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Article

Offspring growth and mobility in response to variation in parental care: a comparison between populations

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Life history theory emphasizes the importance of trade-offs in how time and energy are allocated to the competing demands of growth, fecundity, and survival. However, avian studies have historically emphasized the importance of resource acquisition over resource allocation to explain geographic variation in fecundity, parental care, and offspring development. We compared the brood sizes and nestling mass and feather growth trajectories between orange-crowned warblers *Oreothlypis celata* breeding in Alaska versus California, and used 24-h video recordings to study the relationship between parental care and growth rates. Per-offspring provisioning rates were highest in the smallest broods, and food delivery was positively correlated with nestling growth over the 24-h period only in Alaska. Females in Alaska spent more time brooding, and juveniles there showed faster feather growth and earlier mobility compared with those in California. We also found differences in the energetic and nutritional content of insect larvae that could facilitate the observed differences in nestling growth relative to food provisioning. Our results point to the potential importance of food quality and parental provisioning of warmth, in addition to food, for explaining avian growth patterns. We highlight the need to quantify multiple dimensions of parental care and of offspring growth and development, and to better understand the relationships between feather growth, nestling period length, and fledgling mobility.

Keywords: avian growth, clutch size, Lack's hypothesis, life history trade-off, offspring quality

Introduction

Life history theory seeks to understand the trade-offs that constrain organisms along a slow-fast life history continuum and to identify the ecological processes that favor evolution along that continuum (Roff 1992, Stearns 1992, Ricklefs and Wikelski

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2002). A major challenge is to understand the evolution of resource acquisition and resource allocation strategies, and how these strategies give rise to observed life history variation within and among populations and species (van Noordwijk and de Jong 1986, Reznick et al. 2000). In organisms that provide parental care, acquired resources are directed towards developing offspring until they reach independence (Royle et al. 2012). Life history theory predicts that allocation trade-offs shape variation in parental reproductive effort (i.e. the proportion of resources allocated to current reproduction; Williams 1966) and how that effort is partitioned among offspring (Smith and Fretwell 1974). Per-offspring expenditure is influenced by variation in environmental conditions that alters resource availability or costs for parents (Parker and Begon 1986, McNamara and Houston 1996, Kirkwood 2005, Kindsvater et al. 2011, Kindsvater and Otto 2014), or affects the relationship between per-offspring expenditure and offspring performance and fitness (Brockelman 1975, Sinervo et al. 2000, Jorgensen et al. 2011, Leips et al. 2013, Rollinson and Hutchings 2013). In turn, offspring allocate resources towards the competing demands of growth and development (Arendt 1997, Cheng and Martin 2012). Ecological variation therefore shapes resource availability and both parental and offspring allocation strategies, but few comparisons between populations have explored the links between total and per-offspring expenditure and offspring growth, development, and performance.

Studies of birds have been central to developing and testing life history theory (Lack 1947, Skutch 1949, Ashmole 1963, Martin 1987, 2004, 2015, Ricklefs and Wikelski 2002), and have historically emphasized how variation in the acquisition and delivery of food to the young shapes life history variation across geographic gradients. Higher total provisioning rates should allow for larger brood sizes, and classic hypotheses differ in how day length (Lack 1947), population density (Ashmole 1963), and nest predation risk by visually oriented predators (Skutch 1949) limit provisioning. These hypotheses were developed to explain the latitudinal increase in clutch and brood sizes, and latitudinal variation in per-capita provisioning may similarly explain latitudinal variation in offspring growth (Rose and Lyon 2013). Studies have also described allocation trade-offs in birds (Young 1996, Martin et al. 2000, Martin 2004, Monaghan 2004, Tarwater and Brawn 2010), demonstrating geographic variation in parental strategies and offspring growth rates (Gwinner et al. 1995, Starck et al. 1995, Ghalambor and Martin 2001, Remes and Martin 2002, Martin et al. 2011, 2015). A recent synthesis suggests that increased parental expenditure per offspring may facilitate offspring allocation towards feather growth, allowing for early mobility (Cheng and Martin 2012, Martin 2014, 2015). Nevertheless, few studies have directly measured mass and feather growth and linked latitudinal variation in growth rates to variation in parental care; it remains unclear whether and how the relationships between per-offspring parental expenditure and offspring growth may vary among populations.

To better understand patterns of parental expenditure and offspring growth and performance, we compared populations of orange-crowned warblers *Oreothlypis celata* breeding near their northern range limit in Fairbanks, Alaska, and their southern limit on Santa Catalina Island, California. We focused on the nestling period because nestlings in these populations reach a similar asymptotic mass, but birds in Alaska have a faster growth rate and an earlier inflection point in their growth curve (Sofaer et al. 2013a). Our goal was not to identify the ecological drivers of life history divergence in these populations (e.g. the role of age-specific mortality rates), but rather, to quantify any differences in the consequences of variation in parental care for offspring growth and juvenile mobility. We measured food delivery rates and brooding behavior over 24-h time periods to test the hypothesis that the ability to acquire resources and deliver them to young explains differences in clutch and brood sizes between populations. We predicted that per-offspring expenditure would be higher in California, in line with the smaller clutch sizes observed in that insular population (Gilbert et al. 2010). We then tested for differences in nestlings' resource allocation to growth by quantifying the relationship between how much parents provisioned and brooded nestlings and the amount of nestling mass gain, tarsus growth, and feather growth within and between populations. We also analyzed offspring mobility in relation to morphology to assess the implications of growth for functional performance. Finally, we compared the energetic and nutritional content of insect larvae collected in our study areas to test for variation in food quality. Quantifying multiple dimensions of variation in parental behavior and offspring physiology highlighted understudied aspects of geographic variation in avian life histories.

Methods

Avian field methods and video data

We studied the reproductive allocation and behavior of orange-crowned warblers in Fairbanks, Alaska (64°47′N, 147°53′W) and on Santa Catalina Island, California (33°20′N, 118°26′W). Our study populations are located near the northern (*O. c. celata*) and southern (*O. c. sordida*) ends of the breeding range of this species. During the breeding season, the *sordida* subspecies is largely endemic to California's Channel Islands, so the selective environments underlying population divergence encompass both latitudinal and insular effects, among others. For example, our study population on Santa Catalina Island breeds at high densities (Sofaer et al. 2014) and exhibits a suite of traits associated with strong competition, including high testosterone and male aggression relative to the Alaska population (Horton et al. 2010, Yoon et al. 2012). We studied variation in parental care and its consequences for nestlings, evaluating the assumption that growth should reflect variation in per-offspring provisioning (Lack 1947), and the alternative that populations differ in nestlings' allocation to growth. Nestlings hatch at the same mass in these two populations (CA: 1.33 ± 0.13 g, n = 37; AK: 1.35 ± 0.22 g, n = 107), suggesting that important differences in growth are manifested during the nestling period. All descriptive statistics are given as mean ± 1 SD.

To describe patterns of life history variation, we compared clutch size (number of eggs), brood size (number of nestlings), and nestling period length between populations based on data from 2006–2008 in Alaska and 2003–2009 in California. We modeled clutch and brood sizes assuming a quasi-Poisson distribution (Ver Hoef and Boveng 2007) and compared nestling period lengths using Pearson's chi-squared test (Supplementary material Appendix 1 Methods).

We collected 24-h data on provisioning and growth rates in 2007–2008 in Alaska and 2009 in California, with additional provisioning data from 2008 in California. Twenty-four-hour digital video recordings of behavior at nests allowed us to account for differences in day length, which is otherwise difficult because populations at high latitudes often use a lower proportion of daylight hours (Hussell 1972, Sanz 1999, Rose and Lyon 2013). We recorded 62 24-h videos of parental behavior, both early in the nestling period (noon on nestling day 2 through noon on day 3; AK: n = 8 videos, CA: n = 10 videos), and late in the nestling period (day 5–7 and 6–7; AK: n = 19 videos, CA: n = 25 videos). Cameras were set up a minimum of 30 min. before recording began to ensure cameras were accepted. We observed no major inter-annual differences in parental care within each population (Supplementary material Appendix 1 Fig. A1). Ambient temperature during nest videos did not differ between populations (Yoon et al. 2017). The timing of our video and nestling growth data collection during the late nestling stage was designed to control for both nestling age and nestling position along the growth curve (Supplementary material Appendix 1 Methods). For both mass and feather growth, birds in Alaska reached the inflection point in their growth curve slightly less than one day earlier (see Results). In Alaska we collected 24-h data starting on day 5, and in California we collected data both at the same age (starting on day 5) and at the same stage of growth (starting on day 6).

We transcribed each nest video to quantify the number of active feeding hours, the number of feeding trips, the mean food load size, and the number of hours the female spent brooding (Table 1). We recorded the time of each arrival and departure and defined food load size as the size of the food item(s) relative to the parent's bill size (e.g. 1.5 times the bill size). Total food delivery during each video was defined as the number of feeding trips multiplied by the mean food load size; this value was divided by brood size to estimate per-nestling food delivery (see Supplementary material Appendix 1 Methods for treatment of missing video time and food load sizes and analyses demonstrating that these did not affect our primary conclusions).

To quantify the relationship between provisioning and growth rates, we weighed and measured nestlings before and after our 24-h video recordings. We individually marked nestlings using non-toxic permanent marker on their toenails,

Table 1. Twenty-four hour provisioning patterns and growth over the 24-h period of young (days 2–3) and old (days 5–7) nestling *O. celata* in Alaska and California (mean ± 1 SD). Old nestlings in California were measured on both days 5–6 and days 6–7; the mean across days was first calculated for each nestling, and the mean across nestlings is reported.

Nestling age	Population	Active feeding hours	Total feeding trips	Food load size	Total food delivery	Food delivery per nestling	Brooding hours	Mass gain (g)	Tarsus growth (mm)	Feather growth (mm)
Young	Alaska (n = 8 videos; n = 30 nestlings)	19.4 ± 0.7	66.2 ± 14.8	3.1 ± 1.0 (n = 5)	196.4 ± 59.1	40.2 ± 11.0	15.7 ± 2.0	1.3 ± 0.3	2.2 ± 0.4	1.8 ± 1.0
	California (n = 10 videos; n = 26 nestlings)	13.3 ± 0.4	116.3 ± 36.2	1.2 ± 0.5 (n = 3)	134.5 ± 15.9	53.8 ± 13.7	6.3 ± 1.1	1.2 ± 0.4	1.8 ± 0.4	1.3 ± 0.8
Old	Alaska (n = 19 videos; n = 54 nestlings)	19.2 ± 0.6	105.2 ± 28.8	2.7 ± 0.5 (n = 18)	290.8 ± 86.7	60.8 ± 14.1	11.4 ± 3.3	1.4 ± 0.4	1.7 ± 0.4	4.9 ± 0.7
	California (n = 25 videos; n = 23 nestlings)	13.4 ± 0.5	211.8 ± 55.4	1.2 ± 0.5 (n = 18)	238.6 ± 87.3	91.8 ± 42.6	1.4 ± 1.2	1.3 ± 0.4	1.6 ± 0.3	4.1 ± 0.4

allowing us to calculate the growth of each bird over a 24-h period (Sofaer et al. 2013a). Nestlings were weighed to the nearest 0.01 g. We measured the tarsus and the length of the first primary feather from where it exited the skin to the tip of either the feather sheath or the feather, if it had emerged from its sheath. In Alaska, we weighed and measured 30 nestlings from 6 nests on days 2 and 3, and 54 nestlings from 11 nests on days 5 and 6. In California, we weighed and measured 26 nestlings from 10 nests on days 2–3 and 23 nestlings from 9 nests on days 5, 6, and 7 (to calculate growth for both days 5–6 and 6–7). All handling was complete by 30 min. before the start of each video. Although growth increments over a 24-h period likely include some lag effects of previous conditions and may be buffered by stored energy, food restriction studies have demonstrated growth responses over 1 day in passerines (Searcy et al. 2004), suggesting measured growth increments over a 24-h period can reflect direct responses to observed provisioning rates.

Variation in food quality is often implicitly assumed to be constant within and between populations, despite evidence suggesting dietary quality can influence clutch size (Eldridge and Krapu 1988, Patten 2007) and passerine growth (Boag 1987, Johnston 1993, Wright et al. 1998). We therefore compared the energetic and nutritional content of insect larvae collected at our study sites. Larvae were collected in 2010 from vegetation at randomly generated locations at each study site, and were assayed for energetic and nutritional content (Supplementary material Appendix 1 Methods).

Comparison of mass and feather growth curves

We fit growth curves to mass and feather data to characterize growth trajectories, and used the first derivative at each point along the curve to visualize variation in growth rate (Wang et al. 2014). Previously, we estimated nonlinear logistic mixed models to establish that nestlings in Alaska have faster peak growth rates and earlier inflection points for mass gain than birds in California (Sofaer et al. 2013a). Here, we plot the previously estimated fixed-effect functions of mass gain (and their derivatives) for direct comparison with feather growth curves. Feather growth trajectories have rarely been compared between populations, and we modeled growth of the first primary pin feather using a logistic function. The feather growth model was based on 865 observations from 264 nestlings in 69 nests, and following Sofaer et al. (2013a), included nest and nestling-level random effects to account for the lack of independence between siblings and repeated measures. The final model included these random effects on the inflection point parameter. We included fixed effects that estimated the difference between populations in the growth rate constant and in the inflection point, and estimated a fixed difference in the inflection point for younger asynchronously hatched nestlings. We had relatively little information on the asymptotic value of the length of the first primary feather and therefore did not include nest or nestling-level random effects on the asymptotic length. To minimize potential biases (Austin et al. 2011), we fixed the difference in the asymptote between populations to be 3% larger in Alaska, reflecting the average measured difference in adult wing length between populations. We set the value of the asymptote for California (the population for which data were available at a later age) at the fixed effect estimate based on a model without any random effects. Results were nearly identical when estimating, rather than fixing, asymptotic feather length. Nonlinear-mixed models were estimated using the nlme (Pinheiro et al. 2016) R package.

We note that the logistic curves we estimated are useful for understanding differences between populations in the growth rate constant and inflection point, but are not appropriate for inferring how populations may vary in their patterns of growth rate increase and decline surrounding the inflection point (i.e. patterns in the derivative of the growth curve). This is because the logistic curve is symmetrical – for a given curve, the increase in growth rate prior to the inflection point equals the rate of decline in growth rate after the inflection point. We visually aligned the inflection points of the growth curves from different populations to emphasize this symmetry. Martin (2015) hypothesized that birds with slower life history strategies maintain higher growth rates later in the nestling period, despite having lower peak growth rates. However, as both Martin (2015) and this study estimated growth rates using a logistic function, neither can appropriately test the proposed hypothesis. Instead, symmetry in the logistic curve means that a faster increase in the growth rate will necessarily be linked to a more rapid decline in the growth rate.

Comparison of 24-hour provisioning rates

To test the hypothesis that the differences in clutch and brood sizes between birds in Alaska and California reflected variation in food acquisition and delivery, we compared total and per-nestling provisioning rates over 24 h. For each variable, we tested for a difference between populations using linear mixed models. Nest identity was included as a random effect because some nests were videotaped at multiple ages (AK: n = 4 of 24 nests; CA: n = 9 of 20 nests). Each model included fixed effects of population, nestling age, brood size, a brood size by population interaction, and an age by population interaction. We included the potential for the latter interaction because of differences in nestling growth rate between populations (Sofaer et al. 2013a; Supplementary material Appendix 1 Methods). Models were fit in the lme4 package in R (Bates et al. 2014), and degrees of freedom and p-values were estimated using the Satterthwaite approximation in the lmerTest package (Kuznetsova et al. 2014).

Relationship between per-nestling provisioning and growth

For each nestling, we calculated the increase in mass (g), tarsus length (mm), and primary feather length (mm) over the 24-h video period (Table 1). We modeled the relationship between each measure of growth and per-nestling provisioning rates

Table 2. Estimated effects of per-offspring provisioning and other factors on offspring mass gain (g), tarsus growth (mm), and feather growth (mm) over 24 h. Population effects estimate differences in the responses of nestlings in California compared with Alaska, which was the reference level. All three measures of growth were positively related to per-nestling provisioning in Alaska, while the interaction between population and per-nestling provisioning decreased the slope of the per-nesting provisioning effect to near zero in the California population (i.e. the estimated interaction in each model was of similar magnitude, with the opposite sign).

Model	Effect	β ± SE	Statistic	p
Mass gain	Per-nestling provisioning rate	0.019 ± 0.004	$t_{85.6} = 4.69$	$p < 0.0001$
	Population × per-nestling provisioning rate	–0.021 ± 0.004	$t_{80.8} = -4.81$	$p < 0.0001$
	Population	–0.413 ± 0.253	$t_{28.2} = -1.63$	$p = 0.11$
	Stage	–0.185 ± 0.151	$t_{45.9} = -1.22$	$p = 0.23$
	Population × stage	0.534 ± 0.164	$t_{116.3} = 3.25$	$p = 0.0015$
	Brooding time	0.023 ± 0.022	$t_{28.6} = 1.03$	$p = 0.31$
	Asynchronous hatching	0.026 ± 0.075	$t_{133.24} = 0.35$	$p = 0.73$
Tarsus growth	Per-nestling provisioning rate	0.028 ± 0.004	$t_{128.9} = 6.88$	$p < 0.0001$
	Population × per-nestling provisioning rate	–0.033 ± 0.004	$t_{122.3} = -7.43$	$p < 0.0001$
	Population	–0.773 ± 0.299	$t_{39.5} = -2.59$	$p = 0.014$
	Stage	–0.777 ± 0.165	$t_{68.9} = -4.70$	$p = 0.0001$
	Population × stage	0.899 ± 0.158	$t_{145.5} = 5.68$	$p < 0.0001$
	Brooding time	0.024 ± 0.026	$t_{48.8} = 0.91$	$p = 0.37$
	Asynchronous hatching	0.029 ± 0.066	$t_{124.3} = 0.44$	$p = 0.66$
Feather growth	Per-nestling provisioning rate	0.024 ± 0.008	$t_{15.5} = 2.84$	$p = 0.012$
	Population × per-nestling provisioning rate	–0.026 ± 0.009	$t_{16.4} = -2.86$	$p = 0.011$
	Population	–0.723 ± 0.413	$t_{16.6} = -1.75$	$p = 0.098$
	Brooding time	0.007 ± 0.037	$t_{16.7} = 0.19$	$p = 0.85$
	Asynchronous hatching	–0.187 ± 0.159	$t_{90.0} = -1.17$	$p = 0.24$

using linear mixed models (Table 2). We included a random effect of nest to account for sibling relationships and shared per-nestling provisioning rates for birds in each nest at each age. We initially included a nestling random effect because most birds were measured over multiple intervals (i.e. 2–3, 5–6, and/or 6–7); however, this effect did not explain any variance in mass gain, tarsus growth, or feather growth and was removed from all models. Our models included fixed effects of population, per-nestling provisioning rate, the interaction between population and per-nestling provisioning rate, early versus late stage (nestling day 2–3 vs days 5–7), a population by stage interaction, whether or not the nestling hatched asynchronously (i.e. was younger that its siblings), and the number of hours spent brooding during the active portion of the day. The population effects test for a significant difference in the intercept between populations at the overall mean per-nestling delivery rate (63.7 bill-size equivalents per 24 h) because the delivery rate was centered prior to model fitting. Brooding time was included to test whether higher levels of brooding were associated with increased growth. Diagnostics on the feather growth model showed a poor fit to data from day 2–3, so this model was restricted to data from the late nestling period, and the stage effect and its interaction with population were excluded. As in the previous analysis, models were fit in lme4 and degrees of freedom and p-values were approximated using the lmerTest package.

Offspring mobility

Offspring functional performance provides an integrated measure of physiological condition and interacts with environmental conditions to shape individual fitness (Irschick and Garland Jr 2001). For juvenile birds, predation is the dominant source of mortality in the weeks after leaving the nest (Sullivan 1989, Yackel Adams et al. 2001), and predators can shape selection on offspring mass and mobility (Vedder et al. 2014). However, direct measurements of juvenile mobility in birds have focused on precocial species (Dial 2003). To understand the relationship between juvenile size and performance within and between populations, we measured fledgling jumping distance in the field and compared each individual's maximum jumping distance to its mass, tarsus length, and wing length. Fledglings were captured by hand on the day they left the nest in 2008 in Alaska (16 birds from 11 broods on day 9–10) and in 2009 in California (7 birds from 3 broods on day 12–14); 9 nestlings from 4 broods in California were taken from their nests on day 10, to account for differences in nestling period length and assess mobility at the same age that birds fledged in Alaska.

We constructed an apparatus to test jumping distance. A 120 cm long '2 by 4' piece of lumber (technically 1.5 by 3.5 inches) formed the base and was surrounded by plexiglass. A perch was inserted at a height of 17 cm. The lumber was evenly coated with texture spray and marked at 10 cm and 2 cm major and minor increments, respectively, with permanent marker. The plexiglass surrounding walls were taller in California than in Alaska to allow for higher jumps, but the perch height was consistent. A video recording was made as each juvenile bird was placed on the perch and jumped off (see Supplementary material Appendix 1 for an example video). Motivational measures such as tapping the plexiglass behind the bird, clapping, snapping, or moving hands, and if needed, gently poking the bird, were used to induce jumping. For each jump, distance was determined by taking a still photo from the video at the moment of landing, and using the program ImageJ to measure the distance from the perch to the bird's front foot. This quantification was done by two observers; for four birds processed by both observers without their knowledge, measured jumping distances were highly repeatable between observers (Pearson correlation: $r = 0.96$). Each bird jumped off the perch a median of five times (range 1–9 jumps), and the maximum distance jumped was used as a measure of jumping performance. A linear mixed model with a random effect of nest was used to test for differences in jumping distance among age and population groups (i.e. AK age 9–10, CA age 9–10, CA age 12–14). The relationships between maximum jumping distance and wing length, mass, and tarsus length were evaluated with a linear mixed model that included an effect of population and an interaction with each body size metric and population; these morphological measures were not too highly correlated to include in a single model ($r < 0.3$). Nest ID was included as a random effect. As before, models were fit in the lme4 package in R, and degrees of freedom and p-values were approximated using the lmerTest package.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.sk14mf2> (Sofaer et al. 2018).

Results

Clutch size, brood size, and nestling period length

Our study populations differed in offspring number and in nestling period length. Birds breeding in Alaska laid larger clutches (Fig. 1a; 4.96 ± 0.75 eggs, mode = 5 eggs, n = 77 nests) than those breeding in California (3.15 ± 0.68 eggs, mode = 3 eggs, n = 341 nests; $t_{414} = -22.65$, $p < 0.0001$). Clutch size declined seasonally ($t_{414} = -5.08$, $p < 0.0001$), and this decline was steeper in the Alaskan population, reflecting its shorter breeding season (population by day of year interaction: $t_{414} = 2.74$, $p = 0.006$). Similarly, brood sizes were larger in Alaska (Fig. 1b; 4.63 ± 1.15 nestlings, n = 67 nests) than in California (2.93 ± 0.80 nestlings, n = 240 nests; $t_{303} = -14.88$, $p < 0.0001$). Brood size did not decline seasonally ($t_{303} = -1.14$, $p = 0.25$) or show a population by date interaction ($t_{303} = -0.38$, $p = 0.70$). Nestling period length was shorter in Alaska (Fig. 1c; 9.54 ± 0.82 d, n = 39 nests) than in California (12.26 ± 0.68 d, n = 39 nests; $\chi^2_{df=4} = 65.10$, $p < 0.0001$).

Comparison of mass and feather growth curves

Nestlings in California had lower peak feather growth rates (Fig. 2b, d; difference in growth rate constant: $K_{diff} = -0.09 \pm 0.02$, $t_{597} = -5.81$, $p < 0.0001$) and later inflection points ($I_{diff} = 0.84 \pm 0.12$, $t_{597} = 6.98$, $p < 0.0001$) than nestlings in Alaska ($K = 0.79 \pm 0.01$; $I = 6.08 \pm 0.06$). This estimated shift in the inflection point of feather growth trajectories of slightly less than one day establishes that our 24-h data were not comparing growth rates at fundamentally different points along the growth curve (Supplementary material Appendix 1 Fig. A2). Specifically, during the late nestling stage we measured growth for two days in California in order to span the approximately 1-d shift in growth trajectories for both mass and feather growth (Fig. 2a–d). The greater difference in nestling period length, relative to growth trajectories, reflects the observation that birds in California remain in the nest until a later stage of growth and development. Curves were

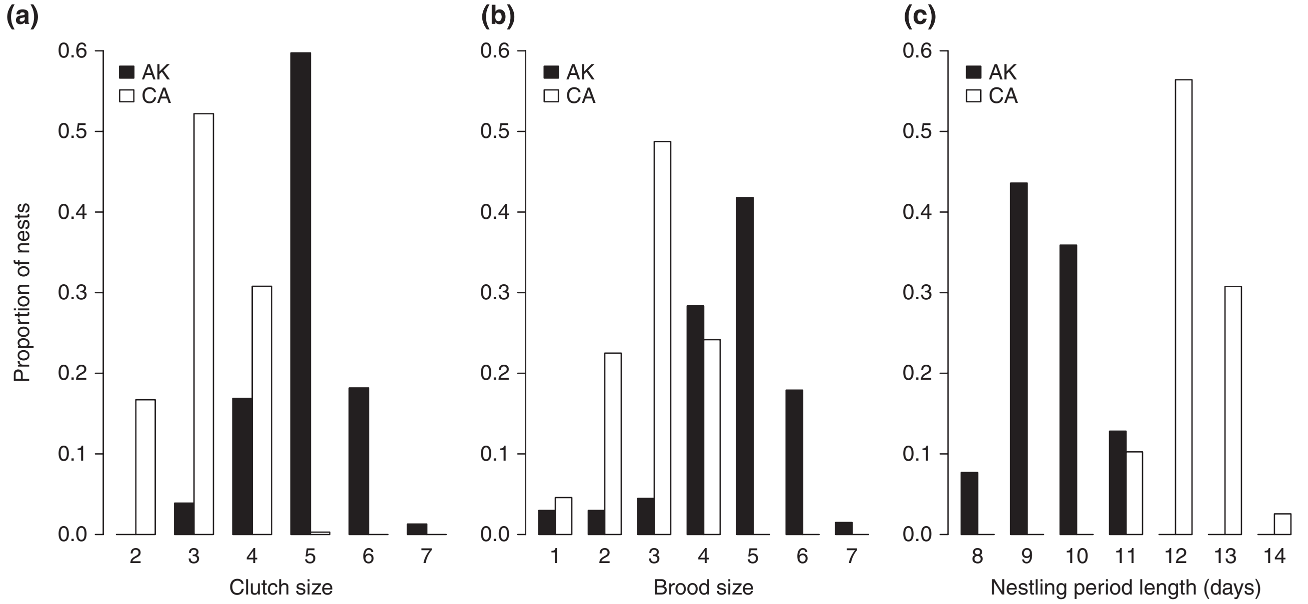

Figure 1. Birds breeding in Alaska had (a) larger clutch sizes, (b) larger brood sizes, and (c) shorter nesting periods than birds breeding in California.

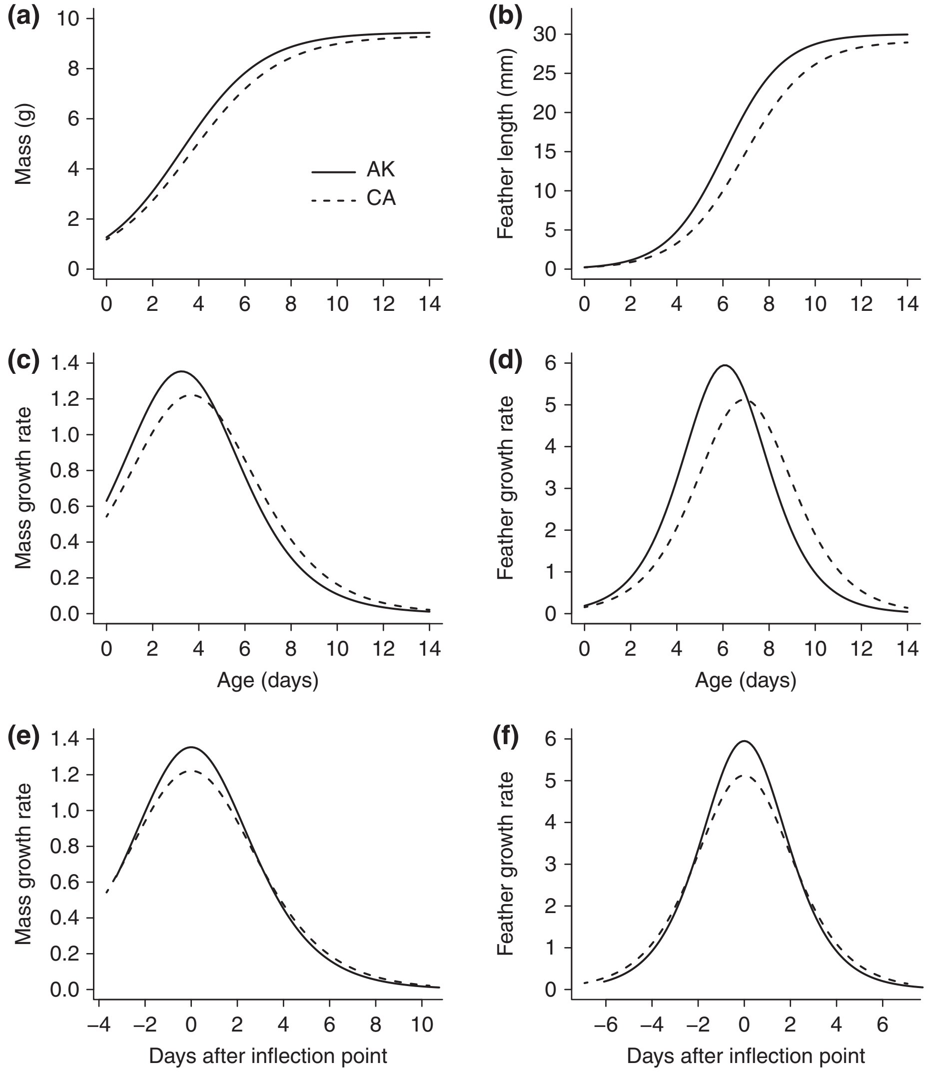

Figure 2. Growth trajectories for (a) mass gain and (b) feather growth in each population, and corresponding derivatives (c–d). Visualizing derivatives when inflection points are aligned (e–f) highlights symmetry in the logistic function. This symmetry means that a faster increase in the growth rate is necessarily associated with a faster decline, so that the apparent maintenance of a relatively high growth rate later in the nestling period for birds with a slower life history can arise simply due to constraints of the logistic function.

aligned by their inflection points to emphasize symmetry in the change in growth rate within the logistic function, i.e. the rate of increase in growth rate equals the rate of decline in growth rate (Fig. 2e–f).

Comparison of 24-hour provisioning rates

Birds breeding in Alaska fed their young for approximately 19 h per day, six hours more than birds breeding in California (Table 1). During each hour, parents in California made more trips to the nest (Fig. 3a), but brought less food per trip (Table 1), which may reflect the absence of avian nest predators in that study population (Peluc et al. 2008, Sofaer et al. 2013b). Over the 24-h period, the net result was that birds in the two study populations delivered a similar amount of total food per hour (Fig. 3b). Because of their smaller brood sizes, birds in California therefore had higher rates of per nestling food delivery during their active hours (Fig. 3c), but nevertheless had similar average per-nestling provisioning rates over the 24-h period (Table 1). Females brooded their young for many more hours per day in Alaska during both the early and late nestling period (Table 1).

Our mixed model of total food delivery showed that birds in Alaska and California brought more food to older nestlings ($\beta = 37.1 \pm 8.5$, $t_{49.0} = 4.36$, $p < 0.0001$) and to larger broods (Fig. 4a; $\beta = 47.6 \pm 14.7$, $t_{48.0} = 3.25$, $p = 0.0021$). Total food delivery did not differ strongly between populations ($\beta = 183.3 \pm 104.3$, $t_{53.3} = 1.76$, $p = 0.08$). The rate of increase in food delivery with increasing brood size did not differ between populations (population × brood size interaction term: $\beta = -37.7 \pm 23.3$, $t_{41.9} = -1.62$, $p = 0.11$), nor

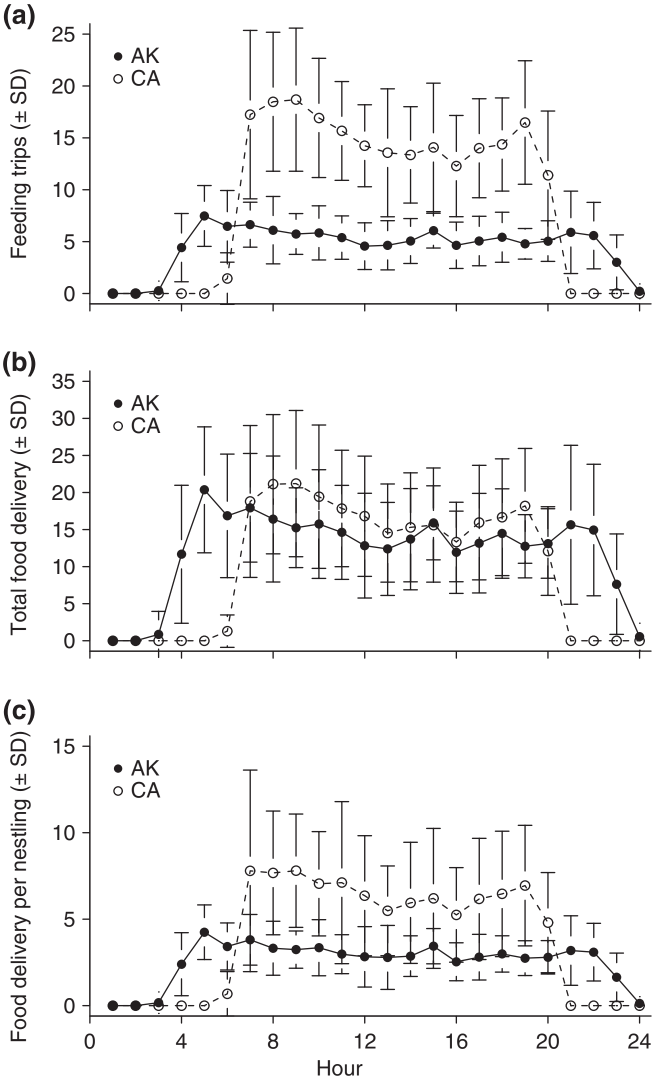

Figure 3. Twenty-four hour feeding patterns in Alaska and California. (a) Birds in California fed for fewer hours of the day but made more trips per hour. (b) Alaskan birds brought bigger food loads on each trip, making total hourly food delivery rates similar between populations. (c) During their active hours, food delivery per nestling was higher in California.

did the effect of increasing nestling age (population × age interaction term: $\beta = -8.4 \pm 10.6$, $t_{46.5} = -0.79$, $p = 0.43$).

Our model of per-nestling provisioning included a strong interaction between population and brood size. California birds fed larger broods at a lower per-nestling rate (Fig. 4b; $\beta = -33.2 \pm 7.1$, $t_{45.6} = -4.67$, $p < 0.0001$), and also had a higher intercept ($\beta = 81.5 \pm 31.9$, $t_{54.2} = 2.56$, $p = 0.013$). Older nestlings received more food ($\beta = 7.2 \pm 2.6$, $t_{51.0} = 2.78$, $p = 0.0077$); this effect tended to be stronger in California compared to Alaska ($\beta = 5.5 \pm 3.2$, $t_{49.2} = 1.70$, $p = 0.096$). There was no main effect of brood size on per-nestling provisioning rate ($\beta = -1.9 \pm 4.5$, $t_{50.3} = -0.43$, $p = 0.67$).

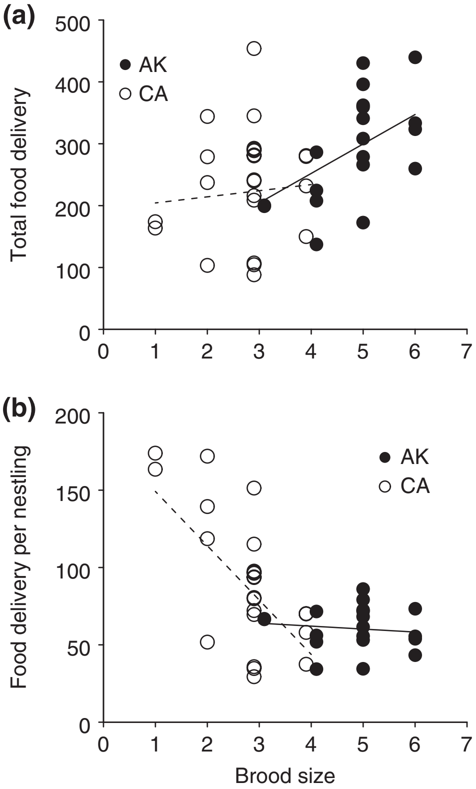

Figure 4. (a) The relationship between total provisioning rates and brood size differed between populations. (b) Per-nestling food delivery decreased sharply with brood size in California, but not in Alaska. Data are shown for the late nestling stage, with each point representing a 24-h period for a single nest. For better visibility, points were shifted horizontally where brood sizes overlap between populations. Lines were fit based on estimates for nestling day 5–6.

Relationship between per-nestling provisioning and growth

The consequences of variation in per-offspring provisioning for offspring growth differed between populations (Fig. 5). In Alaska, nestlings that received more food grew more quickly over the 24-h period, whereas in California a three-fold difference in per-nestling provisioning rates was not associated with faster growth. In each of our models, this pattern was manifested as a positive main effect of per-offspring provisioning rate on growth, along with a population by per-offspring provisioning rate interaction that decreased the slope in California to near zero (Table 2). Relative allocation to feather growth was also higher in Alaska: for a given amount of mass gain, older nestlings in Alaska showed greater growth in their first primary pin feather over 24 h (Supplementary material Appendix 1 Fig. A3).

Offspring mobility

On their fledge day, birds in Alaska could jump farther than nestlings in California of the same age (Fig. 6; nestling day 9–10; AK: 40.1 ± 15.6 mm, n = 16; CA: 20.3 ± 8.7 mm,

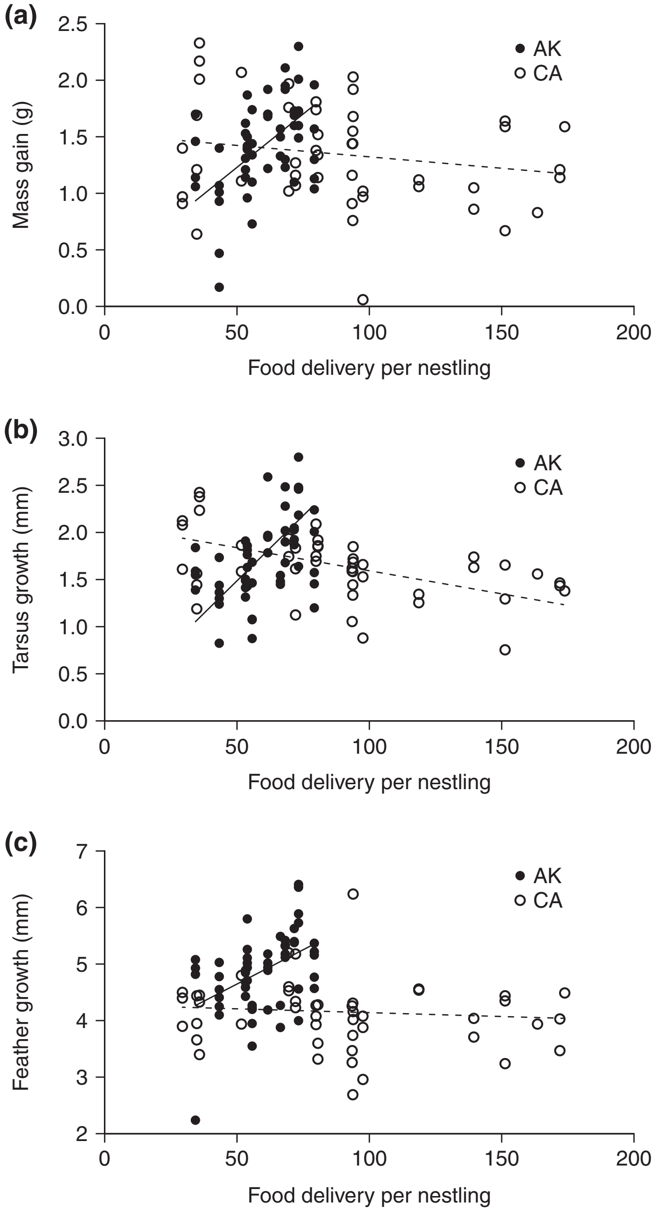

Figure 5. Over a 24-h period, higher per-nestling provisioning rates were correlated with greater (a) mass gain, (b) tarsus growth, and (c) feather growth of nestlings in Alaska but not of those in California. Each point represents a single nestling, and nestmates occur in vertical rows due to their shared per-nestling provisioning rate; our analysis included a random effect of nest to account for this lack of independence. Lines were fit based on model estimates for the late nestling stage.

n = 9), but not compared to fledglings in California, which left the nest at an older age (day 12–14; 49.5 ± 5.9 mm). The linear mixed model supported differences in mobility on day 10 between populations ($\beta = -21.4 \pm 7.1$, $t_{11.5} = -3.03$, p = 0.011), but not fledge day differences between Alaska (day 9–10) and California (day 12–14; $\beta = 8.4 \pm 7.9$, $t_{11.2} = 1.06$, p = 0.31). Wing length had a positive effect on offspring jumping distance (Fig. 6; $\beta = 4.04 \pm 0.96$, $t_{10.2} = 4.23$, p = 0.0017); the effect of wing length did not differ between populations ($\beta = 2.17 \pm 2.06$, $t_{18.4} = 1.05$, p = 0.31) and there was no additional difference between populations ($\beta = -55.64 \pm 140.12$, $t_{20.0} = -0.40$, p = 0.70). Thus, mobility was explained by wing length. Neither mass ($\beta = -6.89 \pm 4.45$, $t_{20.8} = -1.55$, p = 0.14) nor tarsus ($\beta = -3.40 \pm 5.16$, $t_{17.2} = -0.66$, p = 0.52) was related to maximum jumping distance via main effects or interactions with population (interaction terms: $\beta = 13.50 \pm 7.88$, $t_{23.0} = 1.71$, p = 0.10; $\beta = -7.57 \pm 9.95$, $t_{21.0} = -0.76$, p = 0.46).

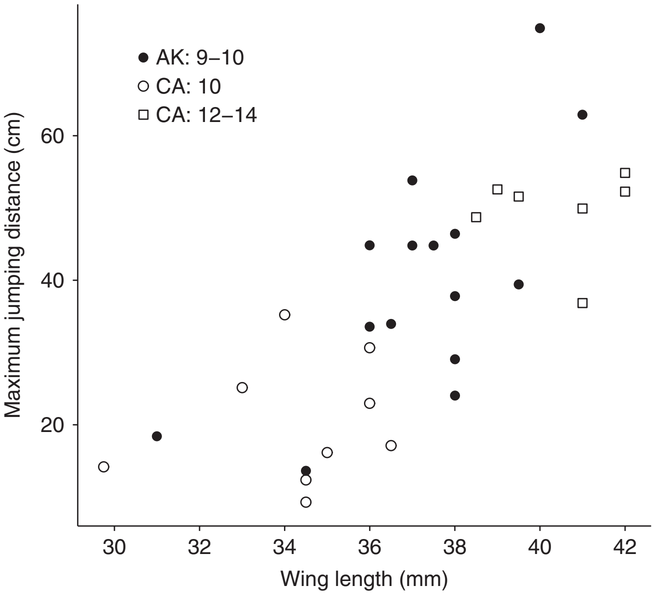

Figure 6. Wing length was correlated with maximum offspring jumping distance across populations and ages.

Energetic and nutritional content of insect larvae

Larvae collected from deciduous plants in Alaska contained nearly 50% less fat than those collected from oaks in California (these are the primary foraging substrates for *O. celata* at each location; Fig. 7a; AK: 12.3 ± 1.0 percent fat, n = 5; CA: 23.2 ± 1.4 percent fat, n = 4). By contrast, the percentage of protein and ash was higher in Alaska (57.4 ± 1.6 percent protein, n = 6; 7.5 ± 0.4 percent ash, n = 5) than in California (52.0 ± 0.6 percent protein, n = 4; 4.8 ± 0.3 percent ash, n = 3). Because fat has high caloric density, samples from Alaska averaged approximately 10% fewer calories per gram of dry matter than those from California (Fig. 7b; AK: 5314 ± 109 cal g^{-1}, n = 6; CA: 5902 ± 99 cal g^{-1}, n = 4). The percentage of gross energy deriving from protein was therefore higher in Alaska (Fig. 7c). The composition of a single sample of larvae collected from spruce trees, an infrequently used foraging substrate in Alaska, was more similar to the larvae collected in California than to larvae collected from deciduous plants in Alaska (Fig. 7b, c); this sample was only large enough to measure caloric and protein content.

Our measures of larval nutritional composition were highly correlated; excluding the single sample from spruce,

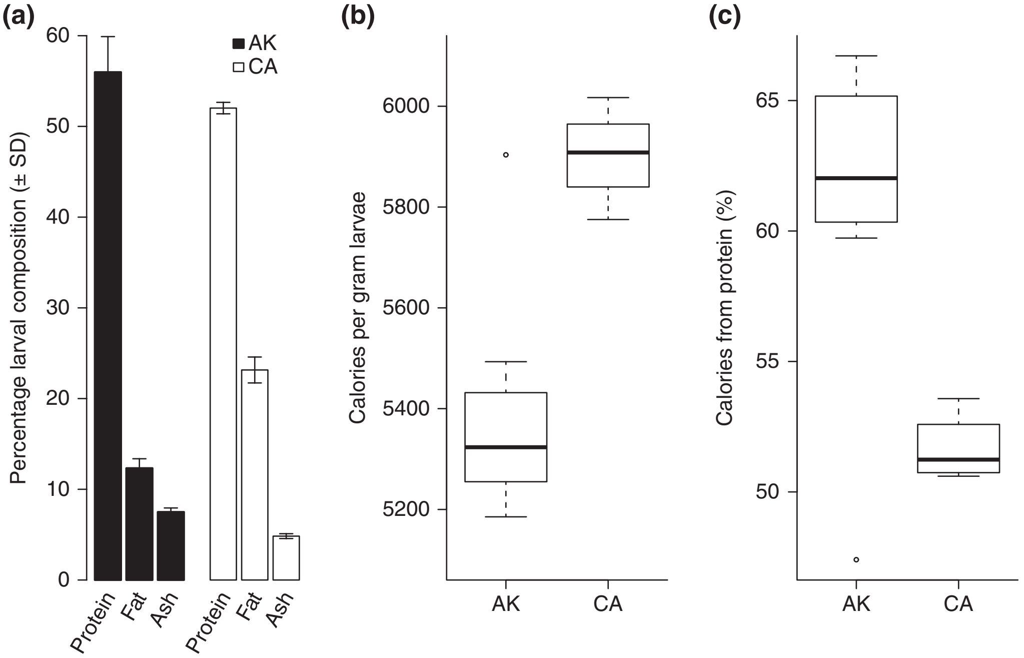

Figure 7. Insect larvae collected in Alaska had (a) higher protein content, lower fat content, and higher ash content than insects collected in California, (b) lower energetic content per gram of dry matter, and (c) a greater percentage of calories deriving from protein. In Alaska, the outlier in (b) and (c) was a sample collected from spruce trees, while other samples were collected from deciduous vegetation.

caloric density was positively correlated with percent fat ($r = 0.93$) and negatively correlated with percent protein ($r = –0.95$) and percent ash ($r = –0.95$). We therefore used a t-test assuming unequal variances to compare the energetic content (cal g^{-1}) of larvae collected in Alaska and California, rather than conducting a multivariate analysis. Based on all samples, larvae collected in Alaska had significantly lower energetic content than those collected in California (AK ± 1 SD: 5398 ± 244 cal g^{-1}, n = 7; CA: 5902 ± 99 cal g^{-1}, n = 4; $t_{8.5} = –4.82$, $p = 0.0011$); excluding the single spruce sample from Alaska increased the difference between the population means ($t_{7.0} = –8.85$, $p < 0.0001$).

Discussion

Avian life histories reflect hierarchical relationships between 1) the ability of parents to acquire resources, 2) how parents allocate resources to reproduction and partition them among offspring, and 3) how offspring allocate those resources to growth, development, and maintenance. Historic hypotheses for the causes of latitudinal life history variation emphasized the constraint of food delivery on brood size (Lack 1947, Skutch 1949, Ashmole 1963), while more recent work recognizes the linkages between parental and offspring acquisition and allocation (Kindsvater et al. 2010, Martin 2015). Our results support the assertion that variation in resource acquisition alone cannot explain geographic variation in clutch and brood sizes, even within a single species. Twenty-four-hour video recordings showed that despite longer days and larger brood sizes in Alaska, total food delivery was similar between populations. Small broods in California therefore received more food per nestling (Fig. 4b). Time spent brooding by females was far higher in Alaska (Table 1), results that do not simply reflect variation in temperature (Yoon et al. 2017). Consequences for nestlings also differed: nestlings in Alaska that received more food grew more quickly, whereas those in California did not (Fig. 5). Nestlings in Alaska also exhibited faster feather growth for a given per-offspring provisioning rate (Fig. 5c) and a given amount of mass gain (Supplementary material Appendix 1 Fig. A3). Faster feather growth enabled nestlings in Alaska to have longer wings and higher mobility at age 9–10 (Fig. 6), when birds in Alaska fledged but those in California remained in the nest (Fig. 1c). Finally, the nutritional content of insect larvae differed between populations (Fig. 7), suggesting the potential for food quality to contribute to geographic variation in avian life histories. Our results highlight the need for an integrative and multidimensional view of both parental care and offspring growth and development; despite the long-standing focus on food delivery, provisioning rates alone provide an inadequate view of parental expenditure and its consequences for offspring.

Nestling provisioning and growth

How offspring grow in response to variation in nestling resource acquisition provides a window into nestling allocation patterns. We found that higher per-nestling provisioning rates had a positive effect on the growth of nestlings in Alaska but not in California (Fig. 5). The lack of a positive growth response to per-nestling provisioning in California is surprising because food limitation is thought to underlie most variation in growth within populations (Ricklefs 1976, Konarzewski et al. 1996, Schew and Ricklefs 1998, Searcy et al. 2004, Killpack and Karasov 2012, Bowers et al. 2014). Potential factors driving differences in the relationship between food delivery and growth between populations include delayed growth responses, higher maintenance costs, higher thermoregulatory costs, and/or lower food quality. Hatchling size, asymptotic mass (Sofaer et al. 2013a), and mean ambient temperature (Yoon et al. 2017) were similar between our study populations. However, nestlings' thermal environments differed, as females in California spent much less time brooding (Table 1). Our models of growth did not support a brooding effect within populations (Table 2), but the much lower brooding rate in California may mean nestlings there invest more energy in thermoregulation at the expense of growth. Brooding represents an underappreciated dimension of variation in parental expenditure, as providing thermal energy is energetically costly (as has been shown during incubation; Nord and Williams 2015), and differences in brooding did not simply reflect weather conditions (Yoon et al. 2017). Quantifying variation in nestlings' thermal maintenance costs across geographic gradients is critical, as intrinsically slow growth rates may promote offspring quality, while slow growth arising from the thermal environment should not. Both intrinsic and extrinsic factors have been shown to contribute to variation embryonic growth (Martin et al. 2013).

Food quality is another underappreciated potential driver of geographic variation in avian life histories. We documented higher protein and mineral (i.e. ash) content in larvae collected in Alaska, and higher caloric and fat content in larvae from California (Fig. 7). The consistency of these patterns and the implications of these differences remain speculative, as the factors limiting growth are poorly understood for insectivorous birds. For example, insectivorous diets are thought to have a surplus of protein (Ricklefs et al. 1998). However, dietary supplementation with fat led to slower growth and a longer nestling period in a wild insectivorous songbird (Johnston 1993), patterns consistent with observations in California where insect larvae contained more fat. Specific dietary elements such as protein, calcium, key amino acids, and tannins are known to influence avian growth (Perrins 1976, Tilgar et al. 2004, Urdaneta-Rincon and Leeson 2004). However, few studies have explored variation in food quality along geographic gradients, between habitats, and across seasons (Wilkin et al. 2009, Arnold et al. 2010). In addition, it is unclear whether variation in food nutritional content can drive adaptive divergence in allocation to growth versus maturation or maintenance. Rapid growth may be facilitated by higher protein and mineral content of available food, a strategy consistent with observations in Alaska, whereas physiological maturation or maintenance (e.g. thermoregulation) relies primarily on energetic inputs (i.e. calories, rather than protein and minerals).

Our work is not the first to find that provisioning and growth rates are not consistently proportional, and previous studies have pointed towards adaptive variation in nestling growth. Comparisons among species have found slower growth was associated with higher provisioning rates (Saether 1994), and high nest predation was correlated with both low provisioning and rapid growth (Ferretti et al. 2005, Martin et al. 2011, Martin 2015). Birds at high latitudes may grow more quickly than those at lower latitudes (Starck et al. 1995, Remes and Martin 2002), but per-nestling provisioning rates are higher in tropical and subtropical regions (Martin et al. 2000, Martin 2015). Artificial selection in poultry has demonstrated the evolutionary capacity for more rapid and efficient growth by increasing mass gain per calorie consumed (Emmerson 1997), but in both poultry and natural populations, rapid growth can be associated with decreased individual quality (Arendt 1997, Bayyari et al. 1997, Metcalfe and Monaghan 2003, Dmitriew 2011). Given high adult survival rates (Sofaer et al. 2014) and strong intraspecific competition (Horton et al. 2010, Yoon et al. 2012) in our insular California population, relatively slow growth could reflect the prioritization of physiological quality compared to birds in Alaska. Yet despite consistent findings that tropical, subtropical, southern hemisphere, and island birds invest more heavily in each offspring than their counterparts in north temperate and mainland areas (Young 1996, Martin et al. 2000, Russell 2000, Tarwater and Brawn 2010, Covas 2012), corresponding gradients in individual quality are less clear.

Martin (2015) proposed adaptive divergence in growth trajectories, with birds with slower life history strategies maintaining faster growth rates late in the nestling period. Tests of this hypothesis should not be based on symmetrical nonlinear functions such as the logistic (Fig. 2). The logistic curve is symmetrical around the inflection point, meaning that a faster increase in the growth rate will necessarily be linked to a faster decline in the growth rate. Apparent higher growth rates later in the nestling period (Fig. 2c–d; Martin 2015) arise from shifts in the inflection point; growth rates during the later nestling period are similar when inflection points are aligned (Fig. 2e–f). Similarly, the average of the derivative of a logistic function, taken over the entire growth period, has been used as an overall measure of growth rate that can be compared between species (Martin 2015). However, symmetry in the logistic function will constrain these averages to be similar when summarized over most (or all) of the growth period; averaged feather growth rate from 0–14 d differed little between our study populations (AK: 0.581; CA: 0.575). A summary that simply reflects the constraints of the logistic function should not be interpreted to indicate that overall growth rates are similar among populations. Recent work in avian growth has emphasized potential advantages of nonlinear functions beyond the logistic (Tjørve and Tjørve 2017); a more flexible approach allowing for asymmetry should be the basis of future comparisons of growth trajectories among populations and species.

Variation in offspring growth and performance

The fitness implications of offspring growth and development depend on ecological conditions. Predation is the major source of mortality for juvenile songbirds in the nest and shortly after fledging (Ricklefs 1969, Yackel Adams et al. 2001, Cox et al. 2014). There is a trade-off between leaving the nest at a later age and with greater mobility, at the cost of longer exposure to nest predation (Roff et al. 2005, Remeš and Matysioková 2016). Longer feathers improve juvenile mobility (Fig. 6; Chin et al. 2009), and studies have demonstrated evolution or plasticity in feather growth in response to pressure for earlier nest departure or higher post-fledging mobility (Miller 2010, Coslovsky and Richner 2011, Cheng and Martin 2012). A recent interspecific synthesis suggested that the higher per-offspring provisioning rates seen in tropical populations with slow life histories facilitates increased investment in feather growth, in turn allowing for higher mobility (Martin 2015). Our intraspecific comparison instead showed birds in the higher-latitude population in Alaska appeared to prioritize feather growth (Fig. 5c; Supplementary material Appendix 1 Fig. A3) and were more mobile at the same age (Fig. 6) than birds in California. These patterns were seen despite the higher daily nest predation rates in California (Sofaer et al. 2014; authors' unpubl), and suggest selective forces beyond nest predation (e.g. migratory phenology and distance) can also drive differences in allocation to feather growth among populations.

Resource acquisition and allocation in avian life histories

The life history traits we observe in nature – clutch size, growth rate, fecundity, and survival – reflect interactions between an organism's underlying allocation patterns and the ecological conditions it encounters. The expectation that resource acquisition and food availability alone explain geographic variation in life history traits therefore implies that populations or species do not dramatically differ in their life history strategies (i.e. their state-dependent allocation pattern), but evidence supporting such views is limited. In their seminal paper, van Noordwijk and de Jong (1986) predicted that variation in resource acquisition should dominate within populations, while allocation strategies should be more variable among populations. These predictions align well with the strong empirical support for Lack's hypothesis within populations (Slagsvold and Lifjeld 1988) and with the insufficiency of food availability as an explanation for life history variation among species (Martin et al. 2000, Martin 2004). Our comparison of two intraspecific populations found more rapid feather growth and earlier nestling mobility in the population with the faster life history strategy. Understanding nestlings' acquisition of thermal energy and of both calories and nutrients will provide a firmer basis for understanding variation and divergence in nestling allocation strategies.

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Supplementary material (Appendix JAV-01646 at <www.avianbiology.org/appendix/jav-01646>). Appendix 1.