perform equally well. Alternatively, a competing hypothesis could be that fall freeze-thaw events cause a decline in reproductive success equally across all levels of territory quality. Following this, we predicted that *per capita* fecundity would be negatively correlated with the number of fall freeze-thaw events and that this effect would be consistent across years, regardless of the proportion of occupied territories that were of high quality. This means that the negative effect of freeze-thaw events will decrease the magnitude, but not the direction, of the slope of the relationship between the proportion of occupied territories that were of high quality and *per capita* fecundity.

5.3 Methods

Study system and field methods

We used demographic and territory occupancy data collected between 1977 and 2018 from an individually marked population of Canada jays in Algonquin Provincial Park, Ontario (45°35'N, 78°30'W). The study area, situated along the highway 60 corridor in the park (Fig 1A), is located within the transition zone of the Great Lakes-St. Lawrence hardwood forest and the boreal forest along the southern edge of the Canada jay's range (Strickland et al. 2011). Each year, 20 - 25 breeding pairs were monitored throughout the late-winter breeding season, which begins in mid-February and ends in May. All nests within the study area were found and monitored until young were approximately 11 - 14 d old, at which point nestlings were marked with a unique combination of three colour leg bands and one aluminum USFWS/CWS leg band (Sutton et al. 2019). Brood size, determined when nests were accessed to band nestlings, was used as an

estimate of fecundity (Sutton et al. *in review*). All territories within the study area were monitored during each population count throughout the study period, regardless of whether or not they were occupied. Occupancy was determined for all territories during bi-annual population counts (late February and mid-October) and a territory was considered occupied if at least one Canada jay was present.

Using these biannual counts, we determined when a territory first became vacant and when it was reoccupied in order to determine the number of years it remained vacant. In many cases, territories were vacated and re-occupied multiple times and we treated each of these re-occupation events separately. For example, if a territory was occupied from 1980-1983, 1990-1996 and 2000-2018, we considered this as two separate periods of vacancy (7 and 4 yrs, respectively). If a territory was vacant at the end of the study period (2018), we considered the number of years it remained unoccupied to be from the point it last became vacant until 2018. Overall the study population has experienced a decline in territory occupancy since the 1980s of approximately 50% (Waite and Strickland 2006, Sutton et al. *in review*). This decline occurred over the course of 27 years from 1977 until 2003 and the population has remained relatively stable since 2003 (Sutton et al. *in review*). Concurrent with this observed population decline, our study area has expanded to allow for the continuous monitoring of 20-25 breeding pairs each year, with 40 territories monitored in 1988, 48 in 1998, 49 in 2009, and 61 territories in 2018.

Territory quality

We used estimates of territory quality calculated by Strickland et al. (2011). Briefly, territory quality was estimated as the proportion of conifers within a 450 m radius buffer around the mean

nesting location based on all known nesting attempts on a territory (Strickland et al. 2011).

Territories were subsequently placed in one of three categories based on the proportion of conifers present (low, 0-40%; medium, 40-58%; and high 58-100%) using Jenks' optimization method (Strickland et al. 2011).

Statistical models for testing predictions of site-dependent regulation

To test the effect of density on territory occupancy, we constructed a series of generalized linear mixed-effect models (GLMM) with a binomial distribution and logit link function that included all possible combinations of density, territory quality (high, medium, low) and the interaction between the two. We also included territory ID as a random effect because territories were monitored each year. Models were then compared using Akaike's information criterion corrected for small sample sizes (AICc) to identify the top model(s) (all models with $\Delta AICc \leq 2$) and AICc weights to further distinguish between top models. To investigate the effect of territory quality on time that a territory remained vacant after abandonment, we constructed a GLMM with a Poisson distribution and a log link function that included territory quality as a fixed effect and territory ID as a random effect. We used occupancy data collected over the course of our entire study period from the point that a territory was monitored until the end of data collection in 2018.

We constructed a simple linear regression to determine the effect of density on the proportion of occupied territories that were of high quality (for a given season, calculated as the number of occupied high-quality territories divided by the total number of occupied territories) and the average number of young produced by each territory class. If site-dependent regulation

was acting on the population, we expected there to be a negative correlation between density and the proportion of occupied territories that were of high quality. Furthermore, the average number of young produced by a given territory class should be constant regardless of population density.

The effect of site-dependent regulation on *per capita* fecundity was assessed using a series of GLMMs with a Poisson distribution and a log link function that included all possible combinations of the proportion of occupied territories that were of high quality, number of fall freeze-thaw events (due to the effect of freeze-thaw events on cached food quality and subsequent reproductive performance; Sutton et al. 2016, 2019) and an interaction between these fixed effects. We used the proportion of occupied territories that were of high quality in this set of models because it represents a more explicit test of site-dependent regulation than using density because site-dependent regulation predicts that *per capita* fecundity should be lower when fewer of the occupied territories in a given area are of high quality. To determine if this was a better predictor of *per capita* fecundity than density, we also constructed a second set of models that included density instead of the proportion of occupied territories that were of high quality. In both sets of models, male and female ID were included as random effects to account for individuals breeding in multiple years.

For all models predicting *per capita* fecundity, we separated the time series into two distinct periods: 1) when the population was declining (1977 – 2003) and 2) when the population remained stable (2004 – 2018; Sutton et al. *in review*). Site-dependent regulation has been proposed to only act on increasing or stable populations (Ferrer et al. 2006), so we fit models predicting *per capita* fecundity using demographic data from the period of time the population

was stable and the entire time series (1977 – 2018) to examine if patterns of regulation were consistent over time.

All statistical analyses were conducted in R version 3.6.0 using the lme4 package (Bates et al. 2015). Visreg (Breheny and Burchett 2017) and ggplot (Wickham 2009) were used to visualize the output of the models and create our figures.

5.4 Results

Territory Occupancy and Length of Territory Vacancy

The top model predicting territory occupancy included density, territory quality, and the interaction between these two effects (AICc weight = 1; Table 1). As predicted by site-dependence regulation, the slope of the relationship between density and territory occupancy was steepest for low-quality territories and shallowest for high-quality territories (Fig 2a).

The time that a territory remained vacant after being abandoned varied widely from 1 – 44 yrs (mean \pm standard deviation; 10 ± 10 , $n = 128$ reoccupation events). As predicted by site-dependence regulation, territory quality was a good predictor of the length of time for which a territory remained vacant (-0.53 ± 0.15), with high-quality territories remaining vacant for a shorter period of time than low-quality territories (Fig. 2b).

The proportion of occupied territories that were of high quality was negatively correlated with density (-0.004 ± 0.0006 , $R^2 = 0.52$), suggesting that, at high densities, a lower proportion of occupied territories were of high quality.

Per Capita Fecundity

Brood size ranged from 0 (for failed nests) to (very rarely) 5 nestlings (mean \pm standard deviation; 1.7 ± 0.4 ; Table S1, $n = 747$ nests surveyed). When the population was stable (2004 – 2018), the top model predicting brood size included the proportion of occupied territories that were of high quality, the number of fall freeze-thaw events, and the interaction between these two effects (Table 2). The interaction between the proportion of occupied territories that were of high quality and the number of freeze-thaw events in the fall suggested that, when breeding conditions were poor (i.e., a higher than average number of fall freeze-thaw events), brood size increased with the proportion of occupied territories that were of high quality (Fig. 3). In contrast to the proportion of occupied territories that were of high quality, density was a poor predictor of brood size when the population was stable ($\Delta\text{AICc} > 4$; Table 2) and throughout the entire time series.

Over the course of the entire time series (1977 – 2018), there was weaker evidence for the effect of the proportion of occupied territories that were of high quality on *per capita* fecundity. Similar to when the population was stable, the top model predicting brood size, included the proportion of occupied territories that were of high quality, the number of fall freeze-thaw events, and the interaction between these two effects (Table S2). However, there was support for two additional models: one included only the number of fall freeze-thaw events ($\Delta\text{AICc} = 1.2$) and the other included the additive effects of the proportion of occupied territories that were of high quality and the number of fall freeze-thaw events ($\Delta\text{AICc} = 1.9$; Table S2). The average number of nestlings produced in each territory quality class did not vary with density over the course of the entire study (low: -0.16 ± 0.17 , medium: -0.056 ± 0.10 , high: $0.097 \pm$

0.086), meaning that changes in density did not cause declines in individual performance regardless of territory quality.

5.5 Discussion

Our work suggests that Canada jay population abundance in Algonquin Provincial Park is regulated, in part, by site dependence. We found strong evidence that density and territory quality influenced territory occupancy and that high-quality territories remained vacant for shorter periods of time. This preferential filling of high-quality territories also resulted in an increase in *per capita* fecundity, but only when there was a higher than average number of freeze-thaw events in the fall preceding breeding. Under this scenario, individuals reproducing on high-quality territories were buffered from weather conditions that negatively influenced cached food quality (Sutton et al. 2019), thereby supporting the hypothesis that environmental conditions modulate density-dependence.

Given that weather could have a pronounced influence on density-dependence, long-term changes in climate could modulate the magnitude of an effect of density on population vital rates (Franklin et al. 2000, Coulson et al. 2001, Jacobson et al. 2004, Previtalli et al. 2009, Flesch et al. 2015). If climate change causes an increase in the fluctuations of either resources or predator abundance (Coulson et al. 2001, Lima et al. 2002a, 2002b, Jacobson et al. 2004, Previtalli et al. 2009), this could result in shifts in territory quality (i.e. territories becoming higher or lower quality). It could also exacerbate differences between territories, resulting in more pronounced density-dependent relationships over time. For example, in high rainfall years, only the best protected nest sites of griffon vultures (*Gyps fulvus*) produced young (Zuberogoitia et al. 2019). Our results suggest that a similar process is likely taking place with Canada jays in Algonquin

Park because, in years with an increased number of freeze-thaw events, we saw a positive effect of the proportion of occupied territories that were of high quality on fecundity. As temperatures continue to increase in the park and more freeze-thaw events are likely to occur, density-dependent regulation of fecundity could become stronger.

Despite site-dependent regulation acting on the Canada jays of Algonquin Provincial Park, the population has not increased over time and instead has remained stable at low abundance. While the number of fall freeze-thaw events may increase the strength of density-dependence, it also influences overall fecundity of the population (Sutton et al. 2019). When a higher than average number of freeze-thaw events occur in the fall, the fewest young are produced (Sutton et al. 2019) and, likely the fewest recruits. This means that despite a greater proportion of the population inhabiting high quality territories, *per capita* fecundity remains low when environmental conditions are not favourable for reproduction and could, in part, explain why the population has not increased over time (Sutton et al. *in review*). Additionally, biased juvenile dispersal into high quality territories outside the study area could mean that fewer individuals will recruit into the population and further limit an increase in abundance.

Despite the evidence for site-dependent regulation on fecundity, it is likely that intraspecific competition also plays a role in regulating Canada jays in Algonquin Provincial Park by acting on vital rates other than fecundity. Results from a detailed population model constructed using demographic data from our study population (Sutton et al. *in review*) provides evidence that density influenced not only fecundity, but also juvenile apparent survival and female immigration. In contrast to fecundity, adult and juvenile apparent survival does not vary with territory quality (Norris et al. 2013). It is, therefore, likely that site-dependence is not acting

on Canada jay survival and instead, intraspecific competition for territories or food resources may be the underlying cause of the relationship between density and apparent survival. While fecundity seems to be the primary vital rate driving variation in population growth in this population (Sutton et al. *in review*), if the relative contribution of apparent survival increased, the underlying mechanism producing density-dependent regulation of this population could also shift. It is, therefore, important to consider how multiple mechanisms may promote relationships between density and vital rates within a single population and the contribution of a given vital rate to population growth in order to understand important factors regulating wild populations (Nevoux et al. 2011, Grünkorn et al. 2014).

One of the challenges of describing how populations are regulated is being able to distinguish between site-dependence and interference competition (Ferrer et al. 2006, Beja and Palma 2008). To distinguish between these mechanisms, previous studies have examined how the coefficient of variance in fecundity (Ferrer and Donazar 1996), skewness of fecundity (Ferrer et al. 2006), and territory-quality-specific estimates of fecundity (Kokko et al. 2004, Zuberogitia et al. 2019) vary with density. However, simulation studies suggest that these metrics are not able to distinguish between site-dependent regulation or interference competition (Beja and Palma 2008). An alternative approach is to more explicitly identify predictor variables that differentiate between the two hypotheses. Our use of the proportion of occupied territories that are of high quality directly tests the relationship proposed by site-dependent regulation and allows for the two hypotheses to be differentiated. If site-dependent regulation is occurring, we would expect a positive relationship between the proportion of occupied territories that are of high quality and fecundity, and a negative relationship if interference competition is acting.

Despite the benefits of using the proportion of occupied territories that are of high quality, it requires detailed knowledge of how territories are distributed across the landscape and the aspects of habitat that promote variation in territory quality. If territory quality can be estimated and remains relatively constant over time, using the proportion of occupied territories that are of high quality is likely a better way to differentiate between site-dependence and interference competition promoting density-dependence.

While our previous work has linked variation in percent conifers to multiple metrics related to reproductive performance and survival (Strickland et al. 2011, Norris et al. 2013, Whelan et al. 2016), our estimate of territory quality is arguably still quite coarse and may account for some of the unexplained variation in models predicting both territory occupancy and *per capita* fecundity. Territory quality was derived from the proportion of coniferous cover in a 450 m diameter circle centred on the mean nest location but may not accurately represent the true area being used by a breeding pair if, for example, nests tended to be located near the edge of the areas the jays actually used. Further, our estimate of territory quality is assumed to be linked to preservation of cached food, which is essential for Canada jays to survive and reproduce during the winter (Strickland et al. 2011), but may not capture other landscape features that contribute to variation in territory quality. Resources and predators may be unequally distributed across the landscape and could increase variation in quality between and within a quality class. Better estimates of territory quality may therefore be derived by measuring resource availability (Barnes et al. 1995, Rodenhouse et al. 2003), predator abundance (Rodenhouse et al. 2003), or measuring patterns of space use at a finer scale in order to accurately assess the habitat an individual or breeding pair uses. Using higher resolution estimates of territory quality could in

turn increase the amount of variation explained by models assessing site-dependent regulation of wild populations.

The degree of habitat heterogeneity can often vary across a species' range and this will likely play an important role in driving variation in how populations are regulated. In Algonquin Provincial Park, a high degree of heterogeneity with respect to forest composition exists at the scale of territories, which is critical for site-dependent regulation to be acting on a population (Dhondt et al. 1992). However, throughout much of the Canada jay boreal forest range, habitat is more uniformly composed of conifers, especially spruce (*Picea*) spp. (Strickland and Ouellet 2018). This suggests that the underlying cause of variation in territory quality in Algonquin may not apply to other Canada jay populations. Studies elsewhere throughout the range could help to determine whether density-dependent regulation occurs in other populations, and if the mechanisms promoting density-dependence vary between populations. In more uniform habitat, competition for resources, or predation risk could be more important regulators of population vital rates (Krüger and Lindström 2001, Nevoux et al. 2011). Few studies have investigated how density-dependent relationships vary between populations of the same species, but this could be a fruitful avenue of research and shed light on how climate and density interact to influence population growth across broad spatial scales.

5.6 Tables

5.6.1 Table 1 AIC table for models predicting territory occupancy in Canada jays

AICc table for models predicting territory occupancy in Canada jays. Fixed effects included in each model are listed in addition to the number of parameters (K), AIC value, Δ AIC value and AIC weight. Top models included all models with Δ AIC \leq 2.

Model predicting territory occupancy	K	AICc	ΔAICc	AICc Weight
Territory Quality * Density	5	1589.9	0	1
Territory Quality + Density	4	1622.0	32.1	0
Density	3	1852.1	262.2	0
Territory Quality	3	1895.3	305.4	0

5.6.2 Table 2 AICc table for models predicting Canada jay brood size while population was stable (2004 – 2018)

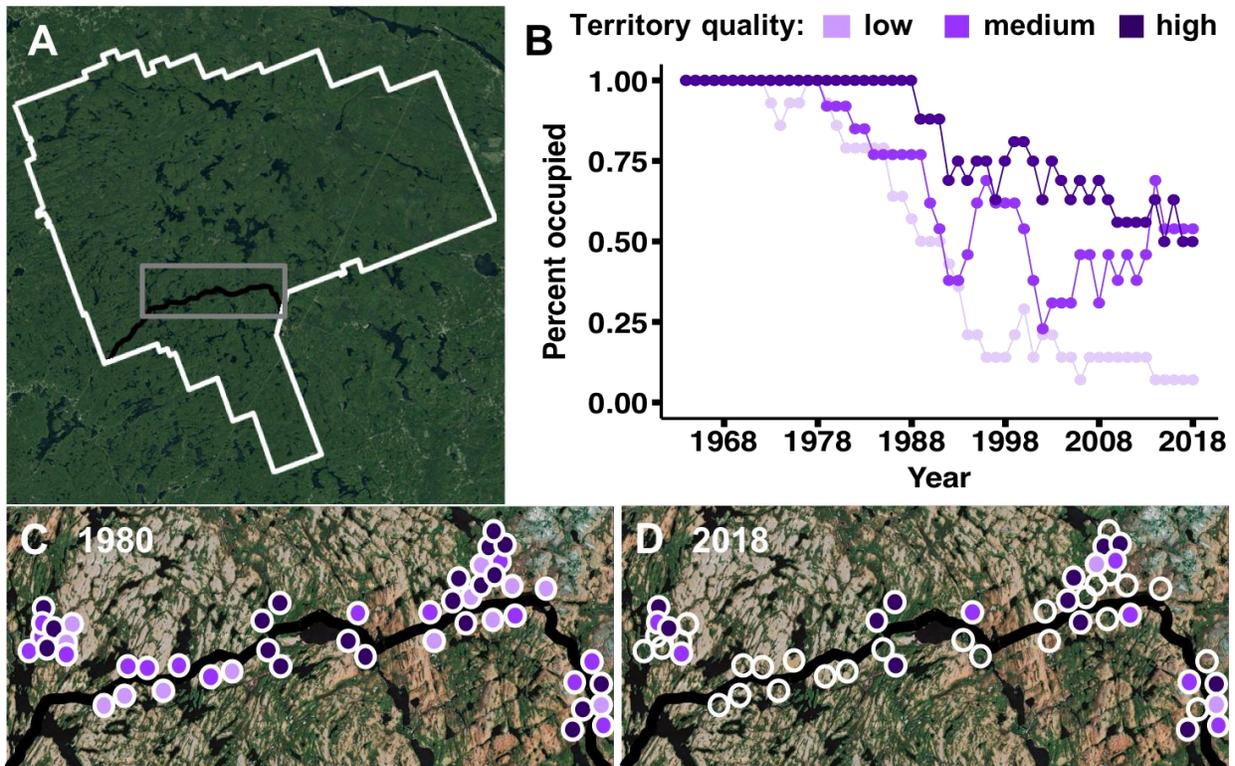
Fixed effects included in each model are listed in addition to the number of parameters (K), AICc value, Δ AICc value and AICc weight. Top models included all models with Δ AICc \leq 2 and AICc weights were used to further differentiate between models within Δ AICc \leq 2.

Model predicting brood size	K	AICc	ΔAICc	AICc Weight
Fall Freeze-thaw * Proportion High	6	1026.2	0	0.59
Fall Freeze-thaw	4	1029.5	3.3	0.11
Proportion High	4	1029.6	3.4	0.11
Density	4	1030.6	4.4	0.07
Fall Freeze-thaw + Proportion High	5	1031.1	4.9	0.05
Fall Freeze-thaw + Density	5	1031.5	5.3	0.04
Fall Freeze-thaw * Density	6	1032.5	6.3	0.03

5.7 Figures

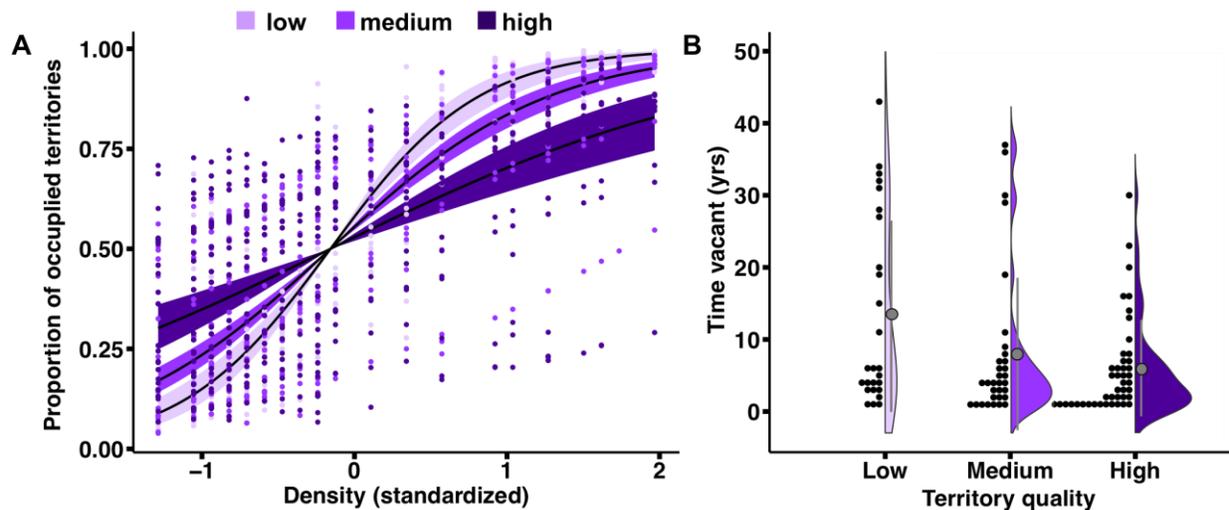
5.7.1 *Figure 1 Study area, distribution of occupied territories and decline in territory occupancy over time of Canada Jays in Algonquin Provincial Park, ON.*

A) Study area (gray box) within Algonquin Provincial Park, ON. B) Decline in territory occupancy in relation to territory quality (as defined by Strickland et al. 2011) indicated by the shades of purple. Circles in C) and D) represent the distribution of occupied territories in a high (1980) and a low density (2018) year, respectively. Territory quality is again indicated by shades of purple, with darker shades representing higher quality territories. Empty circles represent territories that were not occupied during that year. The leafless photography background shows the high degree of habitat heterogeneity that occurs throughout the study area.



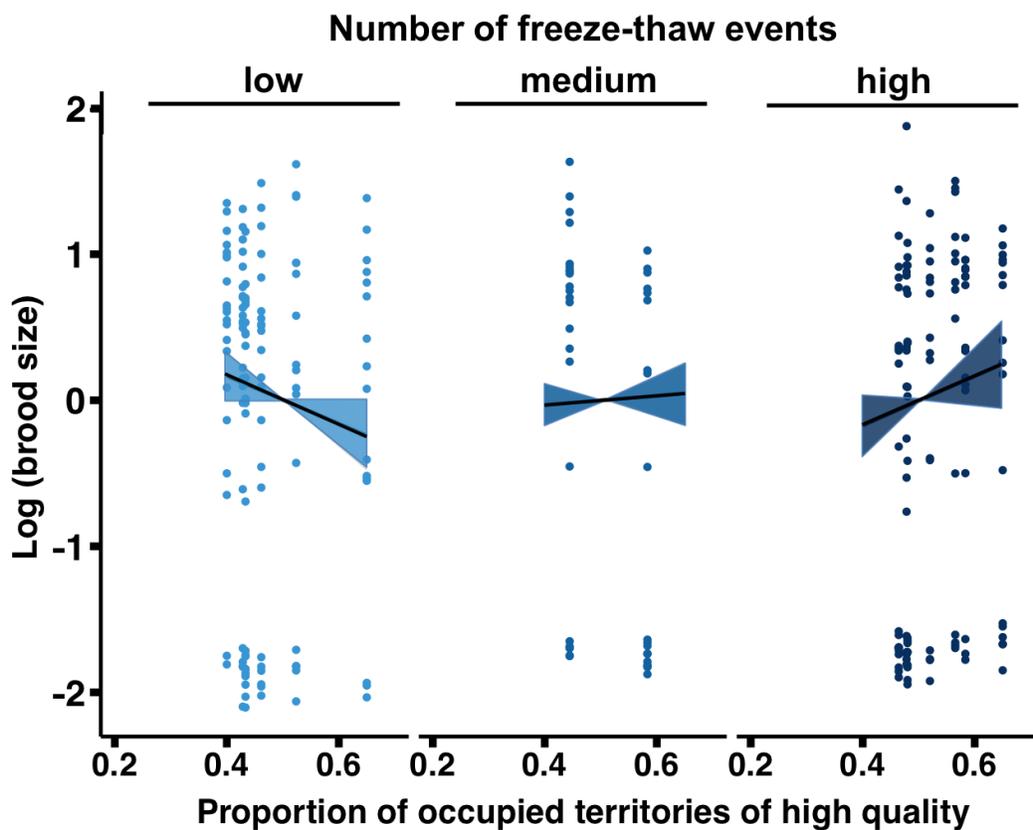
5.7.2 Figure 2 Territory occupancy and time territories remained vacant

A) The effect of population density on territory occupancy depended on territory quality. Density had the strongest effect on occupancy of low-quality territories (indicated by the steepest slope and light purple) and the weakest effect on occupancy of high-quality territories (indicated by the shallowest slope and darkest purple). Points represent partial residuals and the lines represent the predicted slopes from the generalized linear mixed-effect model. B) Territory quality was a good predictor of time that a territory remained vacant. When high-quality territories become vacant, they are more likely to be re-occupied in a shorter period of time than low-quality territories. The large grey dot represents the mean with the grey line representing standard error. Raw data is represented by small black dots on the left side of each violin.



5.7.3 Figure 3 Influence of proportion of occupied territories on brood size

The effect of the proportion of occupied territories that were of high quality on brood size depended on the quality of environmental conditions for breeding, represented by the number of fall freeze-thaw events while the population was stable (2004 – 2018). Only in poor breeding conditions (i.e. a high number of freeze-thaw events, right panel) was there a positive correlation between the proportion of occupied territories that were of high quality and *per capita* brood size. Points represent partial residuals and the lines represent the predicted slopes from the top generalized linear mixed-effect model, as determined by comparing AICc scores. Low, medium and high number of freeze-thaw events represent the 10th, 50th and 90th percentiles respectively.



5.8 Supplemental Material

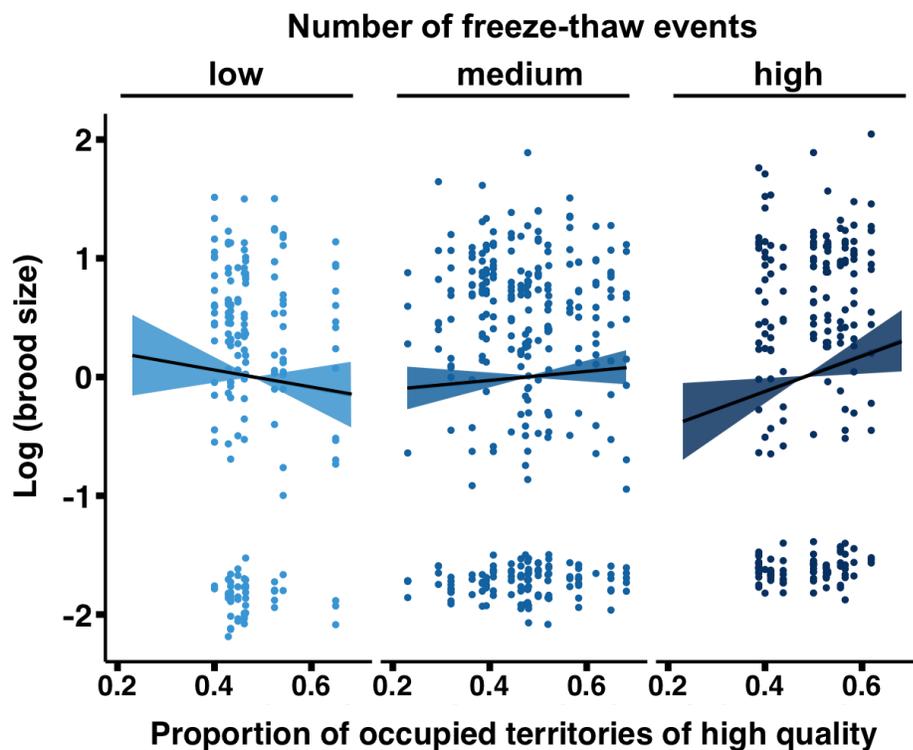
5.8.1 *Table S1 Brood size frequencies during the study period.*

All brood sizes were determined at the time of nestling banding approximately 11-14 days after eggs hatched. Median brood size was 3 and percentages were calculated as the number of nests with a given brood size divided by the total number of nests observed (n = 747).

Brood Size	Percent of total	Number of nests
0	34.6	259
1	7.7	58
2	18.1	136
3	31.1	232
4	7.5	57
5	1	5

5.8.2 Figure S1 Influence of proportion of occupied territories on brood size

The effect of the proportion of occupied territories that were of high quality on brood size depended on the quality of environmental conditions for breeding, represented by the number of fall freeze-thaw events for the entire time series (1977 – 2018). Only in poor breeding conditions (i.e. a high number of freeze-thaw events, right panel) was there a positive correlation between the proportion of occupied territories that were of high quality and *per capita* brood size. Points represent partial residuals and the lines represent the predicted slopes from the top generalized linear mixed-effect model as determined by comparing AICc scores and AIC weight.



6 Epilogue

The objective of my thesis was to address the climatic and demographic drivers of decline of a resident, boreal, food-caching passerine, the Canada jay. By combining long-term demographic data with a novel framework to understand how environmental conditions can influence cached food quality over time, I found strong evidence that environmental conditions throughout the duration of time that cached food is stored can influence not only individual vital rates, but also population growth of Canada jays in Algonquin Provincial Park, ON. Specifically, I found that fall freeze-thaw events carry over to negatively influence fecundity, which in turn is the major driver of variation in population growth. Fall freeze-thaw events also modulated site-dependent regulation that acts on fecundity. Collectively my research synthesizes knowledge from the field of food science and ecology to understand how food caching species may be influenced by environmental conditions and identified key environmental variables that influence population vital rates and growth using long-term demographic data collected from a population living at the southern edge of their range.

Population ecologists are often interested in characterizing changes in abundance over time. However, simply measuring changes in abundance without a view to understanding the mechanisms driving population growth provides only limited information that could be used to predict future trends. Developing a mechanistic understanding of how density and environmental variables contribute to variation in demographic vital rates can help to identify key periods of the annual cycle that have the greatest influence on changes in abundance. Without understanding the mechanisms underlying changes in abundance over time, spurious or biased trend could be produced as a result of when a time series begins and ends or by study-site selection (Fournier et

al. 2019, White 2019). In chapter 1, I identify potential environmental variables that could drive variation in population vital rates. I then apply these potential environmental mechanisms producing variation in vital rates to understand carry-over effects on reproductive performance (chapter 2) and how these effects scale up to influence population growth (chapter 3). Furthermore, I also conduct a field experiment to test the proposed mechanism producing a decline in cached food quality (chapter 3) and find that the number of fall freeze-thaw events that a cached food item experiences is the best predictor of mass when retrieved. The main strength of my thesis is that I have identified mechanisms linking life history traits with changing environmental conditions and the effects that these environmental conditions have on not only individual vital rates but also population growth.

Identifying specific mechanisms driving population growth in a single population also provides the ability to test the potential drivers of growth in other populations across a species' range (Thogmartin and Knutson 2007). One key uncertainty with Canada jays that still remains is whether the drivers of population growth in the Algonquin study population are consistent drivers of population dynamics for other populations across the Canada jays' range. The Algonquin Park Canada jay study provides a detailed mechanistic understanding of both the climatic and demographic drivers of population growth that could be applied to other populations where demographic data is more limited. The identification of proximate mechanisms linking climate and growth rate in one population could, therefore, be used to predict future declines under different climate models and across broad spatial scales if populations respond to proximate climatic mechanisms in a consistent fashion. However, the results presented in chapters 2 and 3 should be applied to populations further North with caution due to the dramatic

change in both climate and habitat characteristics. It is likely that environmental conditions, such as freeze-thaw events, would have consistent negative effects on cached food quality throughout the Canada jays' range, however what remains unknown is whether fecundity contributes as strongly to population growth as in Algonquin and if the strength of density-dependence, and mechanisms promoting it, remain constant over space.

When monitoring a population within a defined study area, it is difficult to disentangle emigration from survival, resulting in the need to use apparent rather than true survival estimates. Using apparent survival can obscure the contribution of both emigration and survival to population growth. For example, if the processes underlying emigration, such as dispersal, or true survival have changed over time they will influence estimates of apparent survival, but changes in either of these vital rates can have very different consequences for population growth. When an individual emigrates from the study site its offspring have the potential to immigrate back to the study area at a future time, but, if an individual dies, it cannot contribute to future population growth. My estimates of adult survival are likely to be closer to true survival due to limited adult dispersal outside of the study area. However, estimates of juvenile survival are likely biased low due to dispersal outside of the study area. Juvenile dispersal is currently a major unknown in Canada jays, but future studies could leverage advances in tracking technology to monitor individuals, especially juveniles, as they disperse within and out of the study area. Incorporating estimates of true survival into population models would allow for more precise estimation of the vital rates and, as a result, a more complete understanding of the processes that contribute to population growth.

One of the limitations of my thesis, and of studying scattering hoarding animals in general, is that it is difficult to assess the quality of individual food caches in the wild. As a proxy, I used simulated caches, but this does not capture all the components that could contribute to the degradation or persistence of food over time. Conducting simulated caching studies in Algonquin allows for the impact of natural variation in temperature and in situ microbial degradation, but still has its limitations. First and foremost, it excludes behavioural and physiological strategies potentially used by Canada jays that could help to preserve caches over time. For example, artificial caches are placed on the north side of trees in order to standardize the conditions that a caching chamber would be exposed to, but Canada jays may exploit particular microhabitats spaced throughout the tree to minimize cache degradation. Furthermore, Canada jay saliva and the oral microbiome could play an important role in caching dynamics by influencing the microbial communities that develop on a cache and potentially limiting microbial growth, but these effects are currently impossible to replicate in artificial caching studies. The type of food used in these studies could also influence the inference drawn from artificial caching studies. Typically, human food is used in an effort to reflect the natural variation in the diet of Canada jays (Strickland et al. 2011, Sechley et al. 2015, chapter 3). This however may not reflect how natural food items actually degrade or reflect the natural microbial components that would be on a food item in the wild. Natural food items could have very different microbial profiles than natural foods and the presence of bacteria from the moment that a food item is cached could increase rates of degradation. Additionally, using human food items does not truly reflect the breadth of food items that are cached by a Canada jay and therefore does not capture the potential variation in rates of degradation over time. It could be important to consider these

factors not only when designing future experiments, but also when interpreting the results of artificial caching experiments to understand the impact that environmental conditions may have on cached food quality.

Throughout chapters 2 – 4, it was assumed that individuals would be consistent in their caching behaviour over time, but the impact of climate change and environmental conditions on Canada jay populations could be mitigated through either learning, or plastic caching behaviour. In chapter 1, I highlighted the diversity of caching behaviour and behavioural strategies that individuals use to mitigate the effects of environmental conditions on cached food (e.g. Elgmork 1982, Hardy 1949). Canada jays could similarly preferentially cache food in locations with antimicrobial properties (Elgmork 1982) or manipulate food before caching to increase its persistence over time (Hardy 1949) to reduce the impact of environmental conditions on cached food over time and this could have implications for understanding how environmental conditions that influence cached food quality may scale up to influence not only individual vital rates, but also population dynamics. Additionally, individual Canada jays could learn either which locations best preserve food, or which food items are most resistant to degradation over time and this could reduce the influence of environmental conditions on cached food quality throughout an individual's lifetime. For example, if individuals can learn to preferentially cache food on conifers, a greater proportion of food caches would be of higher quality when it is retrieved. If individuals preferentially place caches on conifers, it could increase the effect of territory quality on reproductive performance and perhaps strengthen the trends that we observed in chapter 4. Taken together, it is important to develop a more complete understanding of Canada jay caching behaviour and, if this behaviour does vary over time, incorporate this into future models

assessing the impact of environmental conditions on population dynamics. Allowing for plastic responses in caching behaviour throughout the lifetime of an individual could account for some of the inter-individual variation in response to environmental conditions. Further, it could provide a mechanism to understand variation in individual quality and help to account for intra-individual variation throughout an individual's lifetime.

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