

PRIMARY RESEARCH ARTICLE

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

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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, Ontario, and a full annual cycle integrated population model, we examined the influence of environmental conditions and density on the population growth rate of Canada jays (*Perisoreus canadensis*), a resident boreal passerine that relies on perishable 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. Future warming during the fall and winter may compromise the viability of cached food that requires consistent subzero temperatures for effective preservation, potentially exacerbating climate-driven carry-over effects that impact long-term population dynamics.

KEYWORDSannual cycle, Canada Jay, food hoarding, Gray Jay, integrated population model, *Perisoreus canadensis*, population decline, seasonal interactions

1 | INTRODUCTION

Carry-over effects occur when an individual's previous history or experience contributes to explaining their current performance (Harrison et al., 2011; 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 (Cook et al., 2004; Kennedy et al., 2008; Perryman et al., 2002). In some species, non-breeding conditions can explain 7%–40% of variation in annual

breeding success (Morrissette et al., 2010; Norris et al., 2004; Rockwell et al., 2012). At the population level, there is laboratory 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.

Climate often plays an important role in modulating the strength of seasonal carry-over effects (Dickey et al., 2008; Harrison et al., 2013; Juillet et al., 2012). Variation in climatic conditions can alter the abundance, availability, or timing of resource pulses (Durant et al., 2007; Fogden, 1972; Parmesan & Hanley, 2015), which can impact individual condition and then carry over to influence success the following season (Cook et al., 2004; Perryman et al., 2002; 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 shortages of fresh food (Vander, 1990). Depending on the location, duration of storage, and type of food cached, poststorage 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 late-winter/early-spring breeding (Strickland & Ouellet, 2018). Our study population in Algonquin Provincial Park, Ontario, at the southern edge of their range, has declined by over 50% since the 1980s (Figure 1c; Waite & Strickland, 2006) 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 (Sechley et al., 2015; Waite & Strickland, 2006). Although there is some evidence to support the effect of fall temperature on brood size (Waite & Strickland, 2006), fall freeze–thaw events appear to have stronger effects on reproductive performance through simultaneous, negative effects on brood size, nesting success, and nestling condition (Sutton et al., 2019). Despite this, there is no evidence that this 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, we sought to: (a) identify the relative contribution of season-specific vital rates to population growth rate, and (b) 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.

2 | METHODS

2.1 | 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 (Figure 1a; Strickland & Ouellet, 2018). 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 & 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 (Figure 1c; Waite & Strickland, 2006).

Annual monitoring has occurred during two periods of the year. From 1980 to 2018, all nests in the study area were found and monitored beginning in mid-February and monitored until the end of the breeding season in May. Once a nest was found, it was checked

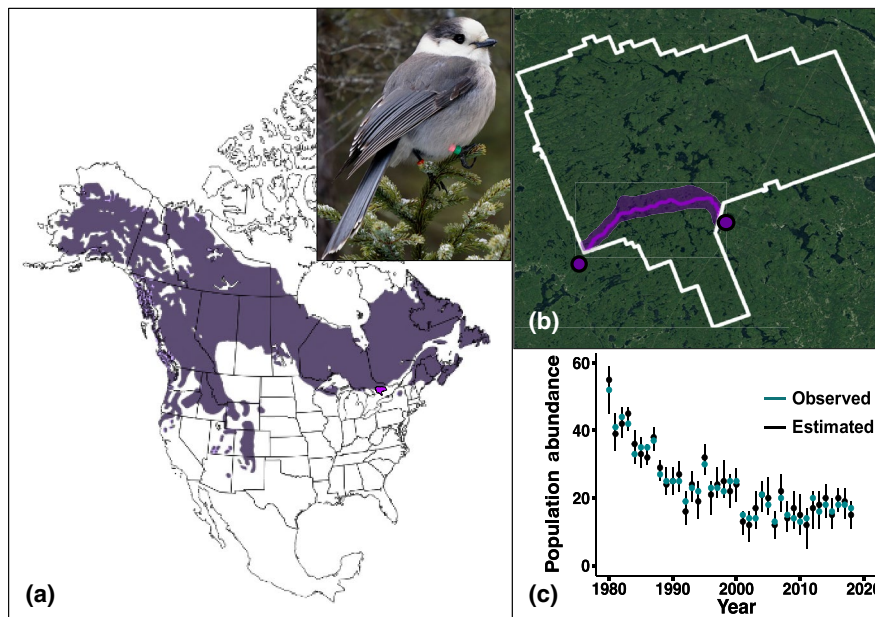


FIGURE 1 Canada jay distribution, study area in Algonquin Provincial Park, ON, and population decline: (a) Range map outlining the distribution of Canada jays (*Perisoreus canadensis*) in purple with Algonquin Provincial Park, ON highlighted in violet. Inset: A color banded Canada jay from the Algonquin study area. All individuals in the study area received a unique color band combination consisting of three colored bands and one aluminum USFWS/CWS band. (b) The core and peripheral study areas (highlighted in purple) are located along the highway 60 corridor in the southern portion of Algonquin Provincial Park. Weather stations used in this analysis are highlighted with black circles outlined in purple, with one located outside the western boundary of the study area (“Dwight”) and the other on the eastern edge of the study area (“East Gate”; Sutton et al., 2019). (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

regularly every 2–4 days until nests were accessed when nestlings were approximately 11 days old. At this time, young were individually marked with three color bands and one aluminum United States Fish and Wildlife Service/Canadian Wildlife Service band. Each year a survey was conducted during the breeding season to count the number of adults and juveniles present. Each October (1980–2018), a second survey 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 resight marked individuals. During both population counts, banded individuals were identified and unbanded individuals were captured and given a unique combination of bands.

2.2 | Study area and long-term data

The integrated population model (IPM; see below) used long-term data from 22 territories that were collected beginning in 1980 (defined as the “core study area”). Both productivity and population count data were restricted to these 22 territories, whether or not they were occupied in a given year. The “core study area” did not include territories that were added after 1980 as the Algonquin Provincial Park study area continued to grow (Sutton et al., 2019; Whelan et al., 2017). In total, 40 territories were monitored in 1988, 48 in 1998, 49 in 2009, and 61 territories in 2018 and these territories formed a “peripheral” study area in addition to the core study area described above. For our capture–recapture analysis, we considered all records of individuals banded and resighted or recaptured in both the core and peripheral study areas. We included all records to develop more precise estimates of survival by leveraging our expanding study to better capture movements of individuals throughout Algonquin Provincial Park.

2.3 | Environmental variables

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 (1980–2004) were corrected so that they would reflect temperatures within the park (see Sutton et al., 2019 for details). 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), prebreeding (Jan–Feb), breeding (Mar–May), and postbreeding (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).

2.4 | General modeling approach

To investigate the direct effects of vital rates on population growth and indirect effects of environmental conditions and density, acting through the vital rates, on population growth, we followed a two-step approach. First, we used an IPM composed of three component models (state-space, productivity, and survival) to estimate apparent survival, immigration, and fecundity from the long-term dataset (Schaub et al., 2013). Second, we used a path model to estimate the direct effects of environmental variables on vital rates, the direct effect of vital rates on population growth, and the indirect effects of environmental variables on population growth via each vital rate. Below, we provide details on each step in this process.

1. 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 IPM developed by Schaub et al. (2013) and similar to that described by Woodworth et al. (2017; Figure 2). We combined the three long-term datasets (described above: population counts, productivity, and capture–recapture) in the IPM to estimate sex-, age-, and season-specific vital rates.

a. State-space model

Central to the IPM is a state-space model, which describes the likelihood of the population count data (Figure 2). The state process represents a population projection model that consisted of three stages (local recruits, surviving adults, and immigrants), two sexes (s , which could be either female, f , or male, m), and a given period of the annual cycle in given year

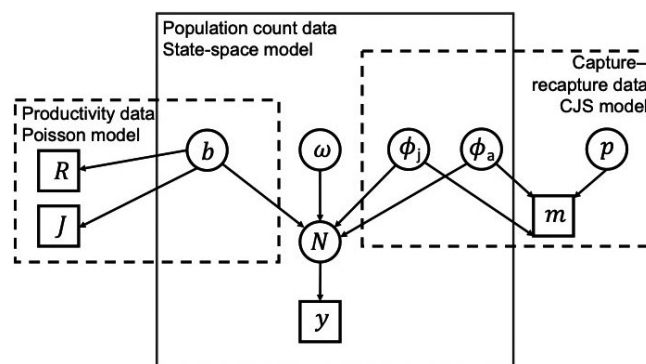


FIGURE 2 Directed acyclic diagram outlining model structure of the integrated population model: Structure of the integrated population model displaying relationships between variables and the three component models composed of: the state-space, productivity, and capture–recapture models. p represents the productivity data (measured as brood size at ~11 days post hatch), m represents the capture/recapture data used in the survival analysis, N represents the true population size, and y is the observed population size (i.e., the number of individuals observed during each population count). All other symbols correspond directly to estimated and measured variables described in Table S3

(t). For example, if “t” is spring/summer in 1982 then “t + 1” would be fall/winter in 1982. The three stages estimated by the IPM included local recruits R (individuals that were born in the study area the previous year; <1 year), surviving adults S (≥ 2 -year-olds that bred in the study area in the previous year), and immigrants I (individuals that came from outside the core study area). Immigrants into the study area fell into two categories: (a) unbanded individuals that were assumed to come from outside the entire study area (i.e., were not born or had bred previously in either the core or peripheral study areas) because all nests were found within the study area and most individuals were counted that were present on a territory during both population counts and (b) banded immigrants that were known to have come from the peripheral study area, but outside the core study area that was used in the population count and productivity datasets. We projected stage-specific abundances as either binomial or Poisson processes to account for demographic stochasticity (Equations 1–6).

$$R_{s, \text{fall/winter}} \sim \text{Binomial} (F_{s, \text{spring/summer}} \cdot \varphi_{ju, s, \text{spring/summer}}), \quad (1)$$

$$R_{s, \text{spring/summer}} \sim \text{Binomial} (\varphi_{ju, s, \text{fall/winter}}). \quad (2)$$

Equation (1) projects the number of local recruits in the fall, which is the product of the number of fledglings of each sex produced in a given breeding year ($F_{s, \text{spring/summer}}$) and sex-specific apparent juvenile survival ($\varphi_{ju, s, \text{spring/summer}}$). Because Canada jays have a single breeding season, the number of local recruits in the spring was a function solely of juvenile survival ($\varphi_{ju, s, \text{fall/winter}}$; Equation 2).

$$F_{f, \text{spring/summer}} \sim \text{Binomial} (F_{s, \text{spring/summer}}, 0.5), \quad (3)$$

$$F_{m, \text{spring/summer}} = F_{t, \text{spring/summer}} - F_{f, \text{spring/summer}}, \quad (4)$$

$$F_t \sim \text{Poisson} (J_t \cdot B_{f, \text{spring/summer}}). \quad (5)$$

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 offspring. Therefore, the number of female fledglings was estimated using a binomial model (Equation 3) and the number of male nestlings was estimated using Equation (4). The total number of fledglings produced was estimated using a Poisson model (Equation 5), where J_t was the per capita number of young produced each year, estimated from brood size, and $B_{f, \text{spring/summer}}$ was the number of females in a given breeding season (spring/summer period).

$$S_{s, t+1} \sim \text{Binomial} (B_{s, t}, \varphi_{ad, s, t}). \quad (6)$$

The sex-specific number of surviving adults was projected using Equation (6), where $B_{s, t}$ was the number of adults in

a given season and $\varphi_{ad, s, t}$ was the sex- and season-specific survival estimate.

$$I_{s, t+1} \sim \text{Poisson} (i_{s, t+1}). \quad (7)$$

Finally, the number of immigrants was projected using Equation (7) where $i_{s, t+1}$ was the expected number of immigrants of each sex in season $t + 1$.

Once all stages had been projected, we estimated annual population growth rate (λ) as the change in population size between spring/summer population counts using the following equation:

$$\lambda_{\text{spring/summer}} = (R_{s, t+1} + S_{s, t+1} + I_{s, t+1}) / (R_{s, t} + S_{s, t} + I_{s, t}). \quad (8)$$

The observation component of the state-space model was used to link sex-specific population count data ($C_{s, t}$) to the true sex-specific population size in each season ($B_{s, t}$; Equation 9) using a log-normal distribution with equal variances for each sex.

$$\log (C_{s, t}) \sim \text{Normal} (\log (B_{s, t}), \sigma_t). \quad (9)$$

The state-space model was initialized in the first year of the IPM using sex-specific priors for each stage-specific abundance.

b. Productivity model

Per capita number of young produced (J_t) was modeled with a Poisson regression using productivity data from our study.

$$J_t \sim \text{Poisson} (\rho_t / C_{f, t}). \quad (10)$$

ρ_t is the total number of young produced in a given year 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.

c. Survival model

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 (ju; <2 years) and adults (ad; ≥ 2 years) and estimated sex- (s; m or f), age- (ju or ad) and period-specific (t; fall/winter or spring/summer) apparent survival and recapture probabilities using a Cormack–Jolly–Seber model (Kery & Schaub, 2011). Therefore, $\varphi_{ju, s, t}$ represents juvenile sex-specific survival from one period of the annual cycle to the next and $\varphi_{ad, s, t}$ represents adult sex-specific survival from one period to the annual cycle to the next (e.g., from spring/summer to fall/winter).

2. Path model

We applied a path model approach (Shiple, 2016) developed by Woodworth et al. (2017) that used estimates of season-specific

vital rates and population growth derived from the IPM and environmental/density variables to estimate the relative contribution of both environmental variables and density throughout the annual cycle on population growth acting through season-specific vital rates. The path model included all possible linkages between environmental/density covariates and season-, sex-, and age-specific vital rates, and these vital rates to population growth (Figure S1). There are two main advantages to using a path model to assess the direct effects of vital rates on population growth and environmental/density variables on vital rates. First, indirect effects of environmental/density covariates on population growth can be estimated (Woodworth et al., 2017). Second, by fitting every linear model in the path diagram to each sample in the posterior distribution estimated by the IPM, uncertainty in the model input are carried forward into the path model (Woodworth et al., 2017). In our analysis, every linear model included in the path analysis was run for a total of 15,000 iterations using each sample in the posterior distribution estimated by the IPM. Once all iterations of the component models were run, mean coefficient estimates and 95% credible intervals were calculated for each model.

At each iteration (i.e., for each sample in the posterior distribution), 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. All statistical analyses were performed in R version 3.6.3 (R Core Team, 2019).

3 | RESULTS

3.1 | Demographic contributors to population growth rate

The population size within the core study area of consistently monitored territories since 1980 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 the 38 year study, population growth rates (λ) ranged from 0.6 to 1.53, with the population increasing ($\lambda > 1$) in only 12 (32%) of these years ($\lambda < 1$, $n = 19$ and $\lambda = 1$, $n = 7$; Figure 3a).

Based on the path 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 4; Table S1). 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 3b–h). Fecundity remained below the level of replacement for most of the years of our study (per capita fecundity was less than two), especially during the period of most rapid decline in the 1980s (Figure 3b). Immigration was highly variable, but spring/summer immigration in both sexes was consistently higher than fall/winter immigration (Figure 3c,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 3e,f). Juvenile apparent survival for both sexes was lower during the spring/summer period compared to fall/winter (Figure 3g,h).

3.2 | 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 = -0.271 , 95% CI = -0.497 , -0.036 ; Figure 5), no other sex- or season-specific estimates of apparent survival were strongly correlated with density or environmental variables (Tables S2–S9). Neither fall/winter and spring/summer male immigration, nor fall/winter female immigration were strongly correlated with any environmental variables (Tables S10–S12). In contrast, spring/summer female immigration was negatively correlated with mean winter temperature (-0.243 , 95% CI = -0.467 , -0.062) and positively correlated with winter precipitation (0.13 , 95% CI = 0.0231 , 0.233) and spring/summer density (0.244 , 95% CI = 0.124 , 0.446 ; Table S13).

Unlike survival and immigration rates, fecundity was strongly correlated with both fall/winter density and several environmental variables (Figure 5; Table S14). Both the number of fall freeze-thaw events (-0.253 , 95% CI = -0.415 , -0.096) and mean fall temperature (-0.17 , 95% CI = -0.317 , -0.024) were negatively correlated with fecundity in the subsequent breeding season. Furthermore, fecundity was negatively correlated with the number of winter freeze-thaw events (-0.212 , 95% CI = -0.369 , -0.052), winter precipitation (-0.213 , 95% CI = -0.381 , -0.032), and fall/winter density (-0.178 , 95% CI = -0.322 , -0.034).

3.3 | 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 indirect effect of fall weather on population growth (-0.426 , 95% CI = -0.876 , -0.00358 ; Figure 6; Table S15). Fall weather had a strong indirect effect on population growth, primarily through its negative effect on fecundity. Density also had a negative indirect effect on population growth (-0.226 , 95% CI = -0.413 , -0.0466), which was primarily

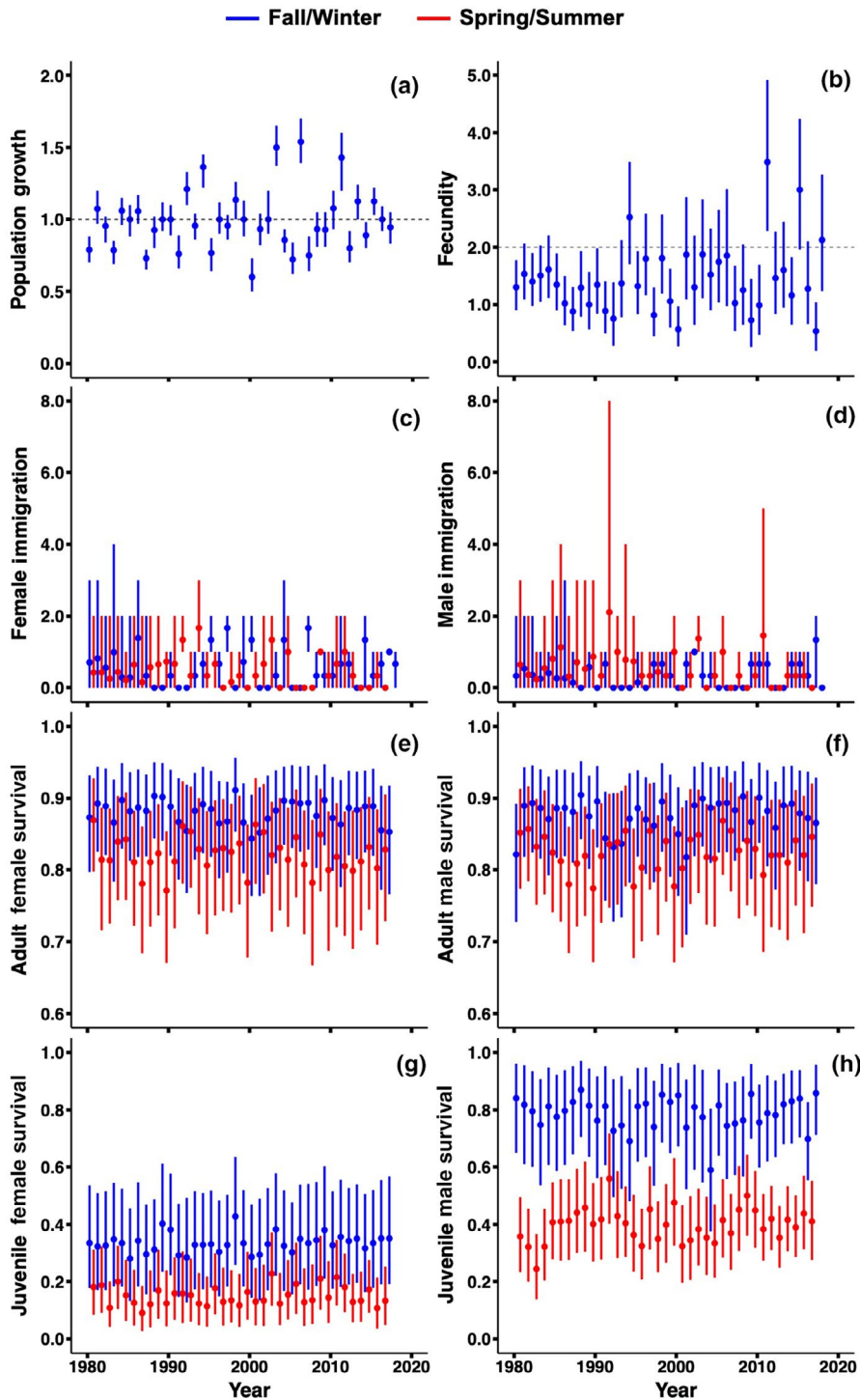


FIGURE 3 Temporal trends of population growth and season-specific vital rates: (a) population growth, (b) fecundity, (c) female immigration, (d) male immigration, (e) adult female apparent survival, (f) adult male apparent survival, (g) juvenile female apparent survival, and (h) juvenile male apparent survival. All points represent means and lines represent 95% credible intervals. Colors represent season-specific estimates of vital rates [Colour figure can be viewed at wileyonlinelibrary.com]

driven by negative effects of density on both fecundity and juvenile male spring/summer survival. However, the overall negative effect was dampened by the positive effect that density had on spring/summer female immigration.

4 | 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 prebreeding weather, on fecundity, which, in turn, was the primary vital rate influencing population growth. Consistent with Sutton et al. (2019), fall freeze-thaw events had the strongest effect on fecundity, and we hypothesize that this 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 (Ali et al., 2015; Boonsumrej et al., 2007; Raji et al., 2016). Our results strongly suggest that a more variable and warmer fall climate likely led to greater food limitation for Canada

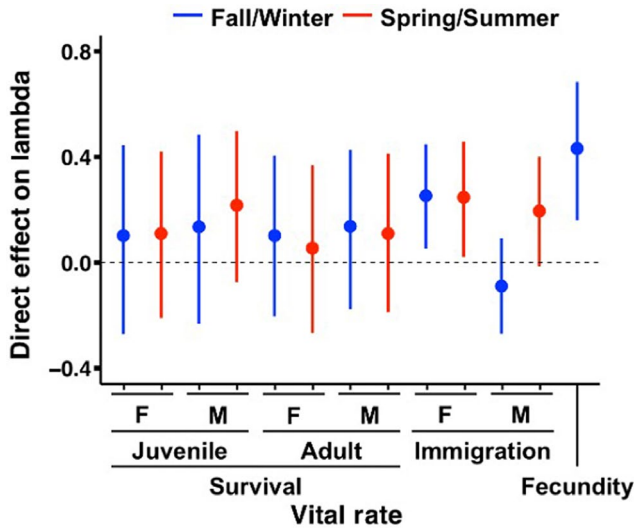


FIGURE 4 Direct effects of vital rates on population growth: Each point represents the mean and the line 95% credible intervals. All vital rates contributed positively to population growth, except over-winter male immigration. Vital rates were considered to contribute strongly to variation in population growth rate if the credible interval did not overlap zero

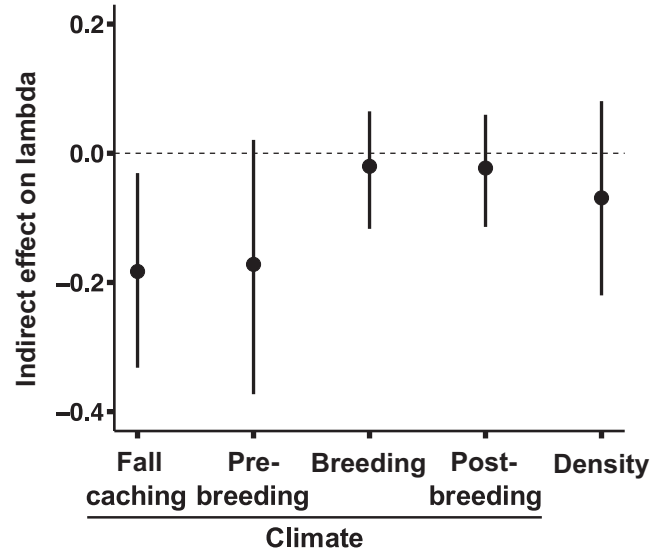


FIGURE 6 Cumulative indirect effects of seasonal climate and density on population growth: Variables were considered to have strong indirect effects if their credible interval did not overlap zero (represented by the dotted line). Each period and density estimate represents the sum of all period-specific climate variables that were included in the path model

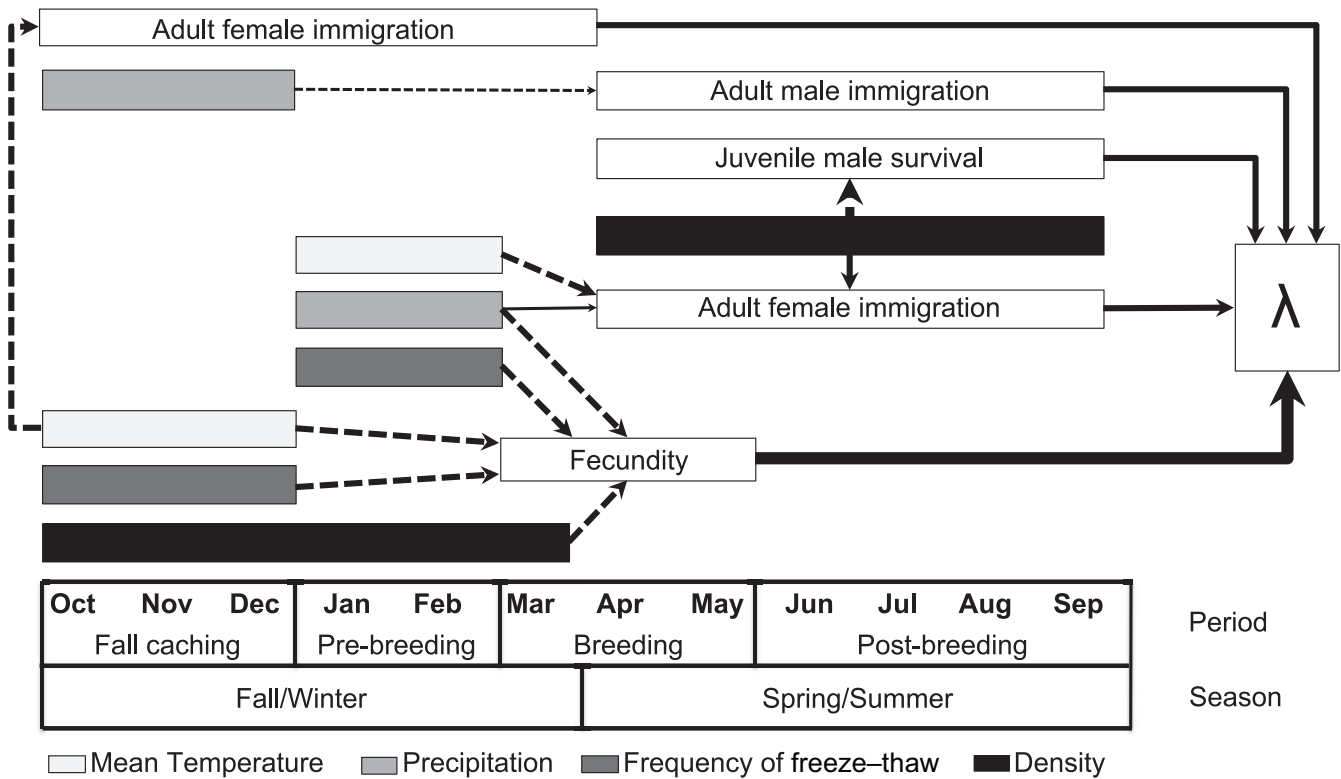


FIGURE 5 Path diagram outlining direct effects of vital rates of lambda and climate variables on vital rates: To simplify the visualization of the path analysis, only vital rates and environmental variables that had the largest direct effects on population growth (credible intervals overlapping zero by less than 10%) were included in the path diagram. 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. Fecundity represents the per capita number of young produced in a given breeding season, while juvenile survival represents the survival estimate of young from fledging to our fall population count

jays during the late-winter breeding period, causing several years of low reproductive output, which in turn produced few juveniles that were available to become breeding recruits.

While our model provides evidence that fall freeze–thaw events contributed to the decline of this population, it seems somewhat contradictory that there is also evidence for a linear decrease in the number of freeze–thaw events over this same time period (Sutton et al., 2019), albeit with high inter-year variability. However, the period of rapid decline in this population actually occurred early in the time series between 1980 and 1996, which was then followed by a period of stabilization at low abundance from 1997 to 2018 (Figure 1c). In the early years of the study, several consecutive years of low reproductive output (Figure 3b) likely contributed to the sharp decline in abundance. Consistent with this, 10 of the 16 years (63%) during this early period had a greater-than-average number of freeze–thaw events in the fall. In contrast, only 8 of 22 later years (36%) had a greater-than-average number of fall freeze–thaw events (Figure S3). In the later period, years with a low number of freeze–thaw events resulted in above average reproductive success (Figure 3). However, it appears these years did not generate a sufficient number of breeding recruits for the population to rebound. This is likely because Canada jays are constrained by low clutch sizes that are typically just above replacement levels (modal clutch size of 3 in the study area with a maximum of only 5; Strickland & Ouellet, 2018). While we did find an effect of density on population growth rates that would presumably provide the capacity of the population to increase at low densities, the strength of this effect was offset by the positive effect of density on female immigration, which implies that fewer females from outside the study area were being recruited into the population during low abundance years. Thus, even a couple of sporadic years of high reproductive output did not result in Canada jays being able to recover from a period of poor environmental conditions that occurred several decades prior.

Seasonal differences in a number of vital rates are a 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 likely 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 neighboring 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. Furthermore, 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.

Variation in the total area monitored within Algonquin Provincial Park may have influenced apparent survival estimates from the IPM. Survival estimates derived from Cormack–Jolly–Seber models depend on how likely an individual is to be resighted or captured after it is initially tagged (Kery & Schaub, 2011; Sandercock, 2003). While we used a consistent core study area of 22 territories for both productivity and count datasets, we incorporated data from both the core and peripheral study areas to estimate apparent survival. Because the total number of Canada jay territories monitored in Algonquin Park increased over time, this also increased the probability of observing individuals when they moved between territories. This higher detection probability likely provided more accurate survival estimates due to our increased ability to differentiate between emigration and mortality. We did not observe any temporal trends in apparent survival, but it is important to note that changes to the overall size of the study area may have obscured possible trends in survival estimates if increasing our area of monitoring increased the probability of detection.

Interestingly, immigration, as estimated by the IPM, decreased after 1988. Although this coincides with an expansion of the study area in Algonquin Park, it is unlikely that expansion of the study area influenced immigration rates. The addition of more monitored territories likely increased the ratio of banded to unbanded individuals but would not have influenced the total number of individuals entering the core study area. However, establishing a causal link between density and immigration remains difficult due to concurrent changes in the size of our study area and population density. Despite these correlated changes, it is important to consider alternative explanations for how density influences immigration. First, given there was a positive correlation between density and female immigration, lower densities would lead to fewer immigrants entering the core study area. Second, a prior analysis showed that adults and juveniles tend to more frequently disperse away from low-quality territories compared to high-quality territories (Norris et al., 2013) and many of the territories in the core study area were of low quality. Consequently, as these territories became vacant over the course of the study, they would be less likely to be reoccupied (Sutton et al., 2020). Furthermore, climate change may have reduced the quality of all territories within the core and peripheral study areas and this may have resulted in biased northward dispersal away from the southern edge of the Canada jay's range.

High-latitude areas, such as the boreal forest, are predicted to experience the greatest changes in temperature, precipitation, and climatic variability. 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 (Menebroeker et al., 2016; Waite & Strickland, 2006) and

under future warming scenarios (Ridgeway et al., 2018), 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 (Soykan et al., 2016).

RESEARCH AND ANIMAL ETHICS

Animal care approval was received from the University of Guelph animal care committee and from Canadian Wildlife Services, which approved all marking of individuals through permits to D.S., N.E.F. and A.O.S. Permission to carry out this study in Algonquin Provincial Park was provided by Ontario Parks.

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CONFLICT OF INTEREST

All authors declare no competing interests.

AUTHOR CONTRIBUTION

A.O.S., D.R.N., and D.S. conceived the study. All authors contributed to data collection, interpretation of data, and writing of the manuscript. All authors approved the final submitted version of the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding authors upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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