Raising young with limited resources: supplementation improves body condition and advances fledging of Canada Jays

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Abstract. Food availability early in life can play a vital role in an individual's development and success, but experimental evidence for the direct effects of food on body condition, physiology, and survival of young animals in the wild is still relatively scarce. Food-caching Canada Jays (*Perisoreus canadensis*) begin breeding in the late winter and, therefore, rely on either cached food or seemingly limited quantities of fresh food to feed nestlings in the early spring. Using a 2-yr food supplementation experiment conducted during the nestling period and 40 yr of observational data on food supplemented by the public, we examined whether food quantity during early life influenced the physiology, body condition, timing of fledging, and survival of young Canada Jays in Algonquin Provincial Park, Ontario, Canada. Experimental food supplementation of breeding pairs advanced the fledging date of young by 24% (5.5 d) compared to controls. In 1 yr of the experiment, nestlings raised on experimentally supplemented territories had lower feather corticosterone concentrations and were in higher body condition than controls. Across treatment and control nests, young that successfully fledged had lower concentrations of feather corticosterone and were in higher body condition than those that did not fledge. Based on 40 yr of observational data, nestling body condition was positively related to the degree of food supplementation by park visitors and nestlings in higher body condition were more likely to be observed in the population in the following fall. Our results demonstrate how food availability early in life can have important downstream consequences on metrics related to individual fitness, including first year survival.

Key words: body condition; early life; feather corticosterone; fledgling; food quantity; nestling; Perisoreus canadensis.

Introduction

Resource availability can be a major constraint in wild animals because the amount of energy available to an individual is intimately linked with its survival and reproduction (Erikstad et al. 1998, Post and Forchhammer 2008). In particular, food quantity during reproduction plays a vital role in the growth and development of offspring. Across taxa, access to greater amounts of food influences offspring body size (Kager and Fietz 2009), growth rates (Woods and Armitage 2003, Vafidis et al. 2016), immune system development (De Neve et al. 2004), and oxidative stress response (Young et al. 2017). Typically, parents aim to maximize access to food during reproduction by timing breeding with pulses in resource availability (Lack 1954, Daan et al. 1989). However, when peak energy demands in reproduction are not matched with pulses of resources, reproductive performance may be severely food limited.

In birds, experimental increases in food during the pre-breeding or breeding periods are often associated with earlier lay dates (Reynolds et al. 2003a, Derbyshire et al. 2015), larger clutch sizes (Derbyshire et al. 2015, Roper et al. 2018), higher quality eggs (Blount et al. 2006), faster nestling growth rates (Vafidis et al. 2016), and increased fledging success (Reynolds et al. 2003b, see review by Robb et al. 2008a). However, because experimental increases in food abundance often influence multiple reproductive metrics, it can be difficult to determine whether supplementation affects all aspects of reproduction independently or if the metrics are correlated with one another (e.g., does early lay date lead to higher quality offspring?). Limiting increases in food abundance to specific periods of the breeding season can help to separate how supplementation influences various metrics of reproductive performance. For example, supplementation during the nestling period precludes any effect of supplementation on timing of breeding and the number of offspring produced and, therefore, the potential effects of food availability on nestling body condition

and timing of fledging can be isolated. However, because artificial spikes in food abundance, such as those administered by experimental protocols, may not reflect normal levels of food acquisition in the wild, the effects of long-term food supplementation, such as feeding by the public throughout the year, may also be important to examine (Robb et al. 2008b).

A variety of physiological responses have evolved to allow young to cope with periods of food limitation (Harding et al. 2009, Fairhurst et al. 2012). In birds, nestlings may respond to low food availability by increasing the secretion of corticosterone to minimize the effects of undernourishment (Kitaysky et al. 2001a, Pravosudov and Kitaysky 2006, Herring et al. 2011). During periods of low food intake, corticosterone maintains blood glucose levels by increasing the breakdown of proteins, glycogen (stored glucose), and fats (reviewed by Sapolsky et al. 2000). In addition, elevated corticosterone can lead to changes in behavior such as increased begging and aggression toward siblings in an effort to outcompete them for food (Ramos-Fernández et al. 2000, Kitaysky et al. 2001b, 2003). Measuring corticosterone in nestlings may therefore provide an indicator of the early-life nutritional environment, especially in species that are food limited.

Canada Jays (*Perisoreus canadensis*) are year-round residents of the subalpine and boreal forests of North America. Before winter, Canada Jays store perishable food items, such as fungi, berries, arthropods, and flesh from small prey and carrion (Strickland and Ouellet 2018). The cached food is used not only for over-winter survival but also to fuel late-winter reproduction (Sechley et al. 2014) including, in some cases, being used to feed their nestlings before fresh food, such as moths and dipteran larva, become widely available as the snow melts (Derbyshire et al. 2019). Previous research conducted in Algonquin Provincial Park, Ontario, Canada (hereafter "Algonquin Park") has shown that Canada Jay pairs supplemented with food during the pre-breeding period began breeding earlier and laid larger clutches (Derbyshire et al. 2015). Furthermore, an analysis of 35 yr of data demonstrated that jays on territories recreationally supplemented by park visitors had earlier lay dates and larger brood sizes compared to those that were not supplemented by visitors (Derbyshire et al. 2015). However, neither form of supplementation had an effect on nestling body condition, suggesting that adults may preferentially use the supplemental food during the pre-breeding period to enhance their own breeding body condition rather than to feed nestlings. In Algonquin Park, Canada Jays feed nestlings as early as March, well before the completion of spring thaw and emergence of many potential food items, implying that parents rely on a limited amount of fresh food or use cached food to feed their young (Derbyshire et al. 2019). Thus, we hypothesized that the amount of food available to a breeding pair during the nestling period could have a strong influence on nestling physiology and development (the "food limitation hypothesis").

To examine this hypothesis, we conducted a food supplementation experiment during the nestling period to assess whether food availability influenced nestling corticosterone, body condition and the timing of fledging. Following the food limitation hypothesis, we predicted that experimentally supplemented nestlings would have lower feather corticosterone levels, be in higher body condition, and fledge earlier compared to controls that were not supplemented with food. In addition, using four decades of reproductive data from the same marked population, we investigated the effect of food subsidies given to breeding pairs by park visitors on nestling body condition. We predicted that, compared to the nestlings of unsupplemented pairs, those of supplemented pairs would be in higher body condition and be more likely to be observed in the autumn.

METHODS

Study area and species

Our study was conducted in Algonquin Park (45°33′ N, 78°38′ W), where a population of Canada Jays (*Perisoreus canadensis*) has been monitored since the mid-1960s (Strickland and Ouellet 2018, Sutton et al. 2019). Within the population, each individual was marked with a unique combination of three color leg bands and a United States Fish and Wildlife Service (USFWS) aluminum band. Canada Jays are an altricial species that produce a single brood per season, but they may undertake a second breeding attempt if the first fails during laying or incubation due to predation (Strickland and Ouellet 2018). In our study area, breeding pairs begin nest construction between mid-February and early March with the first egg laid, on average, on 23 March (modal clutch size = 3; Strickland and Ouellet 2018). Females lay one egg per day and, following clutch completion, incubate for 18 d (Strickland and Ouellet 2018). Following a nestling period that normally lasts 22–24 d ($n = 13$ nests; Strickland and Ouellet 2018), young fledge from their nest and remain with their parents for approximately 6 weeks until they reach nutritional independence in June. Shortly afterward, all juveniles but one leave the natal territory, a reduction consistent with the limited observations of dominance struggles in which the winner stays with the parents and the losers depart and sometimes survive by joining unrelated pairs elsewhere as "immigrants" (Strickland 1991, Strickland and Ouellet 2018). Non-breeders of both classes may remain on their natal or "adopted" territories with the older adults for 1–2 yr during which time they attempt to become breeders elsewhere in the surrounding territorial mosaic (Strickland and Ouellet 2018). The non-breeders are actively chased away from the nest and are not involved in raising the nestlings but may feed

young after they fledged from the nest (Strickland and Ouellet 2018).

Experimental food supplementation

In 2017 and 2018, we conducted a food supplementation experiment during the nestling period from late-March through late-May. We supplemented 18 territories (n = 10 in 2017 and n = 8 in 2018) and compared these to 17 territories that were unsupplemented controls (n = 9 in 2017 and n = 8 in 2018, Appendix S1: Table S1). In 2017, selection for treatment was based chronologically by lay date, where for every two females that began laying, one was randomly selected for supplementation. In 2018, nests were coupled based on lay date and one of each nest pair was selected for treatment with priority given to territories that had not been supplemented in 2017. However, if both pairs had previously been supplemented, supplementation was provided on the territory where one, or both, of the breeders had changed since 2017.

Food supplementation began the day before estimated hatch day and continued throughout the ~23-d nestling period. Canada Jay females begin sitting on their nest with the laying of their first egg but start incubation only when the clutch is complete 2 d later (based on the modal clutch size of 3 and one egg laid per day). Hatch day was estimated as 20 d following the start of sitting to account for 2 d from clutch initiation to completion and 18 d of incubation. Food was supplied to the breeding pair in feeders (Fig. 1), which were refilled every 2 d with 800 g of a blend of wet cat food comprised of a 1:1 mixture of PC Extra Meaty Turkey and Giblets (minimum 11% protein, 5% fat) and Extra Meaty Beef and Salmon (minimum 10% protein, 6% fat; Loblaws, Brampton, Ontario, Canada). Cat food was selected because of its high levels of protein and essential fatty acids, both of which are positively associated with nestling body condition (Twinning et al. 2016), growth, and survival (Reynolds et al. 2003a,b). The amount of food provided every other day was calculated based on the daily expenditure of an adult jay (47 kcal/d, see Shank 1986: Table 1), the maximum number of adults (two breeders and one non-breeder) on a territory in our study area, and the typical number of nestlings (mode = 3) produced by a breeding pair. Feeders were placed ~150 m from the nest, which was close enough to prevent adults from adjacent territories from accessing the food but far away enough to prevent attracting potential predators such as American red squirrels (*Tamiasciurus hudsonicus*) and Merlins (*Falco columbarius*) to the nest. Feeder usage by the breeding pair was confirmed using trail cameras and, of the 18 supplemented territories, 17 had regular visits of the breeding pair to the feeder. The one supplemented territory that had zero visitations to the feeder was removed from the treatment group and was considered a control (now n = 17 supplemented, n = 18 control territories,

Appendix S1: Table S1). During the nestling period, there were no alternative food sources, such as bird feeders, on any of the territories (note: two territories, Boardwalk and Sunday Creek, had access to a feeder in the winter but the feeders were removed in early spring).

Across the 2 yr of supplementation, 23 of the 35 nests contained young that survived to ~14 d post-hatch (supplemented, 25 nestlings from 12 nests; control, 35 nestlings from 11 nests). At day 14, all nestlings were individually marked with a unique combination of four leg bands (three color bands, one USFWS aluminum band). We also took morphological measurements (bill, tarsus, wing chord, seventh primary, tail, body mass). Following Derbyshire et al. (2015), nestling body condition was estimated as the difference between the observed body mass and the predicted mass given body size. Body size was calculated using a principal component analysis on a correlational matrix of bill, tarsus, and seventh primary length. We considered the first principal component (PC1) to be a good estimate of body size because it explained 91% of the variation in the morphometric data set (Appendix S1: Fig. S1). Lastly, to estimate apparent age, we compared measurements of each nestling to daily growth curves of known-age nestlings (D. Strickland and D. R. Norris, *unpublished data*). To determine the age at which nestlings fledged, nests were subsequently monitored every 1–2 d from > 20 m to minimize any disturbance at the nest. When fledglings were observed outside of the nest and capable of short bouts of flight (>5 m) between trees the nest was considered to have fledged. In order to provide a more accurate age at fledging, the estimated hatch day was adjusted to reflect the clutch size observed when the nest was accessed for the marking of nestlings (e.g., for a clutch of 4, hatch day was newly estimated as 21 d

Fig. 1. A pair of Canada Jays (*Perisoreus canadensis*) collecting food from an experimental feeder in Algonquin Provincial Park, Ontario, Canada (photo: N. E. Freeman). Throughout the 2017 and 2018 breeding seasons, breeding pairs were either supplemented during the 22–24 d nestling period every other day with a high protein/fat food or left as unsupplemented controls (see *Methods* for more details).

post-clutch initiation rather than the previously assumed 20 d). Of the 35 territories monitored, 49% had nestlings that successfully fledged (2017, $n = 8$ nests, 15 nestlings; 2018, $n = 9$ nests, 26 nestlings; Appendix S1: Table S1). All protocols complied with the Canadian Council on Animal Care and Canadian Wildlife Services guidelines and were approved by the University of Guelph.

Feather corticosterone

Corticosterone in feathers is believed to reflect circulating levels of corticosterone during the time of feather growth (reviewed by Romero and Fairhurst 2016). Thus, collecting nestling feathers allows for the quantification of corticosterone secretion throughout the nestling period until the feathers are pulled. At the time nestlings were marked and measured, five to seven back contour feathers were collected from each individual and later analyzed using a hormone extraction protocol optimized for avian feathers (Freeman and Newman 2018). Emerged feather (i.e., part of the growing feather not covered by a sheath) was cut and placed in microcentrifuge tubes and pulverized into a powder using ceramic beads in a bead mill (Bead Blaster; Benchmark Scientific, Edison, New Jersey, USA). Based on a serial dilution to determine the optimal sample mass (Freeman and Newman 2018), 2.6 ± 0.1 mg of powdered feather was transferred into a glass test tube and suspended in 5 mL of methanol (HPLC grade; Thermo Fisher Scientific, Waltham, Massachusetts, USA). Samples were placed in a sonicating water bath for 30 min and incubated for 12 h in a shaking 50°C water bath. Feathers were separated from the methanol using vacuum filtration with #4 Whatman filter paper. The empty sample test tube was then rinsed with 1 mL of additional methanol twice. The 7 mL of methanol was dried using a 40°C evaporation plate under nitrogen gas for 50 min. The extract residues were reconstituted with 1:19 absolute ethanol (absolute ethanol; Thermo Fisher Scientific, Waltham, Massachusetts, USA) and phosphate-buffered saline (PBS; 0.05 mol l–1, pH 7.6), vortexed for 30 s, and analyzed using a double-antibody I^{125} radioimmunoassay (RIA; ImmuChem 07-120103: MP Biomedicals, Orangeburg, New York, USA). This assay is highly specific and precise for a range of tissue and sample types and due to limited feather mass, samples were analyzed in a single assay as singletons and concentrations were calculated from a standard curve analyzed in duplicate with an intra-assay coefficient of variation (CV) of 0.3% for the high control and 0.7% for the low control.

Long-term data

For each accessible nest between 1979 and 2018 (excluding experimentally supplemented nests), morphological measurements of each nestling, the age of each parent, and the quality of the natal territory were collected ($n = 1,293$ nestlings). Using the measurements,

body condition of each nestling was estimated with the methods outlined above. Estimates of territory quality derived by Strickland et al. (2011) were based on the proportion of conifers within a 450 m radius of the average location of nests on a given territory (high quality, $n = 20$ territories; medium, $n = 23$ territories; low, $n = 13$ territories). In Algonquin Park, Canada Jay territories are ~140 ha and are defended year-round (Strickland and Ouellet 2018). Canada Jays rely on conifers, primarily black spruce (*Picea mariana*), for nesting locations and to store their caches because conifers preserve cached food better than deciduous trees (Strickland et al. 2011).

In Algonquin Park, Canada Jays may also supplement their diets by actively seeking handouts from humans, storing food items such as nuts, raisins, and suet (Strickland and Ouellet 2018). Thus, we assigned a supplementation level to each territory based on the frequency of public access and location of bird feeders: none (>200 m from roads and walking trails with little to no access of park visitors), fall only (moderate public visitation in the fall but closed off from the public in the winter), fall-winter (moderate public visitation throughout the year), or year-round (had permanent feeders or very high rates of public visitation throughout the year).

Until 2017, nests were usually monitored only until ~11 d post-hatch when the nestlings were marked. Thus, data on the timing and success rate of fledging prior to 2017 is mostly lacking. However, a population census was conducted every October (15–31 October) since 1979, in part, to assess the over-summer survival of young jays. Unfortunately, we could not obtain a true estimate of nestling over-summer survival with this data set because the census did not account for juveniles that dispersed out of the study area.

Statistical methods

From the 2-yr supplementation experiment, we assessed the effect of supplementation on nestling feather corticosterone concentrations, body mass, body size, body condition, age at fledging, and whether a nestling fledged. To test for an effect of food supplementation on feather corticosterone concentrations, we used a generalized linear mixed effects model (GLMM, Gaussian distribution) with treatment (supplemented, control), year (2017, 2018), an interaction between treatment and year, and apparent nestling age as fixed effects. Nest identity was included as a random effect because multiple nestlings were sampled from each nest. Three separate GLMMs were also used to determine whether supplementation influenced nestling body mass, body size (as determined by the PC1 score), and body condition (all Gaussian distributions). All three models included the same fixed and random effects as the first model but also included feather corticosterone as a fixed effect. To test for an effect of food supplementation on the age at which the nestlings were fledging (d), we

constructed a GLMM (Gaussian distribution) with treatment (supplemented, control), year (2017, 2018), an interaction between treatment and year, concentration of feather corticosterone and body condition as fixed effects and nest identity as a random effect. Lastly, to test for the effect of feather corticosterone concentration and body condition on whether an individual successfully left the nest, we used a GLMM (binomial distribution) with year, concentration of feather corticosterone and body condition as fixed effects and nest identity as a random effect.

Using the long-term data, we assessed the influence of the level of food supplementation by park visitors on nestling body size, body condition, and presence during the fall census. We constructed two separate GLMMs, one to predict nestling body size (Gaussian distribution) and the second to predict nestling body condition (Gaussian distribution). In both models, we included level of food supplementation, natal territory quality, age of each parent, number of siblings in a nest, year, banding date, and apparent age of the nestling as fixed effects. Nest identity was included as a random effect in both models to account for multiple young fledging from a single nest. The identities of both parents were also included as random effects because some adults bred across multiple years. To predict whether an individual was observed the subsequent fall, we used a GLMM (binomial distribution) with the same fixed and random effects as the previous two models but also included body condition as an additional fixed effect. All statistical tests were performed using R version 3.5.1 (R Development Core Team 2018) and significance was set at $\alpha = 0.05$.

Results

Supplementation experiment

The effects of the experimental food supplementation on feather corticosterone and body condition were both dependent on year. In the feather corticosterone statistical model, there was a significant interaction between treatment and year where supplemented nestlings in 2018 tended to have lower feather corticosterone concentrations than the 2018 control nestlings and both the control and treated nestlings in 2017 (-0.40 ± 0.21, $t = -1.93$, $P = 0.06$, Fig. 2A, Appendix S1: Table S2). Corticosterone concentrations were also negatively associated with apparent age (-0.22 ± 0.09, $t = -2.51$, $P = 0.02$) but there was no effect of food supplementation on nestling body mass (2.84 ± 2.71, $t = 1.05$, $P = 0.31$) and body size at ~day 14 (0.12 ± 0.43, $t = 0.28$, $P = 0.78$, Appendix S1: Table S3). For the nestling body condition statistical model, there was also a significant interaction between treatment and year, suggesting that food supplementation did not affect nestling body condition in 2017, but led to higher body condition in treated nestlings in 2018 compared to controls (3.58 ± 1.70, $t = 2.11$,

$P = 0.05$, Fig. 2B, Appendix S1: Table S4). There was no effect of feather corticosterone concentrations (0.21 ± 1.22, $t = 0.17$, $P = 0.86$) or apparent age at banding (0.24 ± 0.78, $t = 0.31$, $P = 0.76$) on nestling body condition (Appendix S1: Table S4).

The strongest effect of food supplementation appeared to be on the timing of when birds left the nest (-1.05 ± 0.32, $t = -3.29$, $P < 0.01$, Appendix S1: Table S5). Food supplementation advanced the timing of fledging by 30% in 2017 and 17% in 2018 (7 d and 4 d, respectively; Fig. 2C). Furthermore, nestlings that successfully fledged had significantly lower corticosterone concentrations in their feathers (-28.35 ± 5.16, $z = -5.50$, $P < 0.001$, Fig. 3A) and were of higher body condition than those that did not fledge (7.47 ± 3.31, $z = 2.26$, $P = 0.02$, Fig. 3B, Appendix S1: Table S6).

Long-term data

Over four decades, nestling body size and body condition were influenced by a number of factors. Nestlings hatched earlier in the breeding season were more likely to be larger (-0.06 ± 0.02, $t = -2.97$, $P < 0.01$, Appendix S1: Table S7) and in higher body condition compared to those hatched later in the season (-0.25 ± 0.15, $t = -1.68$, $P = 0.04$, Appendix S1: Table S8). Nestlings with fewer siblings also tended to be larger (-0.07 ± 0.02, $t = -2.90$, $P < 0.01$) and in higher body condition (-0.71 ± 0.16, $t = -4.33$, $P < 0.001$) than those from larger broods. Territories that were food supplemented by park visitors were more likely to have nestlings in higher body condition (0.47 ± 0.18, $t = 2.63$, $P < 0.01$, Fig. 4) but there was no evidence that food supplementation influenced body size (-0.02 ± 0.02, $t = -1.08$, $P = 0.28$). Finally, there was no evidence for a linear change in nestling body size (0.003 ± 0.02, $t = 0.14$, $P = 0.89$) or body condition (0.33 ± 0.21, $t = 1.60$, $P = 0.11$) across years (Appendix S1: Fig. S2).

Whether a nestling was present as a juvenile during our fall census of the study area was positively associated with its body size (0.33 ± 0.17, $z = 1.93$, $P = 0.05$) and body condition (0.10 ± 0.03, $z = 3.01$, $P < 0.01$, Fig. 5) but not level of food supplementation (-0.13 ± 0.09, $z = -1.54$, $P = 0.12$, Appendix S1: Table S9). Nestlings with fewer siblings were also more likely to be observed in the fall than those from larger broods (-0.30 ± 0.13, $z = -2.25$, $P = 0.02$). There was no effect of year (-0.02 ± 0.09, $z = -0.19$, $P = 0.85$), timing of nesting (-0.12 ± 0.10, $z = -1.24$, $P = 0.21$), apparent age of the nestling (-0.43 ± 0.27, $z = -1.61$, $P = 0.11$), or the age of the father (0.02 ± 0.09, $z = 0.23$, $P = 0.82$) and mother (-0.05 ± 0.09, $z = -0.54$, $P = 0.59$) on whether a nestling was observed during the fall census as a juvenile.

Discussion

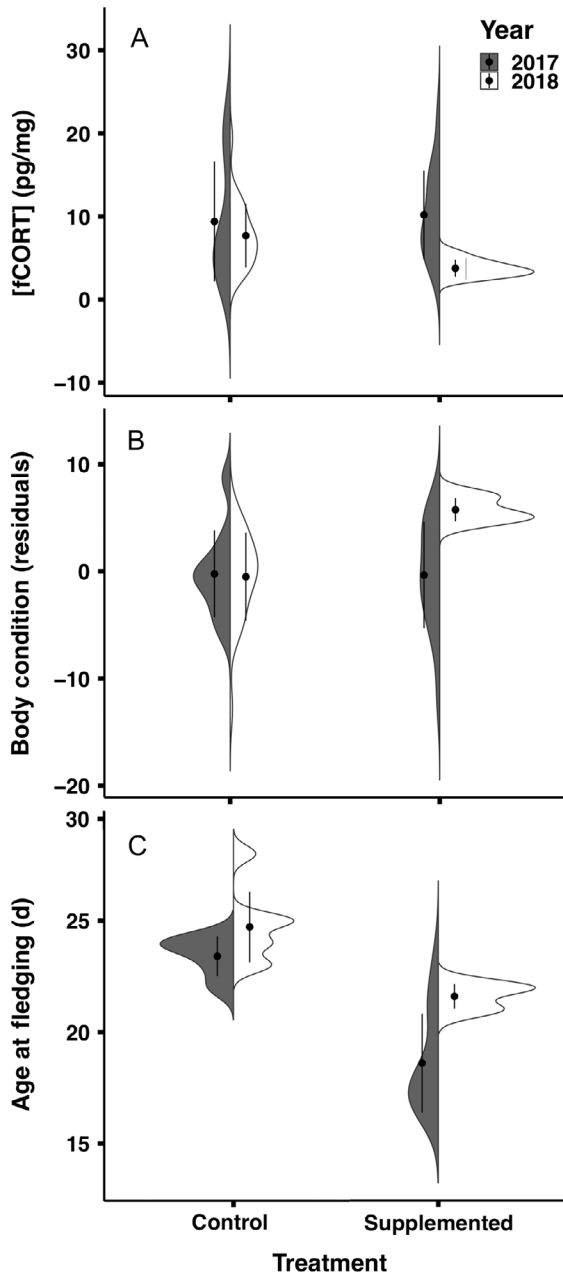Food supplementation influenced Canada Jay nestling feather corticosterone concentrations and body

Fig. 2. The effect of food supplementation on Canada Jay (*Perisoreus canadensis*) nestlings (*n* = 25 supplemented, 35 control nestlings) across 2 yr (2017, dark gray; 2018, white) in Algonquin Provincial Park, Ontario, Canada. (A) Feather corticosterone concentrations ([fCORT] (pg/mg)) of nestlings from food-supplemented territories were lower than controls in 2018 and both control and treatment groups in 2017. (B) Food supplementation had no effect on nestling body condition (residuals of observed mass compared to predicted mass given body size) in 2017 but 2018 supplemented nestlings were in higher body condition than controls. (C) Food supplementation advanced fledging by 30% (7 d) in 2017 and 17% (4 d) in 2018. The violin plot represents a smoothed probability density of the data using kernel density estimation. The black dots with the vertical lines represent the mean and standard error, respectively.
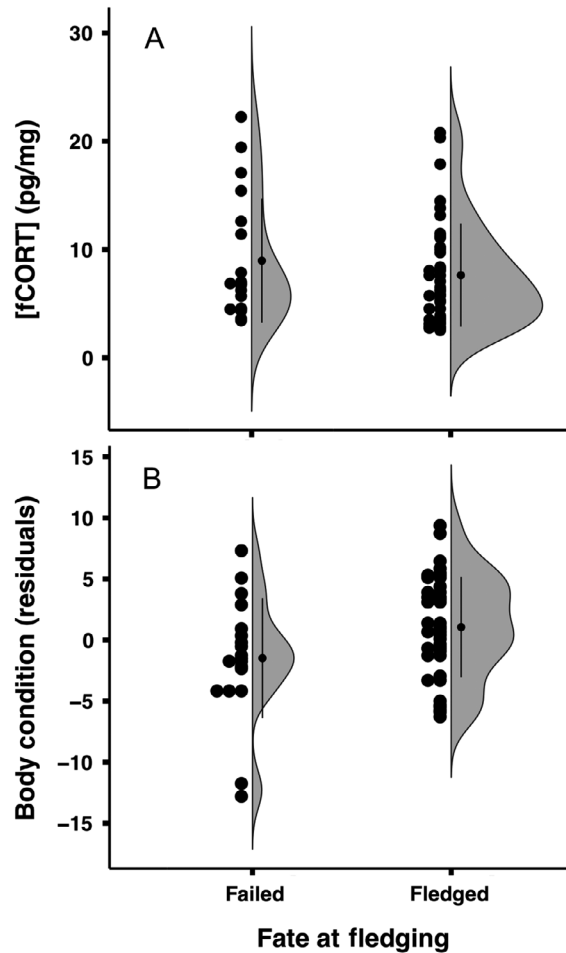

Fig. 3. Canada Jay (*Perisoreus canadensis*) nestlings from a 2-yr food supplementation experiment (2017–2018) that successfully fledged had (A) lower feather corticosterone concentrations ([fCORT] (pg/mg)) and (B) higher body condition (residuals of observed mass compared to predicted mass given body size) than those that failed to fledge in Algonquin Provincial Park, Ontario, Canada. The violin plot represents a smoothed probability density of the data using kernel density estimation. The black dots with the vertical lines represent the mean and standard error, respectively. The smaller black dots are the raw data points (*n* = 41).

condition but, most dramatically, advanced fledging of offspring. Experimental supplementation during the nestling period resulted in a 24% (5.5 d) advancement in fledging, suggesting that the timing associated with being capable of flight in Canada Jays is, at least partly, constrained by food quantity and also has the potential to be highly plastic. Indeed, food-supplemented, early fledging nestlings were developmentally equivalent to nestlings that fledge in the normal 22–24 d range. By fledging early, food-supplemented birds reduced their time in the nest when they are at high risk of predation (Roff et al. 2005) without incurring penalties that might otherwise be associated with leaving the nest prematurely. Leaving the nest early may allow for Canada Jay
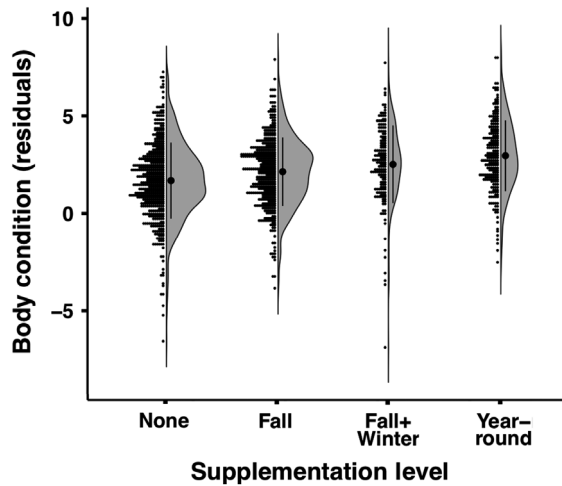
Fig. 4. The effect of food supplementation by the public on the body condition (residuals of observed mass compared to predicted mass given body size) of Canada Jay (*Perisoreus canadensis*) nestlings from 1979 to 2018 in Algonquin Provincial Park, Ontario, Canada. Nestlings from territories that had year-round food supplementation by park visitors or with access to permanent feeders had higher body condition than those with little to no easy public access. The violin plot represents a smoothed probability density of the data using kernel density estimation. The larger black dots with the vertical lines through them represent the mean and standard error, respectively. The smaller black dots are the raw data points (*n* = 1,293).
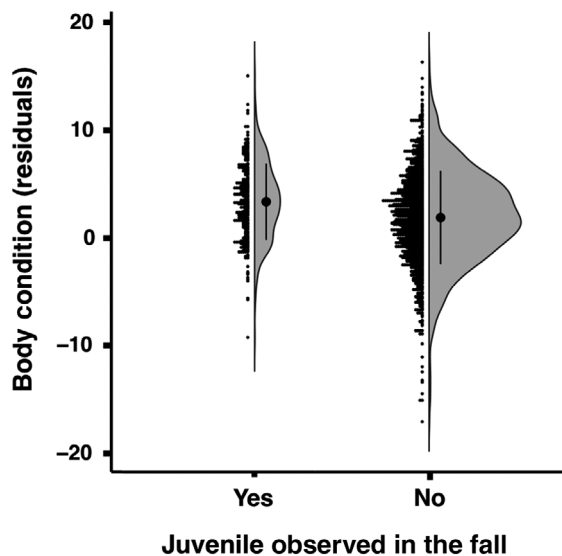
Fig. 5. Canada Jay (*Perisoreus canadensis*) juveniles observed in the fall following hatch from 1979 to 2018 had higher body condition (residuals of observed mass compared to predicted mass given body size) as nestlings than those that were not observed in the fall in Algonquin Provincial Park, Ontario, Canada. The violin plot represents a smoothed probability density of the data using kernel density estimation. The larger black dots with the vertical lines through them represent the mean and standard error, respectively. The smaller black dots are the raw data points (*n* = 1,293).

offspring to avoid nest predators such as red squirrels, Merlins, and other migratory raptors that return in the spring. Furthermore, young that are capable of fledging early may be at a competitive advantage for acquiring a breeding territory in the late summer. Our analysis of long-term data supports this because early-season nestlings are larger and have higher body condition than those hatched later in the season. Larger size and higher body condition due to an individual's diet during development likely confers a competitive advantage when competing for mates and territories (see review by Metcalfe and Monaghan 2001). Taken together, our results emphasize that the amount of food available to a breeding pair during the nestling period has the potential to have profound effects on the timing of early-life events and, potentially, the fitness of their offspring.

Physiological development, particularly of the hypothalamic-pituitary-adrenal axis (HPA), may be a potential proximate mechanism underlying the observed advancement of fledging date due to the role of corticosterone in mediating an individual's response to environmental perturbations and metabolism. Our results are consistent with previous studies by Hudin et al. (2017) and Will et al. (2014), where young birds with access to more food had lower feather corticosterone levels. We used feather corticosterone concentrations as an indicator of environmental stressors, which includes changes in food availability, throughout the nestling period. Feather corticosterone may also reflect the energetic expenditure of the nestling during the period of feather growth (Johns et al. 2018) in part because of the regulation of blood glucose by corticosterone (see Sapolsky et al. 2000 for a review). Therefore, control nestlings may have elevated corticosterone concentrations when compared to the supplemented nestlings due to a physiological response to low blood glucose from low food intake. Additionally, small portions or low frequency of provisioning by parents may result in more intra-brood competition since corticosterone increases begging behavior and aggression. In contrast to our results, Patterson et al. (2015) reported food-restricted Caspian Tern (*Hydroprogne caspia*) chicks had lower levels of feather corticosterone, compared to those fed *ad libitum*. The relationship between food quantity and feather corticosterone may be species specific, possibly due to differences in the deposition of corticosterone into feathers. Therefore, use of feather corticosterone as an indicator of HPA activity must be approached with caution.

Another mechanism that could explain early fledging in our study is nestling body condition. In 2018, body condition was higher in food-supplemented nestlings. Our experimental result was mirrored by the four decades of observational data, where nestling body condition was significantly higher on territories with more exposure to park visitors. Higher food consumption could account for a larger mass given body size and is consistent with several past studies (Kitaysky et al. 2001*a*, Searcy et al. 2004). Furthermore, because food

availability to nestlings is mediated solely by the parents in altricial species, food supplementation may be indirectly influencing nestling body condition by acting on adult body condition and behavior. Elevated food supplies may allow for the breeding pair to improve their own body condition because they do not need to spend as much time foraging, potentially increasing the quality of parental care such as increased defense of the nest. Alternatively, breeding pairs with higher body condition may be able spend more time searching for preferred food items to feed nestlings. In the future, it will be important to disentangle the potential direct and indirect (via parental body condition and behavior) effects of supplementation on nestling body condition.

Environmental conditions, such as temperature and the emergence of fresh food, may also influence nestling development and physiology. Due to the timing of the late-winter breeding season, the weather during the nestling period is highly variable and can range from $-0.3°$ to $7.1°C$. Therefore, it is possible that the lack of effect of food supplementation on nestling feather corticosterone and body condition in 2017 was driven by weather during the nestling period. Average temperature during the nestling period was $6.9°C$ warmer in 2017 ($7.1° \pm 5.0°C$) compared to 2018 ($0.2° \pm 5.6°C$). Unlike in 2018 when substantial snowfalls were regular and the amount of fresh food available was likely low, in the 2017 nestling period, there was fresh food such as moths, caterpillars, and dipteran larvae available (N. E. Freeman and A. O. Sutton, *personal observation*; R. Tozer, *personal communication*). This early pulse of fresh food sources in 2017 could have lessened the impact of experimental food addition on feather corticosterone and body condition (Oro et al. 2013). Intensive monitoring of the amount of food provided to the nestlings should be considered as a natural follow up to this experiment although previous efforts have been stymied by the often high nest locations and the fact the food is almost always held in swollen adult throats until its rapid injection into nestling throats in the form of a mushy and not easily quantifiable brown paste (Strickland and Ouellet 2018). Alternatively, it may not be the quantity of food available to a nestling that is driving differences between years but the quality of food nestlings are consuming. We currently have a limited understanding of the diet of Canada Jay nestlings aside from a few observations (see Strickland and Ouellet 2018). More rigorous study of the diet of nestlings is needed to assess the role of dietary composition and food quality on the growth and development of young jays.

The impact of climate change on Canada Jay food has been the focus of several recent studies on the Algonquin Park population. The hoard-rot hypothesis, proposed to explain the > 50% decline in the Canada Jay population observed since the 1980s, suggests that cached food degrades more quickly with warmer fall conditions, resulting in a reduction of the food available to support the late-winter nesting of Canada Jays (Waite and Strickland 2006). While there has been some support for this hypothesis (Sechley et al. 2015, Whelan et al. 2017, Sutton et al. 2019), we did not detect a decline in nestling body mass, body size, or body condition over the past 40 yr. It is possible that breeding pairs will only continue with a nesting attempt if their cached food stores remain above a certain threshold. This would account for our observed lack of change in nestling body condition over time because only individuals with access to enough resources would be able to successfully rear young. However, it is currently unknown if Canada Jays can assess the amount of cached food that remains and assess if this would be sufficient to raise young.

In a previous study, breeding pairs supplemented with food in the pre-breeding period, either experimentally or through handouts from park visitors, had earlier lay dates and larger clutch sizes but there was no effect of food on nestling body condition (Derbyshire et al. 2015). There are two possibilities to explain the discrepancy between our findings showing the positive effects of food supplementation on nestling body condition and those of Derbyshire et al. (2015). First, it is impossible to estimate how much food the public is feeding to the jays. Second, because the pre-breeding food supplementation resulted in larger brood sizes, there may have been greater intra-brood competition for food than in our study where brood size was not altered. Third, in the pre-breeding experimental manipulation, the quantity or quality of the provided food may have significantly diminished before the nestling period ~3–4 months later, either because the adults consumed it before the young hatched or because, being perishable, it suffered a marked decline in quality.

By understanding the potential mechanisms underlying the timing of fledging and survival of young, we may be able to identify drivers of the long-term population decline. Territory vacancies in this population have increased at a greater rate than reoccupations, particularly for low-quality territories (Strickland et al. 2011), but there is no evidence for a decline in adult survival over time (Norris et al. 2013). Thus, it is likely that reproductive output and recruitment are major drivers of the observed population decline (A. O. Sutton et al., *unpublished manuscript*). From our food supplementation experiment, nestlings were more likely to fledge if they had higher body condition at banding and had lower concentrations of feather corticosterone. Additionally, from the long-term data, nestlings that were observed in the study area the following fall as juveniles were had higher body condition at banding than those that were not observed. This suggests that the quantity of food available to the parents may be indirectly influencing whether or not a nestling survives until the fall by affecting body condition. In Algonquin Park, the juvenile that remains with its parents on its natal territory tends to be male (based on body mass in the fall), but unfortunately, we do not know the sex of the nestlings. Thus, the role of sex in whether a nestling is observed in

the following fall remains unknown. Furthermore, presence in the fall is only an estimate of apparent survival and does not account for emigration out of our study area. Direct estimates of Canada Jay juvenile survival will be necessary to determine whether the quantity of food experienced by young Canada Jays have long-lasting effects on their survival and, ultimately, fitness. Taken together, our results emphasize that the amount of food available to a breeding pair during the nestling period has the potential to have profound effects on the timing of early-life events and, potentially, the fitness of their offspring.

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