



## INVITED PAPER

# Early-Life Corticosterone Body Condition Influence Social Status and Survival in a Food-Caching Passerine

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**Synopsis** Individuals undergo profound changes throughout their early life as they grow and transition between life-history stages. As a result, the conditions that individuals experience during development can have both immediate and lasting effects on their physiology, behavior, and, ultimately, fitness. In a population of Canada jays in Algonquin Provincial Park, Ontario, Canada, we characterized the diet composition and physiological profile of young jays at three key time points during development (nestling, pre-fledge, and pre-dispersal) by quantifying stable-carbon ( $\delta^{13}\text{C}$ ) and -nitrogen ( $\delta^{15}\text{N}$ ) isotopes and corticosterone concentrations in feathers. We then investigated the downstream effects of early-life diet composition, feather corticosterone, and environmental conditions on a juvenile's social status, body condition, and probability of being observed in the fall following hatch. Across the three time points, the diet of Canada jay young was composed primarily of vertebrate tissue and human food with the proportion of these food items increasing as the jays neared dispersal. Feather corticosterone concentrations also shifted across the three time points, decreasing from nestling to pre-dispersal. Dominant juveniles had elevated corticosterone concentrations in their feathers grown pre-dispersal compared with subordinates. High body condition as nestlings was associated with high body condition as juveniles and an increased probability of being observed in the fall. Together, our results demonstrate that nestling physiology and body condition influence the social status and body condition once individuals are independent, with potential long-term consequences on survival and fitness.

## Introduction

Throughout early life, individuals undergo profound changes in morphology, physiology, and behavior. At the same time, threats of predation, low or fluctuating resources, and competition for resources can be potent selective filters. Individuals exposed to good early-life conditions often live longer than those that underwent development in poor conditions (see the “silver spoon hypothesis”; Grafen 1988; reviewed by Lindström 1999 and Monaghan 2008). Young animals may experience adverse conditions during periods of social competition or nutritional restriction due to low food availability or consumption of a diet consisting of low caloric/nutrient foods. While

poor conditions early in life can have pronounced immediate effects (Lindström 1999), they may also result in long-term programming of the endocrine system (Spencer et al. 2009; Grace and Anderson 2018), the immune system (Cole et al. 2012) and behavioral responses (Gardner et al. 2005; Spencer and Verhulst 2007), leading to reduced reproductive success and ultimately, reduced survival. Thus, how individuals cope with the conditions they experience during development can play an important role in modulating offspring mortality and fitness.

Dietary shifts during early life can be drivers of subsequent fitness due to the high nutritional demands associated with growth and development. Diet during

development may shift as individuals become larger because they may be able to expand the range of prey they are capable of catching and consuming (e.g., Olson 1996). As individuals grow, in addition to learning how to forage, they may also change habitats, allowing them to access novel prey species (e.g., Davic 1991). Switching to more profitable food sources, such as those rich in protein and fat, may result in increases in growth rate with positive downstream effects on survival and recruitment (Post 2003; Sánchez-Hernández et al. 2019). Overall, changes in both diet composition and abundance of prey are likely to be important during growth and development.

Concurrent with early life shifts in diet is the ongoing development of physiological systems such as the hypothalamic–pituitary–adrenal axis (HPA). The HPA is activated in response to stimuli such as low resource availability, inclement weather, and threats of predation resulting in the release of glucocorticoids (e.g., cortisol in many mammals and corticosterone in birds). Upon secretion, glucocorticoids act on target tissues to increase glucose in the blood by increasing gluconeogenesis, proteolysis, and lipolysis (Sapolsky et al. 2000) and also by modulating foraging (Kitaysky et al. 2003) and begging behavior (Schoech et al. 2011). Following birth, there is a hyporesponsive period where the HPA is relatively insensitive to many stimuli (fish [HPI axis]: Barry et al. 1995; mammals: Sapolsky and Meaney 1986; birds: Sims and Holberton 2000; Quillfeldt et al. 2009). As the HPA becomes sensitive to stimuli, glucocorticoid secretion increases (Love et al. 2003; Wada et al. 2007). In American kestrels (*Falco sparverius*), for example, baseline levels of circulating corticosterone increased until 22 days post-hatch at which point they were capable of mounting an adult-type response to a stressor (Love et al. 2003). While many studies have focused on the relationship between glucocorticoids and survival (e.g., Romero and Wikelski 2001; Blas et al. 2007; Cabezas et al. 2007; Wilkening and Ray 2016; Lind et al. 2020), few have investigated how the HPA axis shifts in activity across life-history stages in the wild and how this may contribute to divergent life-history trajectories among individuals.

Recent research on a population of Canada jays (*Perisoreus canadensis*) in Algonquin Provincial Park, Ontario, Canada has highlighted how aspects of the early-life environment can influence juvenile survival. In Canada jays, a partial dispersal event occurs approximately 2 months after hatch. During this time, increasingly intense bouts of sibling competition led to the expulsion of the subordinate siblings (hereafter “ejectees”) from the natal territory by the dominant juvenile (Strickland 1991). Because the

siblings fight to remain on their natal territory, it is assumed that becoming the dominant juvenile is the preferred life-history strategy. However, what remains unknown are the proximate mechanisms that link conditions during the nestling period (e.g., body condition, corticosterone concentrations) to juvenile social status. Dominant juveniles that hatched earlier in the season were more likely to be observed in the following fall than those hatched later in the season, possibly because they had more time to develop (Whelan et al. 2016). Nestlings were also more likely to be observed in the fall following hatch if they were raised on territories that received food supplementation from the public (Freeman et al. 2020). Nonetheless, a comprehensive analysis of the intrinsic and extrinsic factors driving variation in juvenile survival, social status, and body condition is necessary to identify mechanisms that contribute to variation in juvenile recruitment. Developing a more robust understanding of these mechanisms may also shed light on the mechanisms of decline that has been observed in this population since 1980, which is, in part, driven by juvenile male survival (Sutton et al. 2021).

Here, we investigated the impact of extrinsic (e.g., age of parents, territory quality) and intrinsic (e.g., feather corticosterone concentrations) factors on juvenile over-summer survival, their social status, and body condition in the fall following hatch. To do this, we characterized the diet and physiological profile of young Canada jays at three time points within the first 6 months of life. In doing so, we tested predictions from the silver-spoon hypothesis, which proposes that individuals exposed to favorable conditions during early life, such as high food availability and low sibling competition, would outperform those raised in poor conditions (Grafen 1988; Monaghan 2008). We predicted that jays would be more likely to be observed in the fall following hatch, achieve dominance, and be in high body condition as juveniles if they were raised by experienced parents (e.g., Whelan et al. 2016), came from smaller broods (e.g., Sutton et al. 2019), were raised on high-quality natal territories with high levels of food supplementation from the public (e.g., Freeman et al. 2020), consumed a higher quality diet rich in protein and fat (i.e., a diet composed primarily by vertebrate tissue), or had low feather corticosterone concentrations.

## Methods

### Study area and species

From 2010 to 2018, we studied young Canada jays in Algonquin Provincial Park, Ontario, Canada

(hereafter “Algonquin Park”; 45°33'N, 78°38'W). The study area in Algonquin Park consisted approximately 30 territories along the Highway 60 corridor. Within the study area, each individual was marked with a unique combination of three color bands and one standard United States Fish and Wildlife Service and Canadian Wildlife Service (USFWS/CWS) aluminum band. Canada jays maintain territories year-round and begin breeding in the late winter (Strickland and Ouellet 2020). Breeding pairs produce a single brood per year but may attempt a second, or even third, nest if their nest fails during laying or incubation (Strickland and Ouellet 2020). Breeding pairs were monitored through nest construction (2–4 weeks) beginning in late-February to mid-March, egg-laying (one egg per day) in March, incubation (18 days) in mid-March and early April, hatching in late March and April, and the nestling period (22–24 days) from late-March through May. Fledged young remain with their parents until they reach nutritional independence (observed foraging for themselves) at 41 days post-hatch (dph) and, shortly after, they undergo a period (55–65 dph) of intense intra-brood competition where the dominant juvenile forces its siblings to disperse from the natal territory. The dominant juvenile then remains with its parents on the natal territory for 1–2 years (Strickland 1991; Strickland and Ouellet 2020). The majority of subordinates, or ejectees, settle either on territories with unrelated breeders with no retained juvenile, while some may fill breeding vacancies (Strickland 1991; Strickland and Ouellet 2020). In the late-summer and throughout the fall, Canada jays cache perishable food items such as berries, mushrooms, arthropods, vertebrate flesh (from carcasses or small mammals and nestlings they have killed themselves) and, when available, human food (e.g., bread, cheese, and raisins) that they depend on for overwinter survival (Strickland and Ouellet 2020). The cached food is also used by females to increase their mass before egg-laying and incubation in February (Sechley et al. 2014) and to, at least partially, feed nestlings from late-March through May (Derbyshire et al. 2019).

### Nestling body condition and sample collection

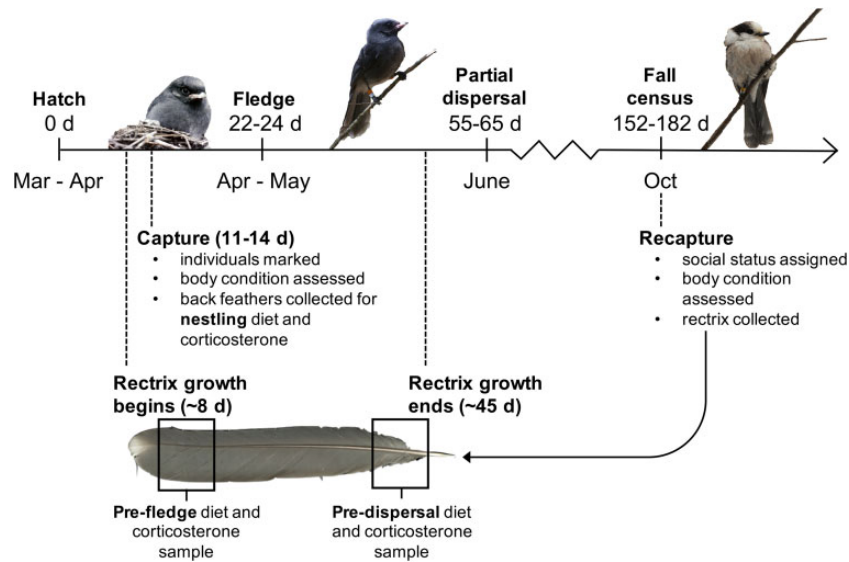
Nestlings were briefly removed from their nest 11–14 dph and were individually marked with three coloured leg bands and one standard USFWS/CWS aluminum band ( $n=143$ ). While out of the nest, mass and the length of the bill, tarsus, and seventh primary were measured and used to estimate the body condition of each nestling.

Nestling body condition was estimated as the difference between observed mass and predicted mass given body size (Derbyshire et al. 2015; Freeman et al. 2020). Body size was quantified using a principal component analysis (PCA) from a correlational matrix of bill, tarsus, and length of the seventh primary. The first principal component (PC1) scores explained 91% of the variation in the morphometric data and was used as an estimate of body size for each nestling (Freeman et al. 2020). The estimated body size was then used to generate a predicted mass using a model generated by Derbyshire et al. (2015) which describes the relationship between body size and mass of known-age Canada jay nestlings. Along with morphological measurements, 8–10 back feathers were also collected and stored in paper envelopes for isotopic and hormonal analysis. The dorsal tract of feathers becomes visible 4 dph and by 11–14 dph the back is well feathered with some emergence from the feather sheaths (Strickland and Ouellet 2020). Therefore, nestling back feathers were estimated to have grown between 4 and 10 dph.

### Juvenile body condition and sample collection

In October of each year, we conducted a population census to monitor the over-summer survival of breeding pairs and their young. If a juvenile was still with its parents on its natal territory, it was considered “dominant” while those found on non-natal territories were considered to be “ejectees”. Immigrant juveniles that had dispersed into the study area were also considered “ejectees” because they had left their natal territory. Juveniles were caught using potter traps or mist nets and morphological measurements including mass, bill, tarsus, and seventh primary lengths were recorded upon capture. Sex was assigned based on mass (male  $>70.5$  g  $>$  female) and if a mass was not collected or if the mass was 70.5 g, the sex was marked as unknown. An estimate for juvenile body size was generated using a PCA on a correlational matrix of bill, tarsus and seventh primary length where the first principal component explained 53% of the variation. Juvenile body condition was then estimated as the residuals of the relationship between mass and the estimated body size of the juvenile.

At capture, the third rectrix on the right side of the tail was collected ( $n=75$ ) and stored in a paper envelope. The rectrix was collected because it begins growing  $\sim 8$  dph, while young are still in the nest (young fledge 22–24 dph) and finishes growing  $\sim 45$  dph, just before the partial dispersal event (55–65 dph; Strickland and Ouellet 2020; Fig. 1). We



**Fig. 1** A timeline of sample collection during the first 6 months of life of Canada jays (*P. canadensis*) in Algonquin Provincial Park, ON, Canada.

conducted isotopic and hormonal analyses at two points along the rectrix that align with 15–20 dph and 40–45 dph. These are two important time periods because they correspond to the lead up to two key life-history events of a young Canada jay: fledge and the partial dispersal event. Pre-fledge diet composition and corticosterone concentrations were analyzed from tissue collected 5–15 mm from the distal end of the rectrix (i.e., the tip of the rectrix), while pre-dispersal diet composition and corticosterone concentrations were analyzed from tissue collected 0–10 mm from the proximal end of the rectrix (i.e., the base of the rectrix). For each section of feather collected, half of the tissue was used for isotopic analysis while corticosterone was extracted from the other half. All feather tissue collected from the rectrix was from the inner vane. A timeline of the life-history events during the early life of a Canada jay and the time points that we sampled are summarized in Fig. 1.

### Stable isotope analysis and diet composition

Diet composition of the young jays at three time points was estimated following methods outlined by Freeman et al. (2021). In brief, potential food items were opportunistically collected across the study area during the breeding season and during the caching period (February to May and October 2016–2017). Food items were grouped into plants ( $n=21$  individual samples), invertebrates ( $n=231$  samples), and vertebrates and human food ( $n=54$  samples, summarized in Supplementary Table S1 in Freeman et al. 2021). For details about sample preparation

and stable-carbon ( $\delta^{13}\text{C}$ ) and -nitrogen ( $\delta^{15}\text{N}$ ) isotope analysis, see Supplemental Information.

Diet composition nestling period (approximately 4–10 dph, back feathers), pre-fledge (approximately 15–20 dph, rectrix tip), and pre-dispersal (approximately 40–45 dph, rectrix base) were quantified using two stable isotope mixing models (MixSIAR, Stock and Semmens 2016). The first mixing model was generated by Freeman et al. (2021) and estimated the nestling period diet composition of Canada jays, which included individual ID as a fixed effect. The second mixing model included a unique ID for each sample timepoint (pre-fledge and pre-dispersal) for each individual to estimate the diet composition of young jays at approximately 15–20 dph and approximately 40–45 dph, respectively. For both mixing models, the raw C and N isotopic signature of each food item, rather than the means of each food group, were input as the source data (Stock et al. 2018) and trophic enrichment factors from the omnivorous yellow-rumped warbler (*Setophaga coronata*,  $1.9 \pm 0.1$  for  $\delta^{13}\text{C}$  and  $3.2 \pm 0.1$  for  $\delta^{15}\text{N}$ ; Pearson et al. 2003) were included. Both mixing models had an uninformative prior and the Markov Chain Monte Carlo parameters were set to three chains with a chain length of 300,000 iterations, a burn-in of 200,000, and a thin of 500. The mean proportion of each dietary source was extracted for each individual for each feather sample. Further statistical analyses were conducted using only the proportions of vertebrate flesh and human food because they represented the vast majority of the diet (Freeman et al. 2021).

### Feather corticosterone

Corticosterone in nestling back feathers (three to five feathers per individual) and juvenile rectrices were analyzed using a protocol optimized for avian feathers (Bortolotti et al. 2008; Freeman and Newman 2018). To minimize any effect of varying feather types and tracts, we only sampled from the vane of both feather types and standardized by mass, thereby avoiding the structural issues that arise with sampling the rachis and reporting corticosterone levels by feather length (Freeman and Newman 2018). For the nestling back feathers, only feather that had emerged from the sheath was analyzed. Feather samples were placed in microcentrifuge tubes with ceramic beads and pulverized into a powder using a bead mill (Bead Blaster: Benchmark Scientific, Edison, NJ). Based on a serial dilution to determine the optimal sample mass (Freeman and Newman 2018),  $2.6 \pm 0.1$  mg of powdered back feather and  $5.0 \pm 0.1$  mg of powdered rectrix were analyzed per sample. Samples were weighed into individual glass test tubes and 5 mL of methanol (HPLC grade: Thermo Fisher Scientific, Waltham, MA) were added to each tube. The test tubes were placed in a sonicating water bath for 30 min and then incubated in a 50°C shaking water bath for 12 h. The feather powder was separated from the methanol using vacuum filtration with #4 Whatman filter paper and rinsed twice with 1 mL of additional methanol. The 7 mL of methanol was dried in a 40°C evaporation plate under nitrogen gas for 50 min. Extract residues were reconstituted with absolute ethanol (5% of the reconstitution volume, absolute ethanol: Thermo Fisher Scientific, Waltham, MA) and phosphate-buffered saline (95% of the reconstitution volume, 0.05 mol l<sup>-1</sup>, pH 7.6) and vortexed following the addition of each solution. The reconstituted samples were analyzed as singletons (back feathers) and duplicates (tip and base of rectrices) using four double-antibody I<sup>125</sup> radioimmunoassay kits (ImmuChem 07-120103: MP Biomedicals, Orangeburg, NY). Feather corticosterone concentrations were calculated from a standard curve from each of the assays. Across assays, the average intra-assay coefficient of variation was 5.1% for the high control and 6.8% for the low control while the inter-assay coefficient was 6.3%.

### Statistical analysis

First, we characterized diet composition and feather corticosterone concentrations at three time points during the early life of Canada jays using feathers collected from 75 individuals across 2010–2018.

Nestlings that were part of a food spiking (Derbyshire et al. 2015) or food supplementation experiment (Freeman et al. 2020) were excluded from the analyses. Shifts in the composition of young jay diets and feather corticosterone concentrations throughout early life were assessed using a linear mixed-effect model (one for diet, one for corticosterone) with sample type (nestling, pre-fledge, and pre-dispersal) as the predictor and individual ID as a random effect. Post-hoc analysis using pairwise comparisons were then conducted to detect differences between each sample type using the package “emmeans” (Lenth 2020).

To assess how early-life conditions might influence whether an individual was observed again in the fall, we used a generalized linear mixed-effect model (GLMM, binomial distribution with a logit link function,  $n=143$  nestlings). Fixed effects included body condition as a nestling, the proportion of vertebrate flesh and human food in the nestling diet, and nestling feather corticosterone concentrations (pg/mg). Pre-fledge and pre-dispersal measures of diet and feather corticosterone were not included in this model because they were only collected from individuals that were present in the fall following hatch. Additional fixed effects included brood size (number of nestlings at the time of marking,  $n=53$  nests), age of the parents (minimum or known age in years,  $n=26$  females,  $n=31$  males), the year, estimated hatch day (20 day since the first day [= day 0] the female was observed on the nest), natal territory quality (percentage of conifers on the territory; Strickland et al. 2011,  $n=28$  territories), and level of food supplementation a territory received. Level of food supplementation was assigned based on the accessibility of the territory 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,  $n=3$  territories, Freeman et al. 2020). Nest ID and the ID of each parent were included as random effects because multiple nestlings were measured in each nest and because some parents bred across multiple years of the study.

We also used a GLMM (binomial distribution with a logit link function) to investigate factors influencing juvenile social status ( $n=46$  juveniles assigned as either a dominant or ejective). The fixed effects were body condition as a nestling, the pre-

dispersal proportion of vertebrate flesh and human food in the diet, pre-dispersal feather corticosterone concentrations, brood size, age of each parent, year, hatch date, natal territory quality, and food supplementation level. Nest ID and the ID of each parent were included as random effects.

The early-life predictors of juvenile body condition (Gaussian distribution with an identity link function) were assessed using a linear mixed model (LMM;  $n = 46$  juveniles). The fixed effects included were nestling body condition, the pre-dispersal proportion of vertebrate flesh and human food in the diet, pre-dispersal feather corticosterone concentrations, brood size, sex, age of both parents, year, estimated hatch date, territory quality, level of food supplementation, and an interaction between brood size and sex. The random effects were nest ID and the ID of each parent. All of the LMMs and GLMMs were run using the package *lme4* (Bates et al. 2015) and all underlying assumptions of the models were met. All analyses were conducted in the R statistical environment (v. 3.6.0; R Core Development Team 2019).

## Results

Over 9 years, we sampled 224 nestlings from 96 nests throughout their first six months of life (Fig. 1). Mean hatch date was April 11 (range = March 24 to May 17) and remained consistent across the study period (linear model:  $0.45 \pm 0.40$ ,  $t = 1.31$ ,  $P = 0.26$ ). Mean brood size was  $2.8 \pm 0.1$  nestlings (range = 1–5) and did not change over time (linear model:  $-0.04 \pm 0.04$ ,  $t = -1.11$ ,  $P = 0.27$ ). Nestling body size increased over time (mean =  $0.23 \pm 0.11$ , range =  $-3.60$  to  $4.30$ , linear model:  $0.13 \pm 0.05$ ,  $t = 2.66$ ,  $P < 0.01$ ), while body condition decreased (mean =  $1.99 \pm 0.29$ , range =  $-15.00$  to  $13.58$ , linear model:  $-0.51 \pm 0.12$ ,  $t = -4.41$ ,  $P < 0.001$ ). Over the course of the study, juvenile body size (mean =  $-0.48 \pm 0.13$ , range =  $-3.86$  to  $3.20$ ; linear model:  $-0.06 \pm 0.06$ ,  $t = -1.08$ ,  $P = 0.28$ ), and body condition (mean =  $-0.15 \pm 0.42$ , range =  $-9.24$  to  $6.48$ ; linear model:  $0.02 \pm 0.20$ ,  $t = 0.11$ ,  $P = 0.91$ ) did not change.

### Early-life diet composition

Diet composition was estimated from back feathers grown during the nestling period ( $n = 196$  nestlings) and from two parts of the rectrix grown at the pre-fledge and pre-dispersal stages ( $n = 75$  juveniles; Fig. 1; Isoplot: Supplementary Fig. S1). Nestling diets were estimated to consist of 51% ( $\pm 7$ ) vertebrate flesh and human food (range = 35–72%), 35%

( $\pm 6$ ) plants (range = 17–48%), and 14% ( $\pm 2$ ), invertebrates (range = 10–20%). Pre-fledge diet (approximately 15–20 dph, rectrix tip) was composed of 74% ( $\pm 5$ ) vertebrate flesh and human food (range = 54–82%), 15% ( $\pm 3$ ) invertebrates (range = 11–26%), and 10% ( $\pm 2$ ) plants (range = 4–21%). Similarly, pre-dispersal diet (approximately 40–45 dph, rectrix base) was 72% ( $\pm 4$ ) vertebrate flesh and human food (range = 53–83%), 16% ( $\pm 2$ ) invertebrates (range = 10–25%), and 12% ( $\pm 2$ ) plants (range = 5–22%). For both mixing models, all chains converged (Gelman-Rubin diagnostic: all variables were  $< 1.05$ , Geweke diagnostic: 5% of variables were  $\pm 1.96$ ).

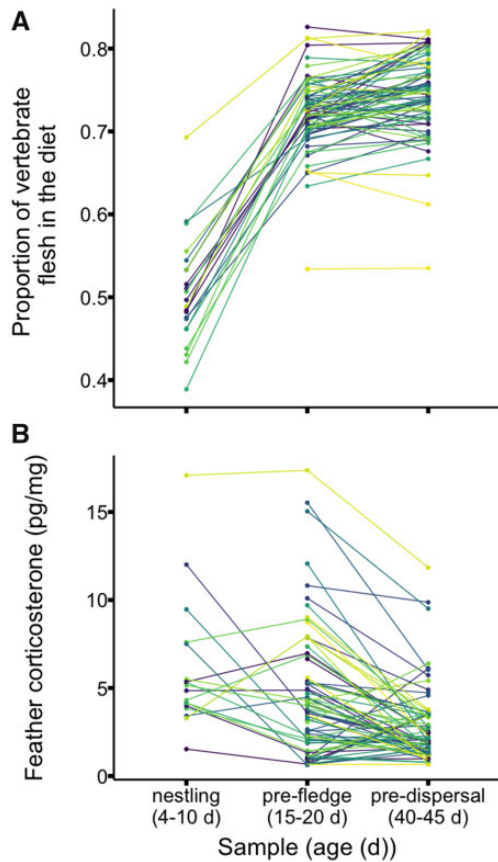
As young Canada jays aged, their diet shifted to include more vertebrate flesh and human food (LMM with post-hoc pairwise comparisons: nestling to pre-fledge:  $-0.22 \pm 0.01$ ,  $t$ .ratio =  $-26.18$ ,  $P < 0.001$ ; pre-fledge to pre-dispersal:  $-0.02 \pm 0.01$ ,  $t$ .ratio =  $-4.20$ ,  $P < 0.001$ ; nestling to pre-dispersal:  $-0.24 \pm 0.01$ ,  $t$ .ratio =  $-28.75$ ,  $P < 0.001$ ; Fig. 2A).

### Feather corticosterone concentrations

Across the study period, we quantified the concentration of feather corticosterone of 148 nestlings and 75 juveniles. Corticosterone concentrations from feathers grown in the nestling period ranged from 1.53 to 22.51 pg/mg (mean =  $6.85 \pm 0.37$  pg/mg). Mean corticosterone concentrations from feathers grown pre-fledge was  $4.36 \pm 0.38$  pg/mg (range = 0.63–17.37 pg/mg) while concentrations in feathers grown pre-dispersal was  $2.78 \pm 0.21$  pg/mg (range = 0.66–11.84 pg/mg). Feather corticosterone concentrations decreased as birds aged (LMM with *post hoc* pairwise comparisons: nestling to pre-fledge:  $1.50 \pm 0.60$ ,  $t$ .ratio = 2.49,  $P = 0.04$ ; pre-fledge to pre-dispersal:  $1.69 \pm 0.34$ ,  $t$ .ratio = 4.97,  $P < 0.001$ ; nestling to pre-dispersal:  $3.20 \pm 0.60$ ,  $t$ .ratio = 5.29,  $P < 0.001$ ; Fig. 2B).

### Juvenile survival, social status, and body condition

Of the 224 nestlings sampled, 66 were observed the following fall (41 males, 22 females, and 3 unknown sex). There were also an additional 30 juveniles that immigrated into the study area (15 males, 15 females), who were presumed to be ejectives from territories outside the study area (note: because the natal history of these individuals were unknown, they were only included in the diet and feather corticosterone analyses). The probability of being observed in the fall following hatch did not change over 9 years (GLMM:  $0.16 \pm 0.54$ ,  $t = 0.30$ ,  $P = 0.76$ ). Juveniles were more likely to be observed in the fall following hatch if they were of higher



**Fig. 2** Shifts in the proportion of vertebrate flesh and human food in the diet (**A**) and feather corticosterone concentrations (**B**, pg/mg) across the early life of Canada jays (*P. canadensis*) in Algonquin Provincial Park, ON, Canada (2010–2018). Each color represents one individual ( $n = 75$ ). Isotopic analysis and corticosterone extraction was conducted on feathers grown during the nestling period (approximately 4–10 dph, back feathers), pre-fledge (approximately 15–20 dph, rectrix tip), and pre-dispersal (approximately 40–45 dph, rectrix base).

body condition as nestlings (GLMM:  $0.90 \pm 0.31$ ,  $z = 2.86$ ,  $P < 0.01$ ; Supplementary Table S1). Extrinsic factors such as hatch date (GLMM:  $-0.26 \pm 0.30$ ,  $z = -0.88$ ,  $P = 0.38$ ), the age of their parents (GLMM, mother:  $-0.42 \pm 0.36$ ,  $z = -1.15$ ,  $P = 0.25$ ; father:  $-0.09 \pm 0.27$ ,  $z = -0.33$ ,  $P = 0.74$ ), brood size (GLMM:  $-0.21 \pm 0.27$ ,  $z = -0.80$ ,  $P = 0.42$ ), and the quality of the natal territory ( $0.01 \pm 0.28$ ,  $z = 0.05$ ,  $P = 0.96$ ) did not influence the probability of being observed in the fall (Supplementary Table S1). Additionally, the proportion of vertebrate flesh and human food in the diet and the concentration of feather corticosterone estimated from nestling back feathers had no effect on whether an individual was observed in the fall (GLMM, proportion of diet:  $0.15 \pm 0.31$ ,  $z = 0.48$ ,  $P = 0.63$ ; feather corticosterone:  $-0.33 \pm 0.39$ ,  $z = -0.83$ ,  $P = 0.41$ ; Supplementary Table S1).

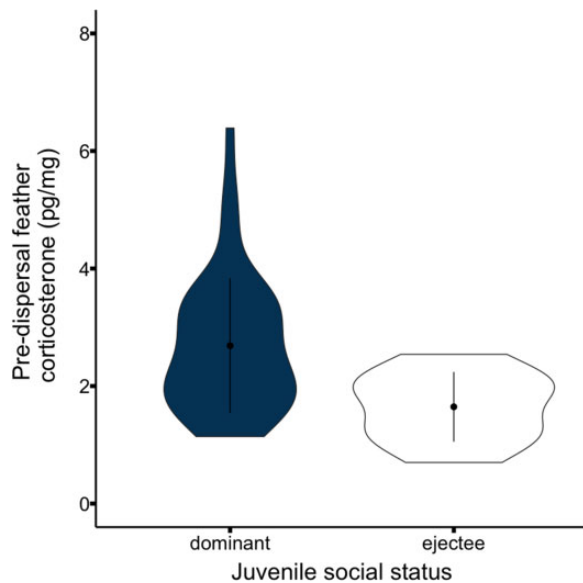
The surviving 66 nonimmigrant juveniles consisted of 50 dominants and 16 ejectees. Social status was associated with corticosterone concentrations in feather grown just before the partial dispersal (GLMM:  $-4.46 \pm 2.06$ ,  $z = -2.17$ ,  $P = 0.03$ ; Supplementary Table S2), where ejectees had lower corticosterone concentrations than dominant juveniles (Fig. 3). Social status was not influenced by the proportion of vertebrate flesh and human food in the diet just before dispersal (GLMM:  $-0.17 \pm 0.53$ ,  $z = -0.32$ ,  $P = 0.75$ ), brood size (GLMM:  $0.14 \pm 0.80$ ,  $z = 0.18$ ,  $P = 0.86$ ) or nestling body condition (GLMM:  $-0.28 \pm 0.77$ ,  $z = -0.36$ ,  $P = 0.72$ ; Supplementary Table S2).

Juvenile body condition was positively associated with nestling body condition (LMM:  $1.57 \pm 0.59$ ,  $t = 2.66$ ,  $P = 0.02$ ) and was higher for males than females (LMM:  $-3.25 \pm 0.93$ ,  $t = -3.52$ ,  $P < 0.01$ ; Supplementary Table S3). There was no correlation between juvenile body condition and pre-dispersal feather corticosterone concentrations (LMM:  $0.14 \pm 0.47$ ,  $t = 0.31$ ,  $P = 0.76$ ) or the proportion of vertebrate flesh and human food in the diet before dispersal (LMM:  $0.19 \pm 0.41$ ,  $t = 0.45$ ,  $P = 0.66$ ; Supplementary Table S3).

## Discussion

Using 9 years of data, we showed that a nestling's body condition carries over to influence its body condition five months later as a juvenile, as well as the probability that it will be observed in the fall. Contrary to the silver-spoon hypothesis, there was no positive influence of having older, more experienced parents, fewer siblings, or being raised on a higher quality territory on either body condition or survival. Higher than average body condition as nestlings may allow individuals to outcompete members of their brood and cohort when searching for resources or breeding vacancies. Additionally, individuals with higher than average body condition may have more energy stores to aid in surviving unpredictable weather events (e.g., late-spring/early-summer snow falls) or the unpredictability of successfully foraging as they learn to forage for themselves. While our findings suggest that nestling body condition is positively associated with apparent survival, it is important to note that our measure of presence in the fall underestimates survival because many individuals were not sampled because they dispersed out of the study area (i.e., ejectees).

Interestingly, dominant juveniles tended to have higher feather corticosterone concentrations before the partial dispersal event than ejectees. Dominance



**Fig. 3** The relationship between pre-dispersal feather corticosterone concentrations (pg/mg) and juvenile social status (dominant = navy, ejectee = white) of young Canada jays (*P. canadensis*) in Algonquin Provincial Park, ON, Canada (2010–2018,  $n = 46$ ).

has been linked with lower circulating corticosterone in mammalian and avian species that do not cooperatively breed (e.g., Louch and Higginbotham 1967; Creel 2001). In contrast, dominant individuals in cooperatively breeding species, such as the Florida scrub-jay (*Aphelocoma coerulescens*), tend to have higher concentrations of glucocorticoids than subordinates (Schoech et al. 1991; Creel 2001). Canada jays in Algonquin are not considered to be cooperative breeders because, during the breeding season, dominant juveniles are actively excluded from the area around the nest, although there are some observations of dominant juveniles feeding their siblings after fledging (Strickland and Ouellet 2020). However, we measured corticosterone in feathers grown long before dominant juveniles had the chance to help feed their future siblings. Therefore, elevated glucocorticoid concentrations in dominant juveniles are likely the result of mechanisms other than assisting with breeding.

Elevated corticosterone could be an indication that an individual is experiencing higher energetic demands (Johns et al. 2018). Leading up to the partial dispersal event, the eventual dominant juvenile competes with its siblings, with each sibling getting ejected from the territory one at a time. Therefore, the dominant juvenile is involved in a greater number of antagonistic interactions than its siblings before the partial dispersal event, possibly resulting in elevated corticosterone levels. In Algonquin Park,

dominant juveniles are typically male (Strickland 1991), which are larger and heavier than females. It is unlikely that male-dominant juveniles have elevated corticosterone due to higher energetic demands than their smaller male counterparts because many studies have found no sex-based differences in feather corticosterone levels (Fairhurst et al. 2012; Robertson et al. 2017; Adámková et al. 2019).

Our results also demonstrate that, as Canada jay young become nutritionally independent from their parents, the proportion of vertebrate flesh and human food increased from 51 to 72% of the diet. The rise of vertebrate flesh in the diet may be due to small mammals and birds becoming more accessible in late spring and early summer. Melting snow could increase the chance of capture as small mammals and reptiles are no longer tunneling under the snow or hibernating (e.g., Bieber et al. 2012). Additionally, Canada jays would have the opportunity to consume more eggs and nestlings with the onset of the breeding season of many migratory songbirds (Ouellet 1970). Human food is likely not playing much of a role in this dietary shift because, after the young fledge, the family group becomes difficult to locate until the late summer when they begin caching food again.

Although we have shown that individuals shift diets as they age, unexpectedly 83% of the diet was composed of vertebrate flesh, especially considering previous reports that food fed to nestlings consisted almost entirely of arthropods and other invertebrates (Strickland and Ouellet 2020; Dan Strickland, unpublished data). One explanation is that we missed sampling some food sources (e.g., nestlings of other species, migrating or newly emerged insects, berries from annual/perennial plants which were covered in snow or had not grown yet) because we only collected potential food items until late-May while rectrices used to estimate diet continued to grow into June. We also cannot rule out the possibility that seasonal changes in the isotopic signatures of prey led to the observed shifts in the Canada jay feathers. Despite some uncertainty in our estimation of diet composition, our results clearly show that there is an ontogenetic shift in the diet of young Canada jays. However, whether the shift is due to seasonal changes in food availability or juveniles learning to forage for themselves, which could result in changes in diet over time, remains unknown.

While the diet of Canada jay young shifted across time, the proportion of vertebrate flesh and human food at any time point sampled (nestling, pre-fledge, pre-dispersal) did not influence the probability of being observed during the fall population count, an

individual's social status, or body condition. Although this does not support the idea that early-life diet quality has downstream consequences for individual success, it is consistent with our recent study demonstrating that diet composition did not impact a nestling's body condition or their probability of being observed in the fall following hatch (Freeman et al. 2021). In other species, however, early-life deficiencies in nutrition can lead to retarded growth, small adult body size, impaired cognitive abilities, and increased mortality (Boag 1987; Kitaysky 1999; Nowicki et al. 2000; van der Ziel and Visser 2001; Pravosudov et al. 2005; Kitaysky et al. 2006). Because Canada jays consume a wide variety of food items rich in protein and fat, it is likely that the juvenile jays were not experiencing a deficiency in macronutrients within their diet, which may be why we see no relationship between diet and various metrics of juvenile body condition, social status, and survival.

Contrary to our predictions, we found that corticosterone concentrations in feathers grown leading up to the partial dispersal event decreased. Circulating corticosterone concentrations in plasma increase throughout development following a period of hyporesponsiveness of the HPA axis (Love et al. 2003; Wada et al. 2007), and as a result, more corticosterone should also be deposited into growing feathers. But, no study has examined whether the hyporesponsive period is detectable in feather corticosterone levels. The decrease in feather corticosterone concentrations across the samples is not likely due to structural (i.e., density) differences between the feathers because it was accounted for by sampling only the vane and standardizing by mass (Freeman and Newman 2018). Future work needs to characterize the relationship of plasma and feather corticosterone concentrations throughout development to determine whether a decrease in feather corticosterone with age is consistent across species.

We showed that body condition during development and, to a degree, feather corticosterone, are associated with whether an individual survives its first summer, its social status, and its body condition as a juvenile. Thus, factors influencing nestling body condition, such as diet quantity (Freeman et al. 2020), have likely played a role in the observed decline of Canada jays in Algonquin Park. We also found that feather corticosterone concentrations and diet of an individual changes during development. While we only focused on the first 6 months of life, continuing to monitor individuals throughout their lifetime may provide some insight into how

events during early life can have lasting effects on fitness.

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## Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

## Supplementary data

[Supplementary Data](#) available at *ICB* online.

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