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Article

Causes and consequences of variation in diet composition of nestling Canada jays

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Diet quality during development can impact growth, physiology, behaviour and survival. The Canada jay is a resident boreal passerine that caches a wide variety of perishable food items in late summer and autumn for its over-winter survival and late-winter reproduction. A previous experiment found evidence that food supplementation of Canada jay pairs during the nestling period had a positive effect on the condition of their nestlings. However, given that foods cached by adults vary widely in nutritional content, the composition of nestling diets could also have an important influence on offspring development. In a population of Canada jays in Algonquin Provincial Park, Ontario, Canada, we investigated the influence of environmental conditions before and during the breeding season on nestling diet composition and the consequences of nestling diet composition on the body condition of nestlings and on their subsequent survival. Using stable-carbon ($\delta^{13}\text{C}$) and -nitrogen ($\delta^{15}\text{N}$) isotopes, we estimated the proportion of three food groups (vertebrates + human food, invertebrates and plants) in feathers from almost 200 nestlings. Nestling diet in March and April was influenced by environmental conditions 5–6 months prior to hatching, with warmer and more variable autumn temperatures associated with a greater proportion of vertebrate flesh and human food in the diet. However, the proportion of vertebrates and human food in the diet had no influence on nestling body condition or whether an individual was observed the following fall. Our results, in conjunction with previous work on Canada jays, suggest that the quantity of food available to a nestling during development may be more important than diet composition.

Keywords: body condition, diet quality, early life, *Perisoreus canadensis*, stable isotopes

Introduction

Both the quality and quantity of food early in life can have profound impacts on the growth, morphology, physiology and survival of offspring (Naef-Daenzer and Keller 1999, Kitaysky et al. 2006, Rossmanith et al. 2007, Wilkin et al. 2009, Freeman et al. 2020a). The effects of food quantity are relatively well-studied where more food is often associated with faster growth rates and larger offspring (Woods and Armitage 2003, Kager and Fietz 2009, Vafidis et al. 2016, Freeman et al. 2020a). In comparison,



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the role of diet quality in development is understudied in the wild due to difficulties associated with quantifying diet composition and the uncertainty associated with gradients of food quality.

Diet quality is an ambiguous term that can mean diet composition (i.e. what an organism is eating), caloric density or nutrient composition (Karasov and del Rio 2007, Twining et al. 2016). Therefore, assessing the role of diet quality during development requires knowledge of food composition and which nutrients are essential for growth. Macronutrients are vital for growth because they are key sources of energy for metabolism and tissue development (Uauy and Dangour 2006, Wu et al. 2014). Diets rich in protein and fat, particularly essential amino and fatty acids, are associated with faster growth rates, higher body condition and increased survival of young (Kitaysky et al. 2006, Twining et al. 2016). The diet of offspring often differs substantially from that of their parents (Radford 2008, Orłowski et al. 2014) and, in some species, adults shift their foraging behaviour during the breeding periods in order to provide food items beneficial for the growth and development of their young (Krebs 1978, Gill 1990). For example, many nectivorous and primarily herbivorous birds have been observed feeding their young protein-rich insects (Gill 1990, Markman et al. 1999, Koenig et al. 2008). However, high-quality food items (i.e. those with high protein and fat content) may not always be available in the environment at any given time.

What young organisms consume or are fed by their parents can be limited by resource availability. Many species time their breeding to coincide with peak resource abundance in order to meet high energetic demands of young (Lack 1954, Perrins 1970, Visser and Verboven 1999, Thomas et al. 2001). However, if the breeding period does not coincide with peak resource abundance in the environment, the diet of developing young may be constrained due to limited food resources (Hipfner 2008, Samplonius et al. 2016, but see Mallord et al. 2016). Young of altricial species may be further constrained because they are unable to forage for themselves and must rely on parental provisioning. However, due to the inconspicuous nature of many altricial birds, identifying what the nestlings are fed is often difficult (Rosenberg and Cooper 1990, Moreby and Stoa 2000, Freeman et al. 2020a).

The Canada jay *Perisoreus canadensis* is an altricial species that breeds in the late-winter when there is little to no fresh food available in the environment (Strickland and Ouellet 2020). As a result, nestling provisioning is supported, at least in part, by cached food (Derbyshire et al. 2019) stored by their parents the previous late-summer and fall (Strickland and Ouellet 2020). Canada jays cache and consume a wide variety of perishable food items including berries, mushrooms, arthropods and vertebrate flesh, the latter from carrion, other birds and the occasional capture of small mammals (Strickland and Ouellet 2020). Jays also take food from people, particularly where they are in frequent contact with humans, such as popular access points in parks. Once cached,

food items are exposed to environmental conditions that can affect their preservation (Sechley et al. 2015, Sutton et al. 2016) and spoilage of food could result in both a reduction in the quantity and quality of cached food available for reproduction and offspring provisioning. This is supported by recent evidence that warmer temperatures and more freeze-thaw events in the fall resulted in reduced reproductive performance in the subsequent breeding season (Sutton et al. 2019, Sutton et al. 2021). While the quantity of food available to the parents impacts nestling physiology, body condition, timing of fledging and survival six months after fledging (Freeman et al. 2020a), the impact of food quality remains unknown. Furthermore, aside from several opportunistic observations (Strickland and Ouellet 2020), we do not have a good understanding of what Canada jay nestlings are fed, or the relative importance of cached versus fresh food items.

Here, we hypothesized that 1) environmental conditions influence the degradation of stored food that then impacts the quality and composition of nestling diets and 2) the quality of nestling diet impacts their body condition and subsequent survival. To examine these hypotheses, we first developed an extensive isotopic map (stable-carbon, $\delta^{13}\text{C}$ and stable-nitrogen, $\delta^{15}\text{N}$, isotopes) of over 300 food items to estimate the composition of Canada jay nestling diets. We then identified drivers of variation in diet composition and the consequences of this variation on nestling body condition and survival. We predicted that warmer and more variable temperatures during the autumn and pre-breeding period would cause a reduction in cache quality and a shift in nestling diets away from highly perishable food items, such as vertebrate flesh. We further predicted that young jays fed a higher proportion foods rich in protein and fat (i.e. vertebrate flesh) would have higher body condition as nestlings and be more likely to be observed in the following fall compared to nestlings fed protein- and fat-deficient foods (i.e. plants).

Methods

Study area and species

Our study was conducted in Algonquin Provincial Park, ON, Canada (45°33'N, 78°38'W; hereafter 'Algonquin Park') where a population of Canada jays has been monitored for 53 years (1964–2018). In Algonquin Park, Canada jays maintain year-round territories in treed, lowland bogs dominated by black spruce *Picea marianana* and in drier areas dominated by mixed forests of white spruce *P. glauca*, balsam fir *Abies balsamea*, white pine *Pinus strobus*, white birch *Betula papyrifera* and aspens *Populus* spp. The Algonquin Park jays cache food in late-summer and fall which they rely on for over-winter survival (Strickland and Ouellet 2020), gaining mass in Feb and early Mar before egg-laying (Sechley et al. 2014), and, albeit to an unknown extent, to feed nestlings mainly in April (Derbyshire et al. 2019). Within the study area, breeding pairs are monitored

throughout nest construction (initiated mid-Feb–mid Mar), egg laying (one egg per day, Mar), incubation (18 d, Mar–Apr), hatching (late Mar–Apr) and the nestling period (22–24 d, Apr–May). Canada jays produce only one brood per year but breeding pairs may attempt to renest if the nest fails during laying and incubation. After leaving the nest, fledglings remain with their parents until they become nutritionally independent in June. At that point (~ 6 weeks post fledging) increasingly intense intra-brood struggles lead to the departure from the natal territory of all but the dominant juvenile (Strickland 1991).

Estimating body condition

When the nestlings were estimated to be ~ 11–14 d, they were removed briefly from their nests and individually marked with a unique combination of one standard US Fish & Wildlife Service or Canadian Wildlife Service band and three coloured leg bands. At that time, we also collected morphological measurements including the length of the bill, tarsus and 7th primary, in addition to mass. To estimate body size, we conducted a principal component analysis (PCA) from a correlational matrix of bill, tarsus and 7th primary and extracted the principal component scores from the first axis (PC1) which explained 91% of the variation in morphometric dataset. We then used a model generated by Derbyshire et al. (2015) that described the relationship between mass and PC1 scores of known-age nestlings to predict mass given body size. Body condition was estimated as the difference between the observed mass and the predicted mass given body size (Derbyshire et al. 2015, Freeman et al. 2020a).

Food sampling for stable isotope analysis

In order to estimate the diet composition of nestlings using stable isotopes, we first collected food samples from Canada jay territories in Algonquin Park and from along the Park's Highway 60 corridor during the 2016–2017 breeding seasons (Feb–May) and in the fall (Oct), when the jays were caching food. Canada jays are generalists that feed on fungi, berries, an array of invertebrates, small mammals and birds, including nestlings (Strickland and Ouellet 2020). They also scavenge from vertebrate carcasses from road kill or wolf kills and consume human food such as raisins, bread and hot dogs, provided primarily by Algonquin Park visitors. Mushrooms were not available during the winter–spring and fall sampling periods so they were collected in August 2017. Plants and invertebrates were collected opportunistically across the jay territories while vertebrate tissue was sampled opportunistically from roadkill, where a portion of abdominal (snake), hind leg (mammals) or pectoral muscle (birds) was excised and collected. Human food was selected based on observations of what the general public offered the jays and was purchased from a local grocery store. All food samples were frozen until preparation for isotopic analysis.

Stable isotope analysis

At the time of handling, 3–5 back feathers were collected from each nestling and stored in paper envelopes (collected in 2011, 2012, 2015–2018; $n = 196$). Prior to isotopic analysis, lipids and surface contaminants were removed from the feathers. Whole feathers were placed in scintillation vials and soaked in a 2:1 chloroform:methanol solution for 24 h, rinsed with fresh solution and then air dried for 72 h (Norris et al. 2006, Sørdeide et al. 2006). The emerged portion of the feathers from the feather sheath were then minced with scissors.

Food samples were prepared in a drying oven at 70°C for 24 h before being powderized with a mortar and pestle. Between 0.30 and 0.50 mg of each feather and food sample was weighed into tin capsules (Elemental Microanalysis, Okehampton, UK). The encapsulated samples were combusted and oxidized in an elemental analyzer (elemental combustion system: Costech Analytical Technologies, Valencia, CA, USA) and run through a mass spectrometer (Thermo Finnigan Delta^{plus}XP Isotope Ratio Mass Spectrometer: Thermo Fisher Scientific, Waltham, MA, USA) at the Queen's Facility for Isotope Research, Queen's Univ. (Kingston, ON, Canada).

Results of the stable isotope analyses are reported in δ ($\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$) where R is the isotopic ratios (C^{13}/C^{12} or N^{15}/N^{14}) in the samples (R_{sample}) and international standards (R_{standard} , carbon: Vienna Pee Dee Belemnite, nitrogen: air). Additional in-house standards were also included every 10 samples: UC-1 Graphite for carbon ($-25.7 \pm 0.3\%$, $N = 19$), EIL-61 KNO_3 for nitrogen ($0.8 \pm 0.2\%$, $N = 16$) and cormorant feather for both elements ($\delta^{13}C: -17.1 \pm 0.2\%$ and $\delta^{15}N: 14.1 \pm 0.2\%$, $N = 21$). Duplicates were included every 10 samples and were replicable to within 0.1‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{15}N$.

Following isotopic analysis, the individual food items were grouped into five categories: mushrooms ($n = 29$), plants ($n = 19$), invertebrates ($n = 231$), vertebrates ($n = 37$) and human food ($n = 17$) for subsequent statistical analyses. However, mushrooms were removed as a group because the fruiting bodies were not available during the sampling period (collected in Aug, sampling period = Feb–May and Oct) and had highly variable isotopic signatures ($\delta^{15}N$ range = -0.1 to 18.1%) and, thus, prevented us from distinguishing it from the other food groups. Vertebrates and human food were combined because of the similarity in their isotopic composition (linear model for $\delta^{13}C: 0.23 \pm 0.53$, $t = 0.43$, $p = 0.67$ and $\delta^{15}N: -0.83 \pm 0.68$, $t = -1.23$, $p = 0.23$; Phillips et al. 2014 for a priori grouping of sources). Similar to other studies on the anthropogenic diets of animals (Newsome et al. 2010, Hopkins and Ferguson 2012), the human food we sampled (e.g. raisins, cheese, peanuts, bread, hot dogs) had heavy nitrogen and carbon isotopic compositions. For nitrogen, this was likely due to the use of fertilizers (Trandel et al. 2018) and, for carbon, because of the prevalence of C_4 plants (e.g. corn and wheat grain; Rangan et al. 2016) in the production of processed foods. The final groups of food items ('plants', 'invertebrates' and 'vertebrates + human food') and

the individual samples within each group that were used in statistical analyses are summarized in Supporting information.

Weather variable extraction

Weather conditions from Oct to Feb were quantified using 40 years of data extracted from the Dwight weather station (45°23'N, 78°54'W, 1977–2005) and Algonquin Park East Gate weather station (45°32'N, 78°16'W, 2004–2018). Data from the Dwight station were transformed following methods outlined by Sutton et al. (2019) because it is located outside of the study area. Daily mean temperature, cumulative precipitation and the number of freeze-thaw events were extracted from the long-term weather data and separated into fall (Oct–Dec) and winter (Jan–Feb) to reflect caching and pre-breeding seasons, respectively (Sutton et al. 2019). We considered these three weather variables due to their role in the degradation and spoilage of cached food (Sutton et al. 2016, 2021). To reduce the number of variables considered in subsequent analyses and because each of the weather variables were highly correlated, a PCA from a correlational matrix of mean temperature, precipitation and the number of freeze-thaw events was conducted for each season (fall and winter). In both the fall and winter PCAs, all weather variables loaded positively along PC1 axis (Supporting information) meaning that a larger PC1 score represented a warmer, wetter and more variable season. PC1 explained 46.5% of the variation in fall weather variables and 43.2% of the variation in winter weather variables (loadings are summarized in Supporting information). We extracted PC1 values from the fall and winter PCAs from fall 2010 to winter 2012 and fall 2014 to winter 2018 in order investigate the effect of fall and winter weather on diet composition. Mean daily temperature during the breeding period (Mar–May) for 2011, 2012, 2015–2018 was also extracted from the 40-year weather dataset due to the potential of conditions during these periods to influence fresh food availability. In an effort to keep the total number of variables used in the analysis to a manageable number, we chose to not include precipitation or number of freeze-thaw events during the breeding season in the statistical model. In a previous analysis, there was no evidence that breeding season precipitation influenced fecundity (Sutton et al. 2021). Freeze-thaw events during the breeding season were not included because thawing is the dominant state as temperatures get warmer and, following sustained thaw, freezing events are likely to have little effect on the preservation of cached food.

Estimation of diet composition

Diet composition of a Canada jay nestling was based on the proportions of plants, invertebrates and vertebrates and human food found in an individual's diet (Fig. 1). Proportions were estimated using MixSIAR, an isotopic mixing model that allows for the inclusion of fixed and random effects (Stock et al. 2018). We included individual ID in the mixing model as a fixed effect and input the raw (rather than mean) source data (isotopic signatures of the food items;

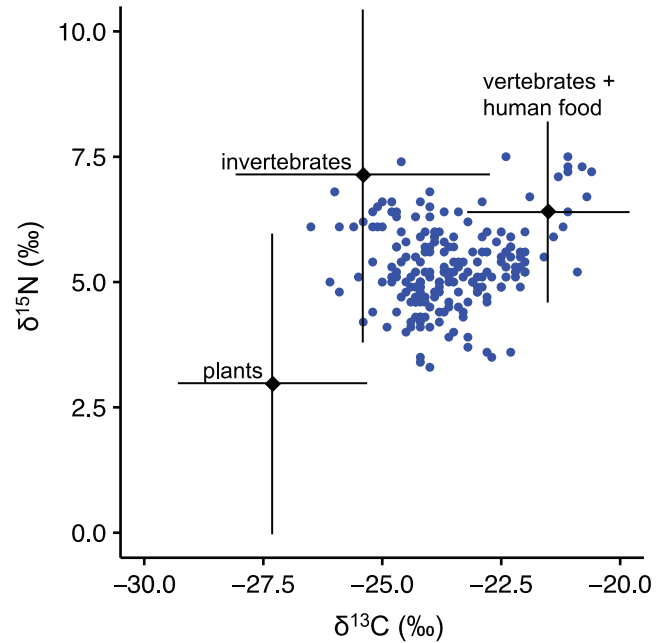


Figure 1. Isotopic ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of nestling Canada jay *Perisoreus canadensis* back feathers (blue circles, $n=196$) and dietary sources (plants, invertebrates and vertebrates) in Algonquin Provincial Park, ON, Canada. Each dietary source is labelled and indicated by the mean (black diamonds) and the standard deviation (black lines).

Stock and Semmens 2016). The raw source data was included because it allows covariance between isotopes to be included in the model. The trophic enrichment factors included in the model were from the omnivorous yellow-rumped warbler (*Setophaga coronata*, 1.9 ± 0.1 for $\delta^{13}\text{C}$ and 3.2 ± 0.1 for $\delta^{15}\text{N}$; Pearson et al. 2003), which were similar to those generated using SIDER (1.8 ± 1.4 for $\delta^{13}\text{C}$ and 3.3 ± 1.3 for $\delta^{15}\text{N}$), a statistical package used to predict trophic enrichment factors in the absence of any field or lab estimates (Healy et al. 2018). Trophic enrichment factors are included in isotope mixing models to correct for the differences in isotopic composition between consumer and prey tissue (Phillips et al. 2014). The majority of the diet of Canada jay nestlings consisted of vertebrate flesh and human food (mean = $50.5 \pm 0.1\%$, range = 34.9–72.3%). The remainder of the diet consisted of plants (mean = $35.3 \pm 0.1\%$, range = 17.4–47.9%) and invertebrates (mean = $14.2 \pm 0.02\%$, range = 10.2–19.9%). We used only the proportion of vertebrates and human food for subsequent analyses because each of the food group proportions were highly correlated (Pearson's correlations: vertebrates and invertebrates, $r = -0.75$; vertebrates and plants, $r = -0.98$; invertebrates and plants, $r = 0.62$), it constituted the majority of the nestling diet, and we predicted flesh to be rich in fat and protein.

Statistical analysis

We evaluated the causes and consequences of the nestling diet using a Bayesian structural equation model that consisted of five sub-models (Fig. 2). The first sub-model related

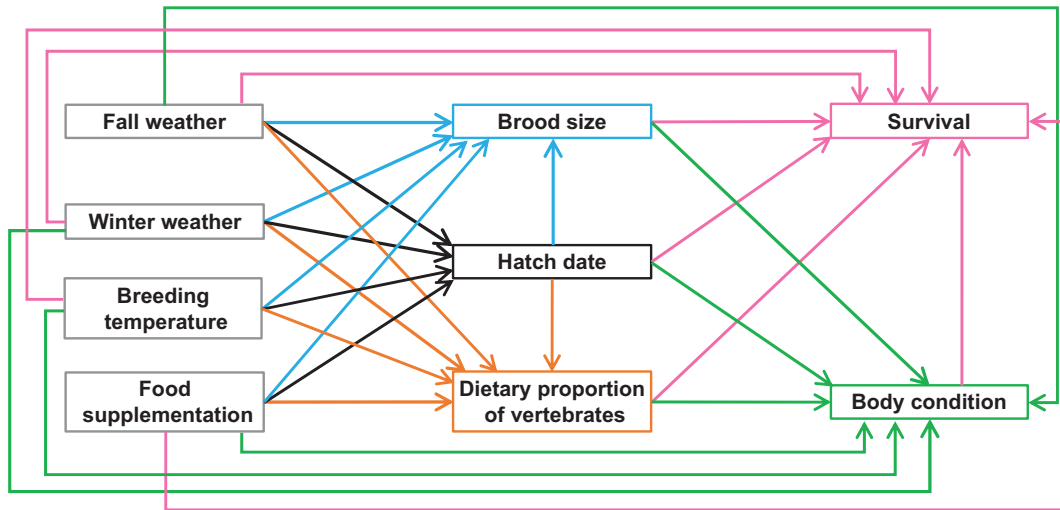


Figure 2. The complete Bayesian structural equation model showing the direct and indirect effects of environmental conditions on Canada jay *Perisoreus canadensis* nestling diet, body condition and survival in Algonquin Provincial Park, ON, Canada (n = 196 nestlings). Each arrow represents a direct effect and each sub-model is denoted by the arrow color.

the estimated hatch date of the nestlings within a nest (20 d following the first day (day 0) the female was observed on the nest; Strickland and Ouellet 2020; Gaussian distribution with an identity link function, n = 114 nests) to weather in the months leading up to and including the breeding season of hatch (fall PC1, winter PC1 and breeding season temperature, n = 6 years) and the level of food supplementation on the territory. A level of food supplementation was assigned to each territory based on its degree of accessibility to the public and the location of permanent feeders: none (> 200 m from roads and trails with no access to park visitors, n = 11 territories), fall (moderate public visitation but closed off from the public in the winter, n = 11 territories), fall + winter (moderate public visitation throughout the year, n = 3 territories), year-round (very high rates of public visitation throughout the year or access to permanent feeders, n = 4 territories; Freeman et al. 2020a). The second and third sub-models related brood size (Gaussian distribution with an identity link function, n = 114 nests) and the proportion of vertebrate flesh in the diet of each nestling (beta distribution with a logit link function, n = 196 nestlings) to the estimated hatch date, weather and level of food supplementation. The fourth sub-model related nestling body condition (Gaussian distribution with an identity link function, n = 196 nestlings) to brood size, the proportion of vertebrate flesh in the diet, estimated hatch date, weather and level of food supplementation. Finally, the fifth sub-model related whether an individual was observed in the fall following hatch (an estimate of post-fledging local survival, Bernoulli distribution with a logit link function, n = 196 nestlings) to its body condition as a nestling, its natal brood size, its estimated hatch date, the weather in the months leading up to and including the breeding season, and the level of food supplementation on its natal territory. All sub-models were generalized linear mixed effects models (GLMM) and included parent IDs and nest ID as random effects, except for the brood size sub-model

which only included parent IDs. The IDs of each parent and the nest were included as random effects because individuals bred in multiple years and multiple individuals were sampled from each nest, respectively. The Bayesian structural equation model was run using the *brms* package (Bürkner 2017, 2018), which uses the probabilistic coding language Stan (Carpenter et al. 2017). The model was run with four chains each run with 200 000 iterations (warmup = 150 000) and a default prior. All analyses were conducted in the R statistical environment (v. 3.6.0; <www.r-project.org>).

Results

Across 6 years, we monitored 196 nestlings from 114 nests. The estimated hatch date of nests ranged from 29 March to 14 May (mean = 11 April) and advanced by an average of over a day per year (linear model: -1.11 ± 0.40 , $t = -2.75$, $p < 0.01$). Average nestling body condition was 2.17 ± 4.09 (range = -12.80 to 13.51) and decreased over the course of the study (linear model: -0.12 ± 0.05 , $t = -2.72$, $p = 0.007$). Of the 196 nestlings, only 36 (18%) were observed again the following fall. Fall weather (fall PC1) remained relatively constant across the six years of the study (mean = -0.64 ± 0.91 , range = -1.70 to 0.75 ; linear model: -0.05 ± 0.04 , $t = -1.28$, $p = 0.20$) while winter weather (winter PC1) became warmer, wetter and more variable (mean = -0.86 ± 1.34 , range = -2.79 to 0.78 ; linear model: 0.40 ± 0.06 , $t = 7.16$, $p < 0.001$) and mean daily temperatures in the breeding season declined by an average of a third of a degree per year (mean = $3.09 \pm 1.87^\circ\text{C}$, range = 1.29 – 6.63°C ; linear model: -0.32 ± 0.04 , $t = -8.10$, $p < 0.001$).

Based on the results of the Bayesian structural equation model, nestling diet was influenced by winter weather and level of food supplementation (Fig. 3, Supporting information). Nestlings consumed more vertebrate flesh and human

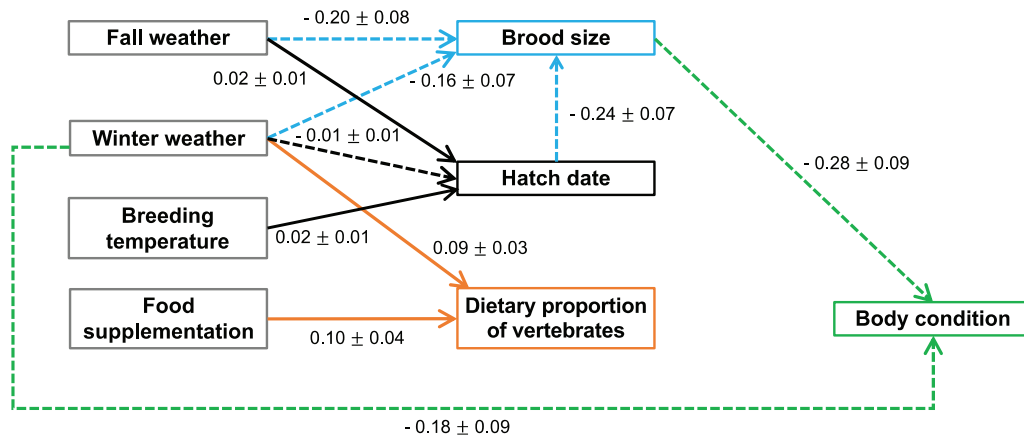


Figure 3. Results from the Bayesian structural equation model showing only the direct and indirect effects of environmental conditions on Canada jay *Perisoreus canadensis* nestling diet, body condition and survival in Algonquin Provincial Park, ON, Canada (n = 196 nestlings) where the credible interval did not overlap zero. Each arrow represents a direct effect (solid = positive, dashed = negative) and each sub-model is denoted by the arrow color.

food following warmer, wetter and more variable winters (0.09 ± 0.03 , 95% credible interval (CI): 0.03–0.15) and when they were raised on territories receiving high levels of supplementation from the public (0.10 ± 0.04 , CI: 0.03–0.18, Fig. 4). Nestlings on territories receiving no supplementation had lower proportions of vertebrate flesh and human food in the diet (mean = $47.8 \pm 0.1\%$) compared to nestlings on territories that were accessible to the public

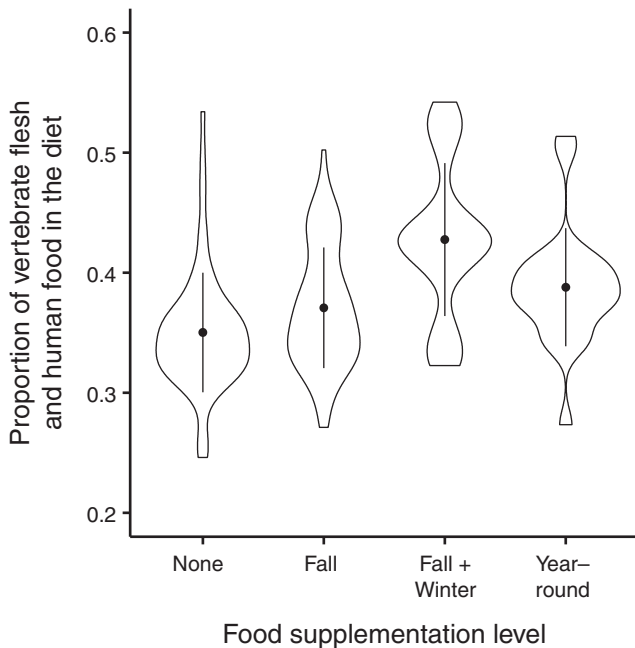


Figure 4. The impact of food supplementation by the public on the proportion of vertebrates and human food in the diet of Canada jay *Perisoreus canadensis* nestlings in Algonquin Provincial Park, ON, Canada (n = 196 nestlings). The level of food supplementation by the public was assigned based on accessibility of the territory to the public (none, fall, fall + winter and year-round; Freeman et al. 2020).

(mean = $52.2 \pm 0.1\%$, t-test: 0.04 ± 0.01 , $t = 4.34$, $p < 0.001$). There was no evidence that the proportion of vertebrate flesh and human food in the diet influenced nestling body condition or survival (Fig. 3). However, environmental conditions and phenological variables did impact nestling body condition. Nestlings had higher body condition in breeding seasons following cooler, drier and less variable winters (-0.18 ± 0.09 , CI: -0.36 to -0.01) and when they had fewer siblings (-0.28 ± 0.09 , CI: -0.45 to -0.11). Smaller broods were associated with later hatch dates (-0.24 ± 0.07 , CI: -0.38 to -0.11) and warmer, wetter and more variable falls (-0.20 ± 0.08 , CI: -0.35 to -0.05) and winters (-0.16 ± 0.07 , CI: -0.31 to -0.02). Fall and winter weather had opposing effects on the timing of hatch day, where warmer, wetter and more variable falls (0.02 ± 0.01 , CI: 0.00–0.04) and colder, drier and less variable winters were associated with earlier hatch dates (-0.01 ± 0.01 , CI: -0.03 to 0.00). Overall, the cumulative effects (sum of the direct and indirect effect estimates) of fall and winter weather on nestling body condition were positive (0.06) and negative (-0.14), respectively (Supporting information).

Discussion

Using stable carbon and nitrogen isotope values from food items and nestling feathers, we show that the majority of the diet of Canada jay nestlings is composed of vertebrate flesh and human food. Our previous understanding of the diet of nestling Canada jays was based on stomach content analysis of 10 nestlings which identified the remains of 75 insects and spiders (Strickland and Ouellet 2020). However, our results suggest that invertebrates constitute a smaller proportion of the nestling diet than expected. Importantly, stomach content analysis directly reflects what nestlings were fed in the hours prior to stomach removal and is biased towards arthropods because of the presence of hard exterior shells (Pierce and Boyle 1991). On the other hand, isotopic analysis of nestling

feathers represent the nestling diet throughout the period of feather growth. The discrepancy between the two methods highlights that using a singular method to determine diet composition may not reveal the entire picture (Horswill et al. 2017).

By incorporating isotopic data with information about environmental conditions, we also demonstrate that weather conditions were a major driver shaping the diet of Canada jay nestlings. Weather conditions two months prior to the breeding season affected the composition of nestling diets but, contrary to our predictions, warmer, wetter and more variable weather in the winter led to a higher proportion of vertebrate flesh and human food in the diet. One possible explanation for this unexpected relationship is that due to the overlapping isotopic signatures of vertebrate flesh and human food, it was impossible to disentangle whether nestlings were fed from natural or artificial sources. Human food may degrade at a slower rate than natural food items if preservatives buffer processed foods from warmer, more variable conditions (Hayman et al. 2004, Alahakoon et al. 2015). Thus, on some territories, it is possible that human food may make up the majority of unspoiled cached food items available in the late-winter. Furthermore, on some of these territories, supplementation by the public persists past the fall caching period, allowing for replenishment of cached food stores and thus, may represent a significant portion of the food provided by parents to their young. It is also possible that warmer temperatures in January and February lead to more visitors to Algonquin Park (Hewer et al. 2016) and increase the chances of human food (and potentially more road kill) being incorporated into the diet of nestlings. This is consistent with our result that public supplementation was linked with higher proportions of vertebrate flesh and human food in the diet. That said, territories with no public access and thus, no access to human food, still had similar proportions of vertebrate flesh (mean=48%) compared to supplemented territories (mean=52%), suggesting that most of the nestling diet is composed of naturally-occurring vertebrate flesh. Discerning how much of the diet is natural versus human food by quantifying additional isotopes (e.g. $\delta^2\text{H}$ or $\delta^{18}\text{O}$) to differentiate food sources (Vander Zanden et al. 2016) or by barcoding fecal sacs (McClenaghan et al. 2019) will be important to better predict the effect of environmental conditions on nestling diet composition.

Despite vertebrate flesh and human food being rich sources of essential amino and fatty acids, variation in the combined amount of these food items in the diet had no effect on nestling body condition or whether an individual was observed in the fall. This could suggest that a threshold exists, where a minimum amount of essential amino and fatty acids are required for development, but a surplus does not increase body condition. Minimum thresholds for dietary protein have been found in broiler chickens (Fanher and Jensen 1989) where low levels of protein in the diet led to depressed weight gain, increased abdominal fat and impaired food conversion efficiency (how well ingested food is converted to body mass, Buysse et al. 1992). An upper threshold

of macronutrients also exists, above which excessive intake may increase mortality (e.g. *Spodoptera littoralis* caterpillars, Raubenheimer et al. 2005; black garden ants *Lasius niger*, Dussutour and Simpson 2012; and see review of several taxa by Simpson and Raubenheimer 2009). However, it is unknown what effect a surplus of macronutrients has on body condition and whether the upper thresholds observed in laboratory settings can also be reached in the wild. In our study population, nestlings may be receiving enough macronutrients, such as essential amino and fatty acids, from either vertebrate flesh and human food or invertebrates (Rumpold and Schlüter 2013, Twining et al. 2016) to meet the minimum requirements for proper growth. As a result, variation in body condition may be driven, not by the amount of protein and fat available in food fed to nestlings, but by other factors such as micronutrients (e.g. vitamins) or the digestibility of food items.

Alternatively, the vertebrate flesh and human food that nestlings consumed may not have impacted body condition or survival because it may be more degraded relative to arthropods and fruit. Vertebrate flesh is more susceptible to warming and variable weather than berries (NEF, AOS, DRN, DS, unpubl.) and may result in the breakdown of macronutrients due to spoilage (Singh and Anderson 2004). If protein has been degraded, it is possible that its reduced value would result in lower growth rates and survival. For example, young Japanese quail *Coturnix japonica* fed 60% freeze-dried spoiled tuna had depressed weight gain when compared to young fed unspoiled tuna (Blonz and Olcott 1978). Similarly, in juvenile blue shrimp *Litopenaeus stylirostris*, a diet of stale fishmeal led to lower final biomass and survival compared to a diet of fresh fishmeal (Tapia-Salazar et al. 2004). Unfortunately, the potential decline in food quality due to environmental conditions cannot be detected by stable isotopes. Thus, a method of estimating nutritional quality and degradation of a food item (e.g. isothermal calorimetry (Wadsö and Galindo 2009) or hyperspectral imaging (Gowen et al. 2007)) would be necessary to identify potential linkages between diet quality, body condition and survival.

Although we did not observe an effect of diet composition on body condition or survival there could be sex-specific differences in response to varying levels of macronutrients in the diet (Maklakov et al. 2008, Lee 2010). For example, female nestling hihi *Notiomystis cincta* supplemented with high-protein food had higher survival within the nest compared to supplemented males (Walker et al. 2013). Similarly, a high-carbohydrate diet decreased the lifespan of males but not female field crickets (*Teleogryllus commodus*, Maklakov et al. 2008). When species are sexually dimorphic, the sex with the larger body mass typically has higher dietary requirements and requires more food (i.e. calories, macro- and micronutrients) to grow and maintain tissues (Anderson et al. 1993) due to their longer digestive tracts and slower digestion (Markman et al. 2006). Because Canada jay females are smaller, they may require lower amounts of protein and other macronutrients to be in high body condition. Thus, if females are responding positively to a given diet while the males show

a negative or lack of response, it could mask the overall effect of diet composition on body condition. Unfortunately, the sex of the nestlings in this study was not known and we were, therefore, unable to investigate an interaction between sex and diet quality on nestling development and survival. Explicitly measuring sex-specific responses to variation in diet composition could help identify potential relationships between diet quality, body condition and survival that are otherwise not apparent in our current analysis.

Based on the lack of support for the effect of diet composition on nestling body condition and survival, it is possible that quantity of food provided by the breeding pair, rather than quality, may be the underlying driver linking fall weather with nestling condition and survival. By coupling a 2-year experiment with 40 years of observational data, Freeman et al. (2020a) showed that the amount of food available to breeding Canada jays plays a role in nestling body condition, timing of fledging and survival. Nestlings from territories with more food had higher body condition, fledged the nest earlier, and were more likely to be observed in the following fall population count (Freeman et al. 2020a). Therefore, it may not be what the nestlings are eating but how much they eat that has lasting impacts on nestling physiology and survival.

Our results also demonstrate how weather can affect different stages of reproduction, sometimes in opposing ways. For Canada jays in Algonquin Park, it appears that warmer, wetter and more variable winters had a negative effect on nestling body condition, possibly by influencing parental condition or the quantity of food fed to young. These types of winters also led to earlier hatch dates (Whelan et al. 2016), likely because warmer periods cued females to begin nesting early (Crick and Sparks 1999, Dunn and Winkler 2010, Townsend et al. 2013). Early hatch dates led to larger broods, which, in turn, resulted in lower nestling body condition likely because of elevated sibling competition (Dijkstra et al. 1990) and more mouths to feed for already food limited parents (Derbyshire et al. 2015, Freeman et al. 2020a). In contrast, warmer, wetter and more variable winter weather had a direct negative effect on brood size that then resulted in improved nestling condition because of lower competition in the nest. This positive indirect effect of winter weather on body condition can, therefore, act to compensate for the negative effect that those same winter weather conditions had via other pathways in the reproductive cycle.

We also saw opposing weather effects between seasons: warmer, wetter and more variable winters had an overall negative effect on nestling condition, whereas similar weather during the fall had an overall positive effect. The later result contrasts with previous analyses on this same population showing how a higher number of freeze-thaw events in the fall (generally warmer and more variable temperatures) tended to result in lower nestling body condition (Sutton et al. 2019). The lack of agreement between these studies could be because our 6-yr time series did not sufficiently capture the full range of inter-annual variation in weather compared to the 40-yr time series used by Sutton et al. (2019). For

example, Sutton et al. (2019) reported a range of 20–57 fall freeze-thaw events within a given year (mean = 40 ± 11), whereas the range of freeze-thaw events from our time series was 23–40 (mean = 31 ± 7), suggesting that the effect of higher than average freeze thaw events was underrepresented in our dataset.

Despite the fact that we found a number of factors influenced nestling body condition, we were unable to explain any variation in first year survival. Our power to detect potential effects was quite low because of the limited number of surviving individuals. However, because our measure of survival was based on presence or absence of individuals within the study site in the fall following hatch (i.e. local survival), we were likely underestimating true survival. Six weeks after the young fledge, increasingly intense intra-brood dominance struggles lead to the departure of all but the dominant juvenile from the natal territory. Departing individuals settle with unrelated, usually failed, breeders elsewhere (Strickland 1991) but marked dispersers rarely do this within our study area (Strickland unpubl.). As a result, our estimates of survival are conservative because any young jays that dispersed outside of the study area were considered to have not survived. Directly tracking young Canada jays from the time of their dispersal using radio transmitters or another remote tracking method, such as satellite tags, will be required to acquire more robust estimates of juvenile survival.

Taken together, despite diet being shaped by a number of environmental factors, variation in diet had no effect on nestling body condition or survival. Canada jays may be buffered from variation in diet because they can obtain essential macronutrients from many of the different perishable food items they consume. However, due to their reliance on cached food, they may be susceptible to long-term changes in environmental conditions (Sutton et al. 2016) and, therefore, investigating inter-annual variation in diet composition and its potential impact on offspring condition could be particularly insightful. Finally, because the amount of food available appears to influence young Canada jays more than the quality of their diet, future studies investigating the role of diet composition during early life should also consider the potential role of food quantity in offspring growth and development.

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Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.xgxd254fb>> (Freeman et al. 2020b).

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