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Research article

Nestling growth rate and food consumption increases under experimentally prolonged daylength in a New World sparrow

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When evaluating avian reproduction, life history theory examines the trade-offs between parental effort, the number and size of offspring, and the rate of nestling development. The growth rates and body sizes of developing birds vary geographically and can diverge with both latitude and migratory strategy. In terms of offspring size, growth rate can deviate in nestlings of the same or similar species due to the correlated influences of weather events, predation pressure, food availability, number of nestmates and parental provisioning. Furthermore, a longer photoperiod for species nesting at higher latitudes increases the duration over which a nestling can be fed each day, and increased nestling provisioning has been positively correlated with growth rate. Whether the amount of time a bird is fed during development drives this variation in growth rate and morphology is unknown. By removing supplemental environmental stressors (e.g. weather, predation) and standardizing feeding rate and environment, we explored the influence of daily duration of nestling provisioning on dark-eyed junco *Junco hyemalis* nestlings. We hand-reared 65 chicks of a sedentary junco subspecies *J. h. carolinensis* under both their natural photoperiod and the longer photoperiod of a closely related migratory subspecies *J. h. hyemalis* and compared growth rate, mass, morphology and the amount of food consumed. Average growth rate, fasted mass, wing length and total daily food consumption were all greater in birds hand-reared under the longer, more northern photoperiod treatment. These findings suggest that increased daily photoperiod at higher latitudes may allow for greater total food provisioning and thus may play a role in the ability of parents in compressed breeding seasons to produce high quality offspring. This points to a trade-off between provisioning effort and nestling growth rate in lower latitude (shorter photoperiod) populations and points to an important role of developmental plasticity on growth rate and morphology.

Keywords: breeding latitude, feeding rate, growth rate, morphology, photoperiod

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Introduction

Reproduction is often considered to be the most demanding life history event for most organisms. During the breeding season, animals must accommodate complex trade-offs in energy, effort and time in ways that maximize both their own and their offsprings' survival. Evaluating how these trade-offs lead to differences in nestling growth rate has proven difficult. However, understanding these differences is important as the rate of development in the nest can influence phenotype and condition, thus having potential direct effects on offspring fitness (Linden et al. 1992, Roff 1992, Arendt 1997, McCarty 2001).

Some life-history trade-offs are well established for songbirds across latitudinal gradients (e.g. investing less in a greater number of offspring versus investing more in fewer offspring), though exactly what drives variation across latitudes is still a subject of debate (Ardia 2005, 2006, Martin et al. 2011, Winkler et al. 2014). Nestling post-natal growth rate often varies with latitude among closely related species; south temperate species typically have slower growth than north temperate relatives (McCarty 2001, Ton and Martin 2016). Furthermore, nestlings from disparate genera also exhibit this trend across latitude (Arendt 1997, Sandvig et al. 2019). The shorter breeding season of high-latitude environments shortens the window of time in which young have access to the resources needed for development and survival, and a fast growth rate can decrease the risk of time-dependent mortality (Skutch. 1949, Ricklefs 1976, Case 1978, Benrey and Denno 1997, Remes and Martin 2002).

Similarly, differences in elevation, which can mimic limitations experienced at different latitudes (e.g. high elevation sites have a shorter breeding season than low elevation sites) and variation across elevational gradients, also correspond to differences in life-history strategies. Songbirds reproducing at higher elevation often invest more in each offspring but produce fewer offspring than low-elevation conspecifics. These groups experience different energetic constraints such as higher thermoregulatory costs or delayed food emergence at higher latitudes (Bears et al. 2009).

In the Northern Hemisphere, migratory species' nestlings often develop faster relative to resident species (Soriano-Redondo et al. 2020), as they must fit two migrations into their annual cycle, thus shortening their breeding season and the time available for nestlings to develop. Not only do egg-laying seasons start later at more northern latitudes (Baker 2009), but relative to resident species, the constraint of fall migration condenses the length of time for nestlings to complete their growth and gain flight capability after hatching (Meiri and Yom-Tov 2004). Rapid growth is advantageous when a minimum body size must be reached quickly (Arendt 1997) as it does for many migrant birds. However, fast growth can negatively affect other traits often associated with an organism's condition and factors that impact fitness (Arendt 2003, Alonso-Alvarez et al. 2007, Arriero et al. 2013), such as longevity (Metcalfe and Monaghan 2003, Hulbert et al. 2007, Lee et al. 2013).

Longer days in more northern latitudes during the breeding season increase the potential number of hours for parents to feed migrant nestlings (Rose and Lyon 2013, Sockman and Hurlbert 2020). Prolonged duration for feeding has the potential to increase total food consumption per nestling per day. Food availability mirrors this trend, as greater local food availability is correlated with increased growth rate (McCarty 2001), whereas food shortages correspond to decreased growth rates (Emlen et al. 1991). For example, the growth rate of both great tit *Parus major* and blue tit *Cyanistes caeruleus* nestlings is positively related to the rate of food delivery, with lower feeding rates resulting in poor relative growth rates (Naef-Daenzer and Keller 1999, Tremblay et al. 2003). As such, a highly influential determinant for the growth of nestlings is the rate at which energy (food) is delivered to the nest (Naef-Daenzer and Keller 1999, Hedd et al. 2002). While a longer photoperiod does not necessitate increased feeding rates by parents, it does increase the overall length of time available for food delivery to the nest each day. Potential increased daily food consumption due to longer feeding duration could therefore play a role in the faster rate of development of northern populations.

To date, numerous factors have been found to be correlated with growth rate: predation pressure (Remes 2007, Martin et al. 2011, Cheng and Martin 2012, Martin 2015), mortality rates (Ricklefs 1969, 1984, Case 1978, Bosque and Bosque 1995, Martin 1995, Ricklefs et al. 1998), parental provisioning rate (Wright et al. 1998, Tremblay et al. 2003, Shutler et al. 2006, Ardia 2007, Martin et al. 2011), food abundance or quality (Boag 1987, Pérez et al. 2016), clutch size and sibling competition (Crossner 1977, Rowe et al. 1994, Nilsson and Svensson 1996, Sanz 1997, You et al. 2009), anthropogenic disturbance (Potvin and MacDougall-Shackleton 2015, Marini et al. 2017), ectoparasitism (Arendt 1985), incubation time and temperature (Nilsson et al. 2008, Nord and Nilsson 2011), egg weight and size (Schifferli 1973, Amundsen and Stokland 1990, Smith and Bruun 1998), latitude (McCarty 2001, Ton and Martin 2016, Tuero et al. 2018, Austin et al. 2020, Remeš et al. 2020), altitude (King and Hubbard 1981, Lu 2005, Johnson et al. 2007, Bordjan 2013), and weather (Murphy 1983, Siikamäki 1996, Pérez et al. 2016). Observational field studies can make it difficult to decouple environmental effects versus intrinsic differences among populations (Arendt 1997).

In this study, given the considerable number of potential influences on nestling growth rate, we held most of the above factors equal to isolate the effects of increased daily feeding duration on growth rate. We hypothesized that latitudinal variation in growth rate could be, at least partially, attributed to phenotypic plasticty and the effects of increased daily feeding duration due to longer photoperiods.

We selected the study species, the dark-eyed junco *Junco hyemalis*, given that this species complex includes a resident *J. h. carolinensis* and migratory *J. h. hyemalis* subspecies that overwinter in the same location but whose migratory population breeds at latitudes much further north (Nolan et al. 2020). In the current study, we hand-raised *J. h. carolinensis* nestlings under photoperiods corresponding to either the *J. h. hyemalis* breeding photoperiod (northern treatment) or the *J. h. carolinensis* breeding photoperiod (southern treatment) and compared their morphological correlates of development and food consumption. Our captive design allowed us to isolate nestling growth in the absence of parental strategies and environmental influences. We predicted that, if daily duration of feeding affects growth rate, then the northern treatment would grow faster. We found that mean growth rate, total daily food consumption, wing length, and fasted mass were all greater in birds that were hand-reared under the more northern photoperiod treatment. There was no difference in peak growth rate between treatments, suggesting the fastest rate of growth was the same during the nesting period. Total daily food intake was greater in the northern photoperiod treatment despite chicks consuming less than their 'southern' counterparts per individual feeding bout. Among other findings, these results suggest a trade-off between provisioning capacity and nestling growth rate and suggest phenotypic plasticity in growth rate and morphology.

Material and methods

Study system

The dark-eyed junco *J. hyemalis* is a songbird broadly distributed across North America. Migratory and sedentary populations can co-occur during winter and early spring where they are exposed to the same environment (i.e. day length, temperature, weather), yet differ in whether they migrate, when they breed, and their morphology (Nolan et al 2020). *Junco hyemalis carolinensis* is sedentary (i.e. non-migratory) and lives and reproduces in the Appalachian Mountains of the eastern United States, while the migratory subspecies *J. h. hyemalis* overwinters with *J. h. carolinensis* but breeds in more northern latitudes of North America, including Alaska, Canada and northern New England (Fudickar et al. 2016, Nolan et al. 2020). *Junco hyemalis carolinensis* have longer bills, wings, tarsi and tails than migratory *J. h. hyemalis (*Miller 1942*)*. In this study, we used 65 nestlings of *J. h. carolinensis* collected at Mountain Lake Biological Station ('MLBS'; University of Virginia) on Salt Pond Mountain, Giles County, Virginia, USA (37.375654°N, 80.522140°W).

Capture and swabbing

Beginning in April 2021, we located and monitored nests at MLBS. Any unbanded females were captured at the nest with either a mist net or butterfly net and marked with a unique combination of color bands and a USGS aluminum band. Females were banded to ensure only one brood was taken from each set of parents. On the day following hatching (hereafter, 'Day 0' refers to hatch day, 'Day 1' is the day after hatch, etc.), the claws of nestlings were uniquely marked with nail polish for future identification, each nestling was weighed, and a buccal swab was collected for DNA extraction and sex determination. To collect the buccal swab, a strip of Whatman paper, held with forceps, was used to sample DNA-containing epithelial cells from the mouth (i.e. a nestling's cheeks and tongue were gently brushed for ~ 20 s until the Whatman paper was damp). The sample was stored in an eppendorf tube with Chelex solution (Adam et al. 2014). We cleaned the forceps with alcohol wipes between each nestling to avoid cross-contamination. On Day 3 or 4, the nestlings were removed from the nest, weighed and randomly assigned to one of two treatments ('Group assignment and housing').

Molecular sexing

To extract DNA, we incubated the buccal swab samples for 15 min at 56°C using a heat block followed by 10 s of vortexing. Next, we incubated samples for 8 min at 100°C. Samples then cooled to room temperature before being centrifuged at 11 000 rpm for 3 min (adapted from (Adam et al. 2014). To identify individual sex, we amplified the chromodomain helicase DNA binding (CHD) gene on the W and Z sex chromosomes using the P8/P2 primer set. 5 µl of the buccal swab DNA extraction was mixed with 2 µl 5× GoTaq green flexi buffer, 0.8 µl 25 mM $MgCl_2$, 1 µl 2 mM dNTP mix, 3 µl primer mix (P2, P8, H_2O), and 0.2 µl GoTaq DNA polymerase. PCR cycling included the following conditions: 95°C for 1 min followed by 30 cycles of 95°C for 20 s, 53°C for 30 s and 72°C for 30 s (adapted from Adam et al. 2014). Sample amplicons, a DNA ladder and positive controls (confirmed males and females) were run on 1.5% agarose gels at 100 V for 1 h. We assigned sex based on the absence (male) or presence (female) of the 380 bp fragment from the W chromosome.

Group assignment and housing

Once in captivity, nestlings were placed under experimental 'Virginia photoperiods' or 'Alaska photoperiods.' One 3.5 × 3.5 × 2.5 m (l × w × h) climate-controlled room was used for each experimental photoperiod treatment. Both rooms were maintained at 22°C with constant airflow. Automatic light timers were used to ensure lights in each room turned on and off according to the appropriate treatment. To control for differences in genetic background and minimize sex as a confounding factor, we assigned nestlings to one of two conditions by splitting broods equally and maintaining an equal sex distribution (i.e. for nests of two male and two female nestlings, one male and one female were randomly assigned to each experimental condition). Nests that contained fewer than four nestlings or an unequal ratio of males to females were separated as equally as possible, with an effort to keep the treatments balanced. Alaska treatment-assigned nestlings developed under the sunrise-sunset schedule of McGrath, Alaska (62.9532°N, 155.5960°W), while Virginia treatment-assigned nestlings developed under the sunrise-sunset schedule of Blacksburg, Virginia (37.2296°N, 80.4139°W), with sunrise and sunset times updated every other day. From the day nestlings were brought into captivity until they reached

Day 7, nestlings were kept in artificial nest-cups with their sibling (when applicable) or solo in an incubator at 29.5°C and 60% relative humidity. On Day 7, nestlings had grown in their down feathers and nests were moved to an incubator maintained at 24.5°C and 60% relative humidity. On or about Day 12, nestlings would hop from their nest cups and could thus be moved into individual cages in the room maintained at 22°C. Once nestlings moved to cages, their food consumption was no longer measured or included in this study, as they were housed individually and provided food ad libitum and also offered mealworms at regular intervals.

Food consumption measurement

In both treatment rooms, we fed nestlings mealworms every 30 min starting at lights on (i.e. 'sunrise') until they turned off (i.e. 'sunset'). Mealworms were sourced by The Bug Company, Fairfield, OH. We soaked mealworms in distilled water prior to feeding to kill the worms and provide hydration to the nestlings. Each nestling was fed until it stopped gaping (i.e. begging for food) and was no longer attentive to the offered mealworm. For nine days, we recorded the mass of worms eaten by a subset of nests between the ages of Day 5 and Day 11 (n = 48 birds). Unlike morphological measurements, food measurments were not taken for all nests due to the timing of nestling rearing and personnel availability. As nestlings were primarily housed in pairs in artificial nest containers and would beg simultaneously in response to stimulation or the presence of a mealworm, each artificial nest had a separate, labeled container of mealworms. We weighed containers before and after feeding and divided each by two for nests with two nestlings to determine food consumption. We measured food consumption in the morning (between 50 min and 2 h after 'sunrise') and in the evening (between 2 h and 30 min before 'sunset') daily. In addition, every other day, we measured midday food consumption by measuring two feedings immediately before and two feedings immediately after the midday point in each treatment. We estimated daily food consumption by averaging morning, midday and evening measures and multiplying by estimated total number of feedings per day (average of 35 for 'Alaska' and 26 for 'Virginia').

Morphology measurements

Weights taken in the nest (Day 0 or 1; not taken on all nestlings and only included in growth rate analysis) were generally taken mid-day. Once in captivity, before the first feeding every morning, we weighed each nestling (n = 65) ('fasted mass'; used for all other analyses). Once per day, between 15:00 and 18:00 h, we measured right wing and right tarsus length (mm) of each bird. Tarsus length, which provides a good predictor of avian body size (Rising and Somers 1989, Senar and Pascual 1997), was used to measure skeletal growth. We measured wing length via 'flattened wing chord' by holding the edge of the wrist flush with the tip of a ruler, gently flattening the feathers down, and measuring the total length from the bird's wrist to the tips of the longest wing feathers. We measured tarsus length and fasted mass through Day 12 and wing length through Day 30, when birds are typically fully developed in each respective measurement (Nolan et al. 2020).

Data analysis

We characterized two components of growth (change in individual mass over time) using R ver. 4.0.2 (www.r-project.org). On a per-bird basis, we fit a standard logistic growth curve (Ricklefs 1968, Martin 2015) using non-linear least squares (NLS):

$$W(t) = \frac{A}{1 + e^{\left(-K_i(t - t_i)\right)}}$$

Here, $W(t)$ denotes mass at time t, A denotes asymptotic mass, t_i denotes the inflection point of the curve, and K_i denotes the instantaneous rate of growth at the inflection point (peak growth rate). We set the lower bounds for all estimated parameters as zero and used starting estimates of A and t_i from each empirical growth curve. Initial estimation used the NL2SOL algorithm (Bates and Watts 1998), and we repeated NLS fitting using initial NLS estimates for more accurate parameter measurement. We then took the derivative of predicted mass with respect to time to obtain the growth rate curve (Wang et al. 2014) and obtained the mean growth rate across the nestling growth period (K_{mean}) (Ricklefs 1968, Martin 2015). When available, weights taken Day 0–1 at the nest were included in this analysis, which spanned up to Day 12 (n = 65). We fit linear mixed-effects models (LMMs) using the *lme4* package to test effects of photoperiod treatment, sex, and their interaction on peak and mean growth rate, accounting for nest as a random effect. We used marginal and conditional R^2 (R^2_m and R^2_c) to partition variance explained by the fixed and random effects.

We similarly used LMMs to test whether age-related changes in body size varied by photoperiod treatment for all chicks (n = 65). We fit a LMM for morning learn mass (Day 4 into Day 12), tarsus length (Day 4 into Day 12), and wing length (Day 4 into Day 30) that included age and its interaction with treatment as fixed effects alongside sex as a covariate; bird identity was nested within nest identity as a random effect. Similarly, we analyzed food consumption measurements using LMs with fixed effects of treatment and age. We tested feedings at different timepoints (i.e. morning, midday and nighttime) and estimated daily food consumption between treatments separately.

Results

Growth rate

By fitting logistic curves to body mass data of junco nestlings, we estimated peak and mean growth rates (Fig. 1).

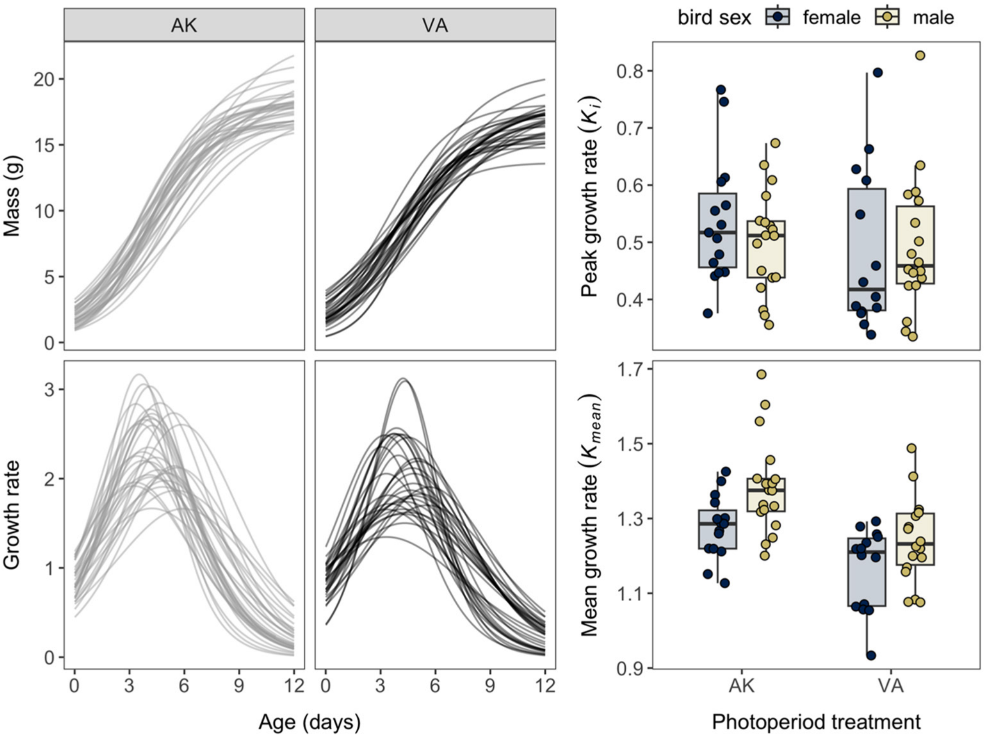

Figure 1. Fitted logistic growth and growth rate curves for nestling junco body mass between Alaska (gray lines, n = 33) and Virginia (black lines, n = 32) photoperiod treatments. Lines represent individual bird trajectories. Boxplots show the median and interquartile range of peak growth rate (K_i) and mean growth rate (K_{mean}) per treatment and sex extracted from the curves, with individual data overlaid and jittered to reduce overlap.

LMMs showed that peak growth rate did not vary by photoperiod treatment ($\beta_{\text{VA}} = -0.06$, $t = -1.76$, $p = 0.33$), sex ($\beta_{\text{male}} = -0.05$, $t = -1.56$, $p = 0.45$), nor their interaction ($\beta = 0.06$, $t = 1.49$, $p = 0.14$). However, mean growth rates were significantly lower for birds in the Virginia treatment ($\beta_{\text{VA}} = -0.12$, $t = -3.67$, $p < 0.001$) and greater in males ($\beta_{\text{male}} = 0.08$, $t = 2.47$, $p < 0.01$), with no interactive effect ($\beta = -0.03$, $t = -0.61$, $p = 0.54$). For both analyses, nest identity explained between 30–48% the variance in nestling growth parameters (K_i: $R^2_m = 0.03$, $R^2_c = 0.50$; K_{mean}: $R^2_m = 0.34$, $R^2_c = 0.63$).

Morphological variables

Morning lean mass

Morning lean mass varied significantly by age and treatment (age-by-treatment interaction: $\chi^2_8 = 27.39$, $p < 0.01$; Table 1) but not by sex ($\beta_{\text{male}} = 0.16$, $t = 0.74$, $p = 0.46$). After adjusting for multiple comparisons, birds in the Alaska photoperiod differed in mass from those in the Virginia photoperiod starting from Day 5 onward and especially starting on Day 9 (Fig. 2A, Table 2). Bird and nest identity explained 9% of the variance in morning lean mass ($R^2_m = 0.84$, $R^2_c = 0.93$; $\sigma^2_{\text{bird}} = 0.49$, $\sigma^2_{\text{nest}} = 0.52$).

Tarsus length

Tarsus length increased over time ($\chi^2_8 = 5788$, $p < 0.01$; Table 1) but did not vary not by treatment ($\chi^2_1 = 1.44$, $p = 0.23$) or their interaction ($\chi^2_8 = 3.87$, $p = 0.87$), nor sex ($\beta_{\text{male}} = -0.04$, $t = -0.27$, $p = 0.77$; Fig. 2B). Bird and nest identity explained 9% of the variance in tarsus ($R^2_m = 0.84$, $R^2_c = 0.93$; $\sigma^2_{\text{bird}} = 0.27$, $\sigma^2_{\text{nest}} = 0.24$).

Wing length

Wing length increased over time ($\chi^2_{26} = 199539$, $p < 0.01$; Table 1), was greater for birds in the Alaska photoperiod treatment ($\chi^2_1 = 3.93$, $p = 0.05$; Fig. 2C), and was greater in males ($\beta_{\text{male}} = 1.84$, $t = 5.37$, $p < 0.001$); the age-by-treatment interaction was not significant ($\chi^2_{26} = 14.10$, $p = 0.97$). Bird

Table 1. ANOVA ncluding comparisons of mass, tarsus, and wing by day (age), treatment, sex and the interaction between day and treatment.

Response	Factor	χ	df	p-value
Mass	Day	6840.25	8	0.00
Mass	Treatment	24.42	1	0.00
Mass	Sex	0.55	1	0.46
Mass	Day:treatment	27.39	8	0.00
Tarsus	Day	5821.12	8	0.00
Tarsus	Treatment	1.43	1	0.23
Tarsus	Sex	0.06	1	0.80
Tarsus	Day:treatment	3.89	8	0.87
Wing	Day	201661.88	26	0.00
Wing	Treatment	4.02	1	0.05
Wing	Sex	28.95	1	0.00
Wing	Day:treatment	14.54	26	0.97

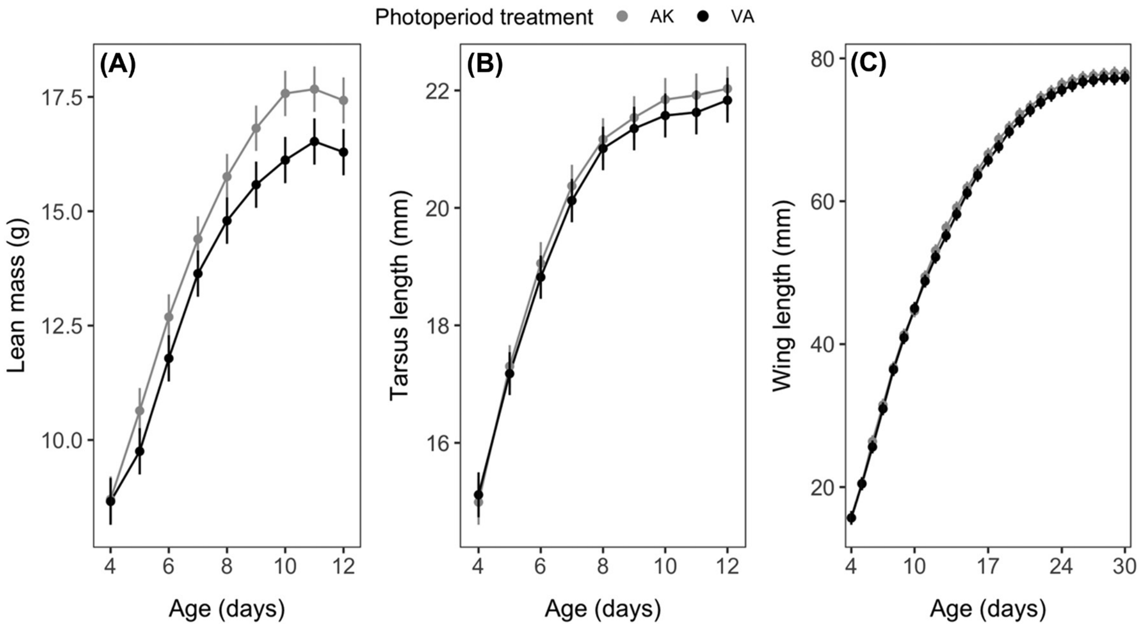

Figure 2. (A) Morning lean mass for Days 4–12 of nestlings under Virginia (black lines, n = 32) and Alaska (gray lines, n = 33) photoperiod treatments. (B) Tarsus length for Days 4–12 of nestlings under Virginia (n = 32) and Alaska (n = 33) photoperiod treatments. (C) Wing length for Days 4–30 of nestlings under Virginia (n = 32) and Alaska (n = 33) photoperiod treatments. Data points represent estimated means and 95% confidence intervals by age and treatment from each corresponding LMM, adjusting for bird sex and random effects.

and nest identity explained less than 1% of the variance in wing length ($R^2_m = 0.98$, $R^2_c = 0.99$; $\sigma^2_{\text{bird}} = 1.39$, $\sigma^2_{\text{nest}} = 1.37$).

Food consumption

Food consumed per feeding

During all three timepoints measured (n = 24), food consumption per feeding was greater for the nestlings raised under Virginia photoperiod than those raised under Alaska photoperiod (n = 24) in the morning (VA avg = 0.57, AK avg = 0.44, $F_{1,104} = 25.85$, $p < 0.01$), midday (VA avg = 0.55, AK avg = 0.45, $F_{1,46} = 7.86$, $p = 0.01$), and at night (VA avg = 0.59, AK avg = 0.46, $F_{1,92} = 21.97$, $p < 0.01$; Fig. 3). In the morning, food consumption increased as age increased ($F_{1,104} = 3.17$, $p = 0.01$), but this effect was not observed midday ($F_{1,46} = 0.49$, $p = 0.82$) or at night ($F_{1,92} = 1.84$, $p = 0.10$). Food consumption at each time point within treatments was not significantly different ($F_{1,278} = 1.33$, $p = 0.27$).

Table 2. Comparison of mass of Virginia and Alaska treatments from day (age) four to day twelve.

Contrast	Day	Estimate	SE	df	T-ratio	p-value
AK – VA	4	0.05	0.28	182.20	0.16	0.87
AK – VA	5	0.89	0.28	170.47	3.19	0.00
AK –VA	6	0.9	0.28	170.47	3.26	0.00
AK –VA	7	0.76	0.28	170.47	2.73	0.01
AK – VA	8	0.96	0.28	170.47	3.47	0.00
AK – VA	9	1.24	0.28	170.47	4.46	0.00
AK – VA	10	1.46	0.28	170.47	5.26	0.00
AK – VA	11	1.14	0.28	170.47	4.13	0.00
AK – VA	12	1.13	0.28	176.33	4.04	0.00

Total daily food consumption

Estimated total daily food consumption was greater for nestlings under Alaska photoperiods ($F_{1,104} = 4.60$, $p = 0.03$; Fig. 4). All birds increased daily food consumption with age ($F_{1,104} = 2.19$, $p = 0.05$) and average food consumption per feeding increased with age ($F_{1,104} = 2.36$, $p = 0.04$).

Discussion

North temperate and migratory birds, breeding at higher latitudes, develop faster relative to conspecific south temperate and resident species.Whether this phenomenon results from local adaptation or increased time for food provisioning due to longer photoperiod remains untested. Here, we removed environmental stressors (e.g. weather, predation pressure), standardized feeding rate, and hand-raised *J. h. carolinensis* nestlings under either *J. h. carolinensis* or *J. h. hyemalis* (further north) breeding photoperiods to investigate the influence of the duration of daily provisioning on growth rate. We found that total daily food consumption, wing length, fasted mass, and average growth rate were all greater in the chicks reared under the longer *J. h. hyemalis* day length suggesting the potential for differences in daily provisioning duration to influence population differences in these developmental paramaters.

Growth rate and life history

The junco nestlings reared under two different photoperiod treatments had significantly different average growth rates.

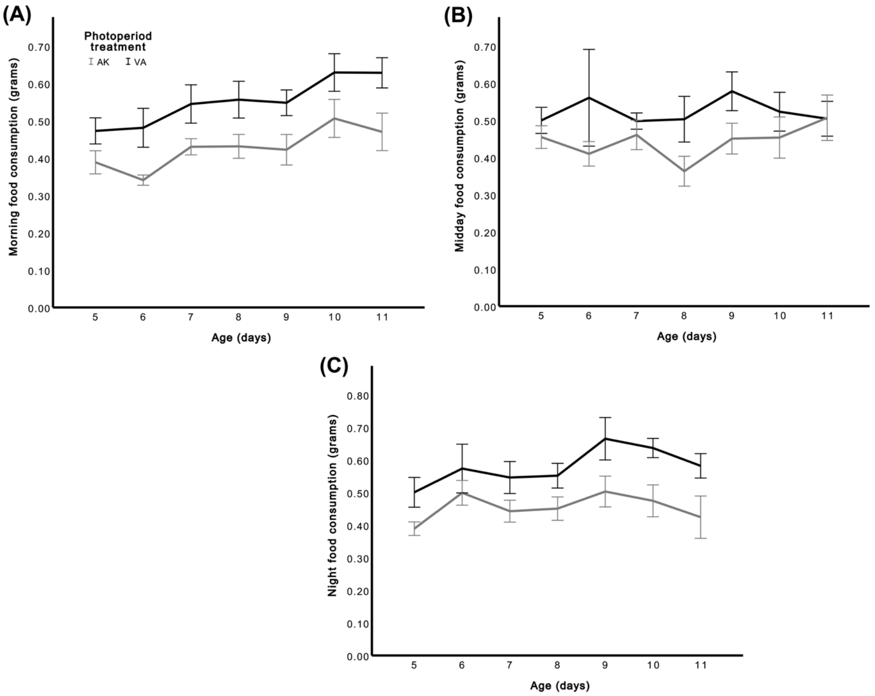

Figure 3. (A) Morning, (B) midday, and (C) night food consumption per feeding for nestlings aged Day 5–11 under Virginia (black lines, n = 24) and Alaska (gray lines, n = 24) photoperiods. Each data point represents mean ± 1 SE.

Longer photoperiods increase the timeframe over which a nestling is fed (Sockman and Hurlbert 2020), and increased food supply has been positively correlated with growth rate (McCarty 2001). While many studies have concluded that external influences (e.g. predation pressure, weather, parental provisioning) drive variation in growth rate, we eliminated or standardized many of these influences and still found differences in growth rate due under different photoperiods. As food consumption per feeding was greater for nestlings under the Virginia photoperiod, but total daily food consumption was significantly greater for nestlings under the Alaska photoperiod, we can conclude that a longer photoperiod increases food consumption when birds are offered food at consistent and regular intervals (i.e. standardized parental investment). We propose that variation in growth rate and morphology between the two treatments was caused, to some extent, by differential total daily food consumption due to differences in available feeding time (photoperiod).

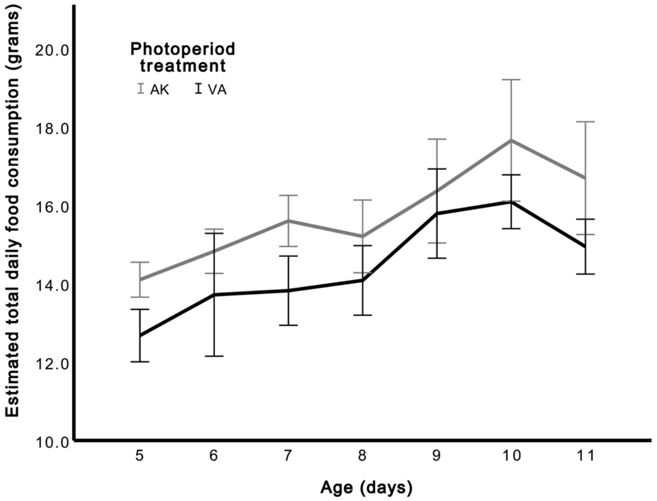

Figure 4. Estimated total daily food consumption by nestlings aged Day 5–11 under Virginia (n = 24) and Alaska (n = 24) photoperiod. Each data point represents mean ± 1 SE.

While nestlings reared in the Alaska photoperiod ate more overall per day and were offered food more times a day due to longer day length, they ate significantly less during each individual feeding than the nestlings in the Virginia treatment. Given this, it is possible that nestlings have a maximum caloric intake per day; thus, increasing the number of feedings per day results in decreased food consumption per feeding which maintains the caloric maximum. As songbirds are visual foragers, they are able to feed their offspring for a longer duration and rear larger broods in higher latitudes than their counterparts living further south (Lack 1947). Our results suggest two possible life history trade-offs: First, the longer photoperiods of northern environments may not increase food consumption of individual nestlings but rather increase the number of nestlings a parent can feed. This may result in the ability of parents to maintain a larger clutch size, thus maximizing fecundity in the shortened breeding season of higher latitudes. Counterintuitively, growth rate has been found to be slower in smaller broods (Ricklefs 1973). Feeding rate per chick decreases when clutches are small, which likely leads to the slower growth rate of smaller broods (Nur 1984). In larger clutches, rapid nestling growth may improve the competitive position of a nestling within the brood (Magrath

1990, Stouffer and Power 1990). Latitude tends to correlate positively with clutch size, both intra- and interspecifically (Lack 1947, 1948, Skutch 1949, Dunn et al. 2000, Cardillo 2002), which is consistent with migrants breeding at more northern latitudes having faster growth rates than residents breeding at more southern latitudes. Secondly, decreased foraging time and energy necessary per feeding bout provides adults with more time for predator avoidance and self maintenance, thus potentially increasing individual fitness. A faster growth rate may allow for nestlings to fledge more quickly or become fully independent faster once they leave the nest sooner, allowing parents the possibility of a second clutch (Arendt 1997, Martin et al. 2011).

The interpretation of our results must be considered within the limitation of our study. First, the birds in our treatments were offered food at fixed time intervals from lights on to lights off. However, we do not have evidence that wild juncos at northern latitudes provision their nestlings uniformly from sunrise to sunset. While we are not aware of studies that report the daily duration of junco nestling provisioning at high latitudes, several studies have reported daily activity patterns of breeding birds at high latitudes (Ashley et al. 2012, Steiger et al. 2013). These studies found that birds that breed at high latitudes experience extended quiescence periods during daylight hours, suggesting periods of parental inactivity during the nestling stage. Therefore, our results should be considered as the potential maximum difference in growth rate. Additionally, we brought nestlings into captivity in mid-May at our Virginia study site which is roughly one to two weeks before *J. h. hyemalis* juncos begin hatching at northern latitudes in the wild. Therefore, our Alaska photoperiod treatment was likely shorter than daylengths experienced by wild Alaska-raised junco nestlings. Lastly, when comparing our results to the experience of free-living juncos, by holding temperature equal and constant across treatments, we have removed any effect of temperature differences on total energy available to the nestlings during development (Mertens 1977, Degen et al 1992, Olson 1992).

Growth rate and plasticity

Growth rates of many organisms positively correlate with both the latitude and migratory tendency of a species (Ricklefs 1976, Ricklefs 1984, Martin 1995, Martin et al. 2011, Martin 2015, Ton and Martin 2016, Soriano-Redondo et al. 2020). However, it is unknown whether growth rate is genetically predetermined or driven by the environmental conditions under which an organism develops. Our observed effect of duration of daily feeding on growth rate during development is consistent with previous findings that growth rates are influenced by both hereditary and environmental factors (Garnett 1981, Heath et al. 1993). Further, nest ID explained only 30–48% of growth rate in our model, suggesting a considerable contribution of feeding treatment. In the wild, migratory juncos that breed in Alaska *J. h. hyemalis* and resident populations that breed in Virginia *J. h. carolinensis* are morphologically different, with the *J. h. hyemalis* being smaller in mass, wing length, bill length, tail length and tarsus (Miller 1942). Interestingly, this is opposite of our results, with birds reared under Alaska photoperiod having higher mass and longer wings. Since both of our experimental groups contained nestlings from the same subspecies *J. h. carolinensis*, our results suggest that mass and wing length are plastic traits that are influenced by caloric intake during development. We suspect that as *J. h. carolinensis* juncos do not migrate, they have not been selected to be smaller in size, thus they have the genetic flexibility to grow larger. Juncos in the current experiment that were reared with a feeding schedule consistent with a more northern latitude grew larger in size (demonstrated by mass and longer wings). It is therefore possible that increased photoperiod and prolonged daily feeding at northern latitudes may contribute to the general pattern that is observed of animals being larger at higher latitudes (Bergmann 1848).

There are undoubtedly disparate environmental pressures affecting daily food consumption for residents developing at lower latitudes and migrants developing at higher latitudes in the wild. Populations often vary in size at maturity depending on where on the globe they reproduce. Migratory birds, breeding at higher latitudes, are typically smaller than residents (Hedenström 2003, Soriano-Redondo et al. 2020). Because the smaller surface area to volume ratio in the larger body size of endotherms would increase heat retention, Bergmann (1848) argued that larger bodies would be favored in lower temperature environments, i.e. at higher latitudes (Mayr 1956, James 1970, Salewski and Watt 2017). However, many migratory birds overwinter at the same latitude and in the same climate as their resident counterparts, so they have no need for a larger body size for thermoregulation as it relates to heat retention. Migrants may be smaller than their resident counterparts because increased body mass is associated with an increase in energetic costs when using flapping flight, so larger birds have to refuel more frequently than small birds during migration (Klaassen 1996, Klaassen and Lindström 1996, Lindström 2003). In addition, smaller birds can travel far distances at a faster speed, enabling them to meet seasonality-induced time constraints and increasing their chances of arriving early to claim limited resources (Klaassen 1996, Alexander and McNeill Alexander 1998, Hedenström 2007). Lighter species tend to show faster rates of development (Ricklefs 1973, Pennycuick et al. 1984), which is consistent with migrants' faster growth rate. In the wild, the constraints of migration on *J. h. hyemalis* ultimately select for a smaller body size despite the possibility of growing larger at higher latitudes. Raising *J. h. hyemalis* chicks under the *J. h. carolinensis* photoperiod (the opposite conditions of this experiment) would further test the plasticity of growth rate and the influence of daily feeding duration on this metric.

Finally, our results lend support to the 'daylength availability hypothesis' outlined by Sockman and Hurlbert (2020) regarding the evolution of photoperiodism and migration. This hypothesis posits that migrants alter the amount of daylight available to them with the assumption that this incurs some fitness benefits not available at lower latitudes. Migration to longer day lengths has the possibility to increase fitness given our finding that high latitude photoperiods allow for smaller individual feeding bouts to raise faster-growing nestlings than in lower latitude conditions.

Conclusions

We conclude that available day length for nestling feeding drives the larger average growth rate, mass, wing length, and total food consumption observed under the Alaska treatment. These findings suggest a trade-off between parental provisioning and, 1) growth rate in lower latitude populations and 2) parental fitness in higher latitude populations. Furthermore, the capacity of numerous traits of a single population to significantly diverge under two photoperiods indicates phenotypic plasticity influenced by increased food provisioning possible under increased day length.

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Author contributions

Allison J. Byrd: Conceptualization (equal); Data curation (supporting); Investigation (equal); Methodology (supporting); Project administration (supporting); Visualization (supporting); Writing – original draft (lead). **Colleen S. Mullins**: Conceptualization (supporting); Data curation (lead); Formal analysis (supporting); Investigation (equal); Methodology (equal); Writing – original draft (equal). **Daniel J. Becker**: Formal analysis (equal); Writing – original draft (supporting). **Adam M. Fudickar**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (lead); Writing – original draft (supporting).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.f7m0cfz24 (Byrd et al. 2023).

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