

# Timing of Breeding Determines Growth and Development in a Long-Distance Migratory Bird

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## ABSTRACT

The timing of breeding can have significant consequences for adult and offspring fitness, yet our current hypotheses of seasonal timing focus on the parent perspective. When offspring survival is affected by timing of breeding, we expect to see offspring mechanisms to detect and respond to cues of seasonal timing. Avian embryos respond to photoperiod and seasonal cues during development and in this study we evaluate the influence of photoperiod and season on posthatching growth and development in Franklin's gull (*Leucophaeus pipixcan*). Early- and late-season chicks exposed to short and long photoperiods during development were reared under common garden conditions. Photoperiod had no effect on posthatching growth and development, but seasonal effects present in the egg (maternal egg effects or genetic) did influence posthatching growth and development. Late-season chicks grew body mass and primary flight feathers at faster rates than early-season chicks, which we hypothesize facilitates independence and readiness for migration. Growth rates are complex phenotypes and we propose a general growth model that incorporates delays in negative feedback systems regulating growth. We show that the timing of breeding programs intrinsic growth rates in offspring, which suggests that many of the metrics used to describe seasonal patterns of reproductive success may be biased. *J. Exp. Zool.* 325A:467–477, 2016. © 2016 Wiley Periodicals, Inc.

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## INTRODUCTION

Seasonal declines in reproductive success are well established and the effects of reproductive timing generally explain more variation in reproductive success than other metrics of reproduction such as fecundity, parent condition, or offspring size (Williams, 2012). The hypotheses proposed to explain seasonal patterns of reproduction can be broadly classified into two categories in which (1) factors extrinsic to the parent (e.g., food availability, temperature, predation risk) or (2) factors intrinsic to the parent (e.g., parental condition, age or experience, genotype) regulate reproductive timing and success. Both categories focus on consequences of timing of breeding on parental performance. However, offspring face the immediate consequences of parental decisions on the timing of reproduction. Therefore, we expect strong selection for offspring to be responsive to seasonal cues in ways that optimize their phenotypes given the timing of their birth. The perspective of offspring is not well integrated into our current understanding of reproductive timing.

Parental and offspring traits and fitness are closely aligned. For example, offspring growth and development are intrinsic properties of the offspring, which are used as a proxy for off-

spring fitness with consequences for future phenotypes (Metcalf and Monaghan, 2001, 2003; Jonsson and Jonsson, 2014). But offspring growth and development are also products of parental behaviors and condition, which are used to quantify parental investment and quality (Beamonte-Barrientos et al., 2010; Garcia-Navas and Jose Sanz, 2011; Estramil et al., 2013). However, if offspring are capable of responding to seasonal cues and optimize growth and development relative to their birth dates, we may misinterpret the factors that regulate seasonal variation in performance and overestimate the influence of intrinsic parental factors. For example, if selection has favored slow growth rates in late-season offspring, a study measuring these

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growth rates might interpret this pattern as poor parental provisioning, poor parental quality, or decreased food availability. Understanding the mechanisms that regulate seasonal variation in growth and development from both offspring and parent perspectives can provide a comprehensive interpretation of seasonal reproductive dynamics.

Growth and developmental rates exhibit considerable plasticity in natural populations and the variation can have long-term consequences on individual phenotypes. Early-life events may program or change subsequent growth trajectories (Huchard et al., 2014). For example, periods of reduced food availability, poor nutrition, or suboptimal temperatures can decrease growth rates, but some individuals may compensate (e.g., achieve faster rates of growth) at a later period if favorable conditions return. However, these changes in early growth rates can have long lasting effects on phenotypes (Metcalf and Monaghan, 2001; Dantzer et al., 2013). In species with discrete breeding seasons, offspring produced at different times within the season experience different conditions during development. For example, in Great tits (*Parus major*), the food available for nestlings is an insect larva that is highly seasonal, and the timing of hatching is functionally linked with realized growth rate and probability of survival (Visser et al., '98; Visser et al., 2006). Whether offspring produced at different times within the season can compensate or alter their growth trajectories to optimize for natal timing is not known. Furthermore, costs due to compensation or alternative development within season have not been identified. Finally, a mechanistic framework for understanding within-season regulation of growth has not been developed.

We make a comprehensive evaluation of within-season variation in offspring growth to address these gaps in knowledge. Here, we describe an experiment to evaluate the effects of season, specifically the timing of egg laying, and photoperiod on the posthatching growth of a migratory bird, Franklin's gull (*Leucophaeus pipixcan*). Franklin's gulls are seasonal breeders that migrate between breeding grounds in the northern great plains of North America and their wintering grounds along the western coast of South America (Burger and Gochfeld, 2009). Hence, offspring produced early versus late in the season face different temporal constraints on growth in order to complete development for migration soon after the end of the breeding season. We previously identified the ability of offspring to alter growth in response to season and photoperiod cues during embryonic development (Clark and Reed, 2012). During embryonic development, longer days and late-season egg environments resulted in faster developmental rates and smaller structural size at hatch than shorter days and early-season egg environments. It is unclear if these effects persist after hatching and in this study we quantify multiple aspects of chick growth from hatching to adult size in a common-garden experiment. This experimental approach allows us to focus on growth as an intrinsic

offspring phenotype while controlling for extrinsic factors such as parental provisioning or seasonal changes in the environment.

## MATERIALS AND METHODS

### Ethics Statement

All work was conducted in accordance with permits from North Dakota Game & Fish Department, U. S. Fish & Wildlife Service, and North Dakota State University Institutional Animal Care and Use Committee.

### Study Site, Egg Collection, and Artificial Incubation

To evaluate our hypothesis about the influence of season and photoperiod on posthatching growth, we collected freshly laid eggs from the beginning and end of the nest initiation period and artificially incubated them in the lab. We collected eggs from a Franklin's gull colony nesting at Rush Lake Waterfowl Production Area in north-central North Dakota (48.3817°N, 100.2199°W). We identified first-laid eggs from nests initiated early (i.e., within the first week of the nest initiation period in the colony when approximately 25% of birds had initiated laying) on May 8, 2010 (when there is approximately 14.6 hr of daylight) and late (i.e., within the third week of nest initiation when approximately 75% of birds had initiated laying) on May 24, 2010 (when there is approximately 16.3 hr of daylight), and collected those eggs determined to be freshly laid (i.e., within 24 hr of laying) based on the flotation method (Nol and Blokpoel, '83; Ackerman and Eagles-Smith, 2010). We moved eggs to the lab within 12 hr of collection where we measured size (i.e.,  $\pm 0.01$  g for mass using an electronic balance;  $\pm 0.1$  mm for length using digital calipers,  $\pm 0.1$  mm for breadth), let the eggs sit overnight, and the following morning randomly assigned them to clear plexiglass incubators (Brinsea, Products Inc., Somerset, UK) maintained at 37.5°C and 55% relative humidity. The incubators included egg turners and automatically rotated the eggs every hour for the first 20 days of incubation after which time we stopped the egg turners, increased relative humidity to 70%, and checked eggs daily for evidence of hatching. We placed each incubator in an environmental chamber that maintained either a 14:10 light:dark cycle (LD 14:10) or an 18:6 light:dark photoperiod cycle (LD 18:6) for the duration of the incubation period, which are the same photoperiod treatments used in a previous study (Clark and Reed, 2012) selected to simulate photoperiods experienced across the nest initiation period as well as the latitudinal breeding range. The environmental chambers maintained temperatures at 25°C and 25% relative humidity. We recorded time of hatching (within 4 hr) and measured mass ( $\pm 0.01$  g) and tarsometatarsus (henceforth tarsus) length ( $\pm 0.1$  mm) of newly hatched chicks, once they had dried from the hatching process (typically within 4–8 hr of hatching).

### Chick Rearing and Body Size Measurements

We reared all chicks under common conditions until approximately 40 days of age. Chicks were exposed to room lighting with a photoperiod of approximately LD 15:9, which is the approximate photoperiod experienced by the first chicks to hatch at the Rush Lake site. We reared chicks in warmed brooders maintained at 32°C for 4 days after hatching and maintained at 25–27°C thereafter (chicks were reared for approximately 40 days). We fed chicks moistened kitten food (Royal Canine Babycat 34; 34% minimum crude protein, 24% minimum crude fat, 3.5% maximum crude fiber, 4,406 kcal/kg) every 2–3 hr (from 0600 to 2000 hr; eight feedings for the first week after hatching and six feedings thereafter) until chicks indicated satiation by refusing more food. Franklin's gull chicks are semiprecocial at hatching, which required us to feed chicks by hand for approximately the first week after which the chicks were able to feed themselves. Chicks had continuous access to fresh water. Until chicks were 14 days old, we measured mass ( $\pm 0.01$  g) of each individual prior to each feeding, then again just after feeding to estimate the amount of food it consumed. To quantify both body and structure growth, we measured body mass ( $\pm 0.01$  g) and tarsus length ( $\pm 0.1$  mm) of chicks each morning prior to daily feedings.

### Primary Feather Area Measurement

We measured area of the primary flight feathers from digital images of the right wing taken at 3- to 4-day intervals for each chick. When chicks were 2–3 days old, we positioned the right wing on a flat board, which was covered with graph paper and to which a perpendicular edge was attached (i.e., similar to an extended wing rule), so that a digital image of the wing could be obtained from a camera fixed approximately 250 mm above the wing. We captured subsequent images of the right wing every 3–4 days until the chick was at least 30 days old. We used ImageJ analysis software (Rasband, '97; Abrámoff et al., 2004) to measure the primary flight feather area from the alula and anterior edge of the wing, along the posterior tips of primaries 1–10, and back to the alula ( $\text{mm}^2$ ).

### Statistical Analysis and Quantification of Growth

We checked for differences in size at hatching and development time due to effects of early versus late season, incubation photoperiod (LD 14:10 vs. LD 18:6), the interaction between season and photoperiod, and egg size using a general linear model with corresponding terms. Because previously it was shown that season and photoperiod affect embryonic development, specifically hatchling tarsus length and duration of the incubation period (Cooper et al., 2011; Clark and Reed, 2012), we included this analysis to distinguish hatchling differences that might confound our examination of posthatching growth.

We used a general linear model to statistically analyze the influence of early versus late season, incubation photoperiod,

and the interaction between early versus late season and photoperiod on metrics of chick growth and food consumption. However, terms for incubation photoperiod and the interaction term did not explain a significant amount of the variation for any dependent variable quantifying posthatching development, so for clarity we present only the results for a reduced general linear model with a term for early versus late season. Dependent variables included maximum daily exponential growth rates for mass and tarsus length, the ages at which maximum daily exponential growth rates for mass and tarsus occurred, mean rate of food consumption in the first 7 days posthatching, peak mass and the age at which peak mass was observed, median mass and tarsus length after age 35 days (which are equivalent to the asymptotic mass and asymptotic tarsus length, respectively), and growth rate of primary flight feather area. We computed daily exponential growth rates for mass ( $\text{GR}_{\text{mass}}$ ,  $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) as  $\text{GR}_{\text{mass}} = \ln\left(\frac{M_{\text{age}}}{M_{\text{age}-1}}\right)$ , where  $M_{\text{age}}$  is the mass at a given age (and  $M_{\text{age}-1}$  is the mass 1 day prior), and tarsus ( $\text{GR}_{\text{tarsus}}$ ,  $\text{mm}\cdot\text{mm}^{-1}\cdot\text{day}^{-1}$ ) as  $\text{GR}_{\text{tarsus}} = \ln\left(\frac{L_{\text{age}}}{L_{\text{age}-1}}\right)$ , where  $L_{\text{age}}$  is the tarsus length at a given age (and  $L_{\text{age}-1}$  is the tarsus length 1 day prior). We computed the rate of increase in daily food consumption ( $\text{g}\cdot\text{day}^{-1}\cdot(\text{day from hatch})^{-1}$ ) over the first 7 days posthatching from the slope of a linear regression of the observed daily food consumption by age for each individual (9–10 days after hatching, the amount of food consumed per day begins to plateau). All of the individual regressions explained over 80% of the variation in daily food consumption. We computed the growth rate of primary flight feather area ( $\text{mm}^2\cdot(\text{day from hatch})^{-1}$ ) from the slope of a linear regression of the primary flight feather area measurements obtained for each individual between ages 10 and 30 days posthatching. All of the individual regressions explained over 80% of the variation in primary flight feather area growth.

## RESULTS

We measured growth in 40 chicks hatched from first-laid eggs collected early and late in the season for the captive growth study. Hatching success exceeded 80% and did not vary with treatment group, and we selected the first 10 chicks that hatched from each of the four groups for inclusion in the growth study. Of the 40 chicks in the growth study, one died at age 17 days and was removed from all analyses. We had 19 chicks in the early-season treatment (10 chicks from the LD 14:10 photoperiod and nine chicks from the LD 18:6 photoperiod), and 20 chicks in the late-season treatment (10 from the LD 14:10 photoperiod and 10 chicks from the LD 18:6 photoperiod).

Size at hatching did not vary between early versus late season or incubation photoperiod, but chicks from early-season eggs took significantly more time to hatch than did chicks from late-season eggs. Over 60% of the variation in chick mass at hatching was explained by early versus late season, incubation photoperiod, the interaction between early versus late

season and photoperiod, and egg mass ( $F_{4,34} = 14.927$ ,  $P < 0.001$ ,  $r^2 = 0.637$ ), but only egg mass explained a significant amount of the observed variation ( $F_{1,34} = 0.001$ ,  $P = 0.972$ ,  $r^2 < 0.001$  for early versus late season;  $F_{1,34} = 0.015$ ,  $P = 0.904$ ,  $r^2 < 0.001$  for photoperiod;  $F_{1,34} = 0.046$ ,  $P = 0.831$ ,  $r^2 < 0.001$  for early versus late season  $\times$  photoperiod;  $F_{1,34} = 51.516$ ,  $P < 0.001$ ,  $r^2 = 0.560$  for egg mass). Approximately 30% of the variation in tarsus length at hatching was explained by early versus late season, incubation photoperiod, the interaction between early versus late season and photoperiod, and egg mass ( $F_{4,34} = 3.583$ ,  $P = 0.015$ ,  $r^2 = 0.297$ ), and only egg mass explained a significant amount of the observed variation ( $F_{1,34} = 1.404$ ,  $P = 0.244$ ,  $r^2 = 0.029$  for early versus late season;  $F_{1,34} = 1.109$ ,  $P = 0.300$ ,  $r^2 = 0.023$  for photoperiod;  $F_{1,34} = 0.552$ ,  $P = 0.463$ ,  $r^2 = 0.011$  for early versus late season  $\times$  photoperiod;  $F_{1,34} = 8.499$ ,  $P = 0.006$ ,  $r^2 = 0.176$  for egg mass). A power analysis indicated the differences in tarsus length at hatching between early versus late season and between photoperiod treatments would have been significant with a sample size of approximately 100 (consistent with previous findings (Clark and Reed, 2012), in which sample size was 80). More than 50% of the variation in time to hatch was explained by early versus late season, incubation photoperiod, the interaction between early versus late season and photoperiod, and egg mass ( $F_{4,34} = 8.567$ ,  $P < 0.001$ ,  $r^2 = 0.502$ ), because chicks from early-season eggs took significantly longer to hatch (mean and SE of  $24.7 \pm 0.34$  days) than chicks from late-season eggs ( $22.5 \pm 0.33$  days) ( $F_{1,34} = 21.09$ ,  $P < 0.001$ ,  $r^2 = 0.309$ ). Neither incubation photoperiod ( $F_{1,34} = 0.991$ ,  $P = 0.327$ ,  $r^2 = 0.015$ ), the interaction between early versus late season, and photoperiod ( $F_{1,34} = 2.058$ ,  $P = 0.161$ ,  $r^2 = 0.030$ ) nor egg mass ( $F_{1,34} = 2.246$ ,  $p = 0.143$ ,  $r^2 = 0.033$ ) explained a significant amount of the variation in time to hatch.

The pattern of increase in chick mass differed between early- and late-season eggs, and differed from the pattern of growth in tarsus. Chick mass increased with age to a peak before declining to a lower asymptotic level in chicks hatched from early-season eggs (Fig. 1a), but chicks hatched from late-season eggs increased mass with age before reaching an asymptotic level with no or only slightly discernible peak (Fig. 1a). Tarsus length increased with age before reaching an asymptotic level with no discernible peak for all chicks (Fig. 1b).

Maximum rates of exponential growth in mass and tarsus differed between chicks from early- and late-season eggs, as did the ages at which maximum growth rates were observed. A significant amount of variation in maximum growth rate of mass was explained by early versus late season ( $F_{1,37} = 21.910$ ,  $P < 0.001$ ,  $r^2 = 0.372$ ), with chicks from early-season eggs having significantly slower growth rates ( $0.26 \pm 0.0073$   $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) than rates from chicks hatched from late-season eggs ( $0.31 \pm 0.0071$   $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) (Fig. 2a). A significant amount of variation in maximum tarsus growth rates was also explained by early versus late season ( $F_{1,37} = 12.759$ ,  $P = 0.001$ ,

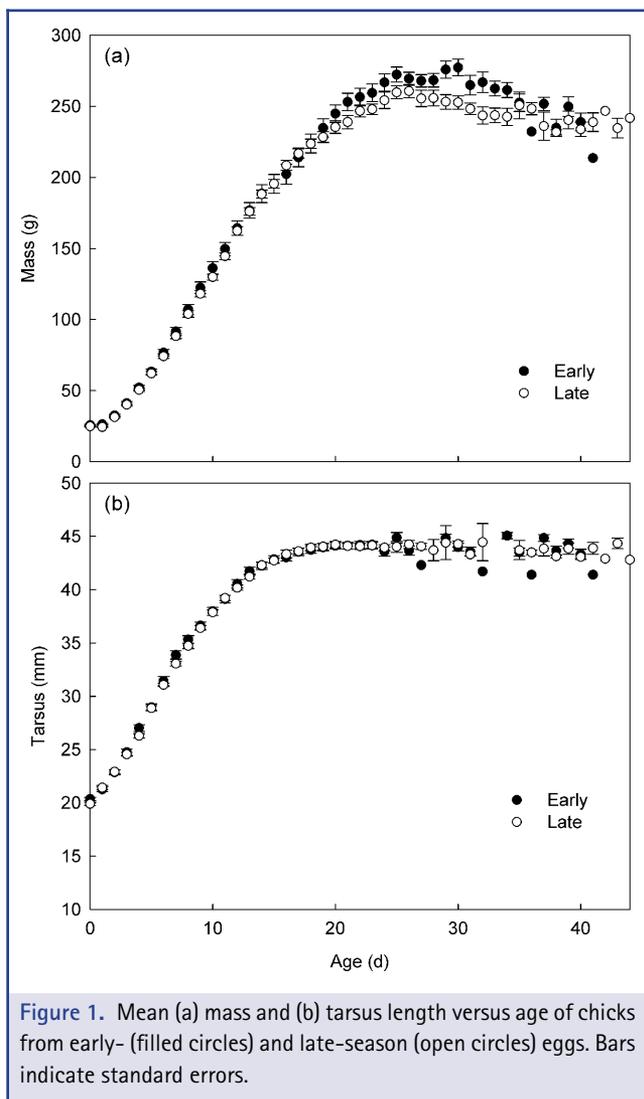
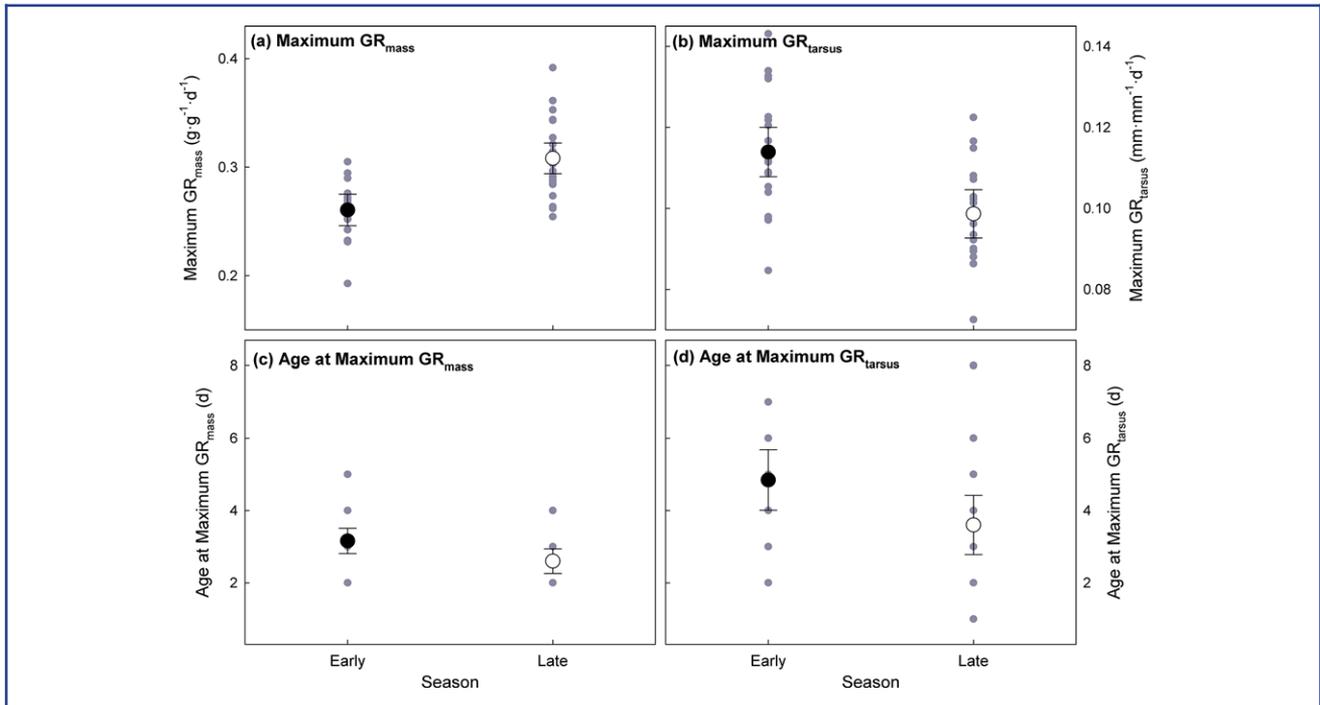


Figure 1. Mean (a) mass and (b) tarsus length versus age of chicks from early- (filled circles) and late-season (open circles) eggs. Bars indicate standard errors.

$r^2 = 0.256$ ). However, chicks hatched from early-season eggs had significantly faster tarsal growth rates ( $0.11 \pm 0.0031$   $\text{mm}\cdot\text{mm}^{-1}\cdot\text{day}^{-1}$ ) than chicks from late-season eggs ( $0.10 \pm 0.0030$   $\text{mm}\cdot\text{mm}^{-1}\cdot\text{day}^{-1}$ ) (Fig. 2b). Chicks hatched from early-season eggs also reached maximum mass growth rate at a significantly older age ( $3.16 \pm 0.174$  days from hatch) than chicks hatched from late-season eggs ( $2.60 \pm 0.170$  days from hatch) ( $F_{1,37} = 5.261$ ,  $P = 0.028$ ,  $r^2 = 0.124$ ) (Fig. 2c). Chicks hatched from early-season eggs also reached maximum tarsal growth rate at a significantly older age ( $4.84 \pm 0.419$  days from hatch) than chicks hatched from late-season eggs ( $3.60 \pm 0.408$  days from hatch) ( $F_{1,37} = 4.510$ ,  $P = 0.040$ ,  $r^2 = 0.109$ ) (Fig. 2d).

The rate of increase in daily food consumption with age differed between chicks from early- and late-season eggs. Early

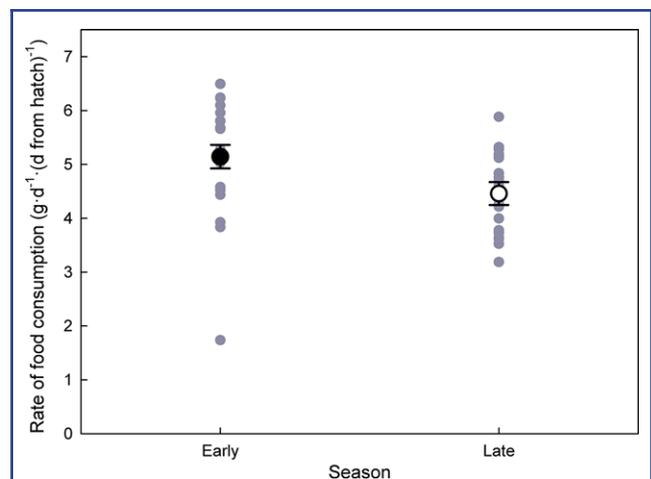


**Figure 2.** Maximum instantaneous growth rate was significantly (a) slower for mass ( $F_{1,37} = 21.910$ ,  $P < 0.001$ ,  $r^2 = 0.372$ ), but (b) faster for tarsus ( $F_{1,37} = 12.759$ ,  $P = 0.001$ ,  $r^2 = 0.256$ ) in chicks from early-season eggs compared to chicks from late-season eggs. However, the age at which the maximum growth rate was observed was significantly older for both (c) mass ( $F_{1,37} = 5.261$ ,  $P = 0.028$ ,  $r^2 = 0.124$ ) and (d) tarsus ( $F_{1,37} = 4.510$ ,  $P = 0.040$ ,  $r^2 = 0.109$ ) of chicks from early-season eggs compared to chicks late-season eggs. Observed values are shown with gray filled circles, with mean and 95% confidence intervals for chicks from early-season eggs indicated by filled circles with bars and from late-season eggs indicated by open circles with bars.

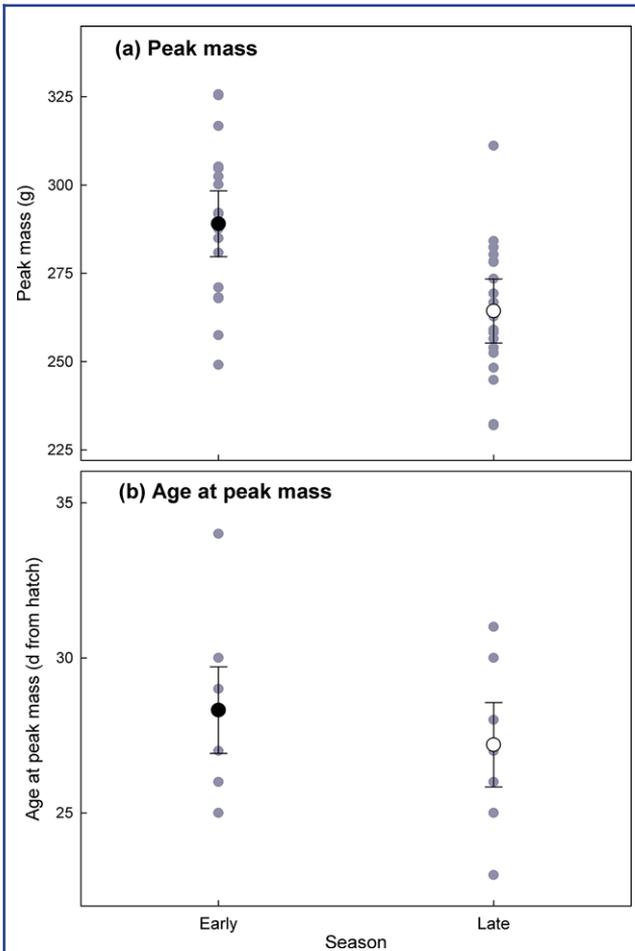
versus late season explained 12% of the variation in the rate of food consumption ( $F_{1,37} = 5.030$ ,  $P = 0.031$ ,  $r^2 = 0.120$ ) (Fig. 3), as chicks from early-season eggs consumed more food as they aged ( $5.14 \pm 0.219 \text{ g}\cdot\text{day}^{-1}\cdot(\text{day from hatch})^{-1}$ ) than chicks hatched from late-season eggs ( $4.46 \pm 0.213 \text{ g}\cdot\text{day}^{-1}\cdot(\text{day from hatch})^{-1}$ ).

The peak mass observed for chicks from early-season eggs was greater than the peak mass observed for chicks from late-season eggs, but the ages at which the peak mass was observed did not differ with season. Chicks hatched from early-season eggs exhibited a significantly greater peak mass ( $289.02 \pm 4.656 \text{ g}$ ) than chicks hatched from late-season eggs ( $264.34 \pm 4.538 \text{ g}$ ) ( $F_{1,37} = 14.419$ ,  $P < 0.001$ ,  $r^2 = 0.280$ ) (Fig. 4a). However, the age at which the peak mass was observed was not significantly different for chicks from early- and late-season eggs ( $28.32 \pm 0.700$  days from hatch for chicks from early-season eggs versus  $27.20 \pm 0.681$  days from hatch for chicks from late-season eggs;  $F_{1,37} = 1.307$ ,  $P = 0.260$ ,  $r^2 = 0.034$ ) (Fig. 4b).

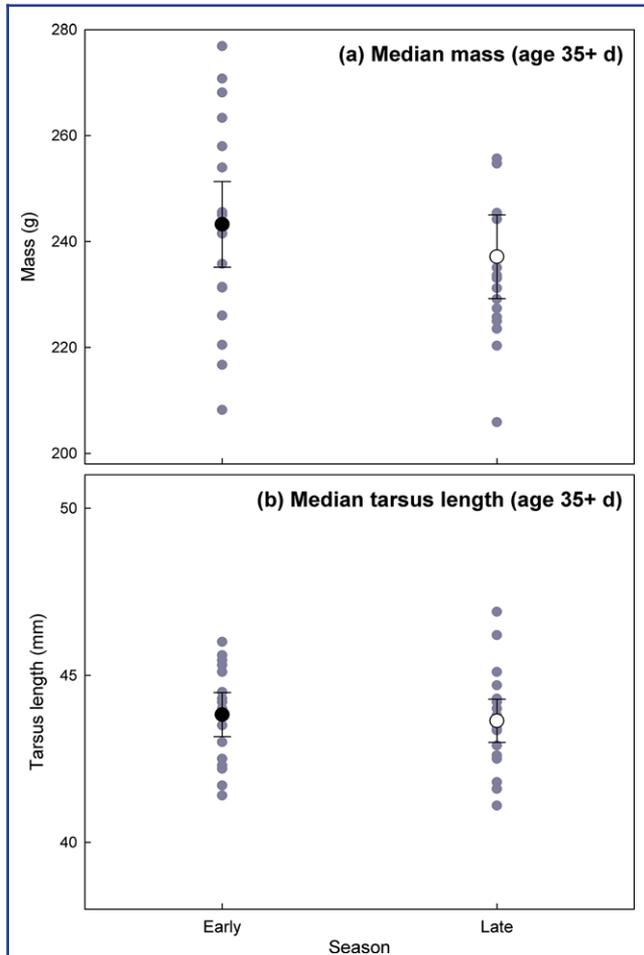
Asymptotic size of chicks, as measured by the median mass and tarsus length after age 35 days, did not differ between



**Figure 3.** Chicks from early-season eggs had greater rate of daily food consumption than chicks from late-season eggs ( $F_{1,37} = 5.030$ ,  $P = 0.031$ ,  $r^2 = 0.120$ ). Symbols as in Figure 2.



**Figure 4.** Chicks from early-season eggs had greater (a) peak mass than chicks from late-season eggs ( $F_{1,37} = 14.419$ ,  $P < 0.001$ ,  $r^2 = 0.280$ ), but (b) the age at which mass peaked did not differ between chicks from early- versus late-season eggs ( $F_{1,37} = 1.307$ ,  $P = 0.260$ ,  $r^2 = 0.034$ ). Symbols as in Figure 2.



**Figure 5.** Asymptotic size did not differ between chicks from early- versus late-season eggs for (a) mass ( $F_{1,37} = 1.167$ ,  $P = 0.287$ ,  $r^2 = 0.031$ ) or (b) tarsus length ( $F_{1,37} = 0.163$ ,  $P = 0.689$ ,  $r^2 = 0.004$ ). Symbols as in Figure 2.

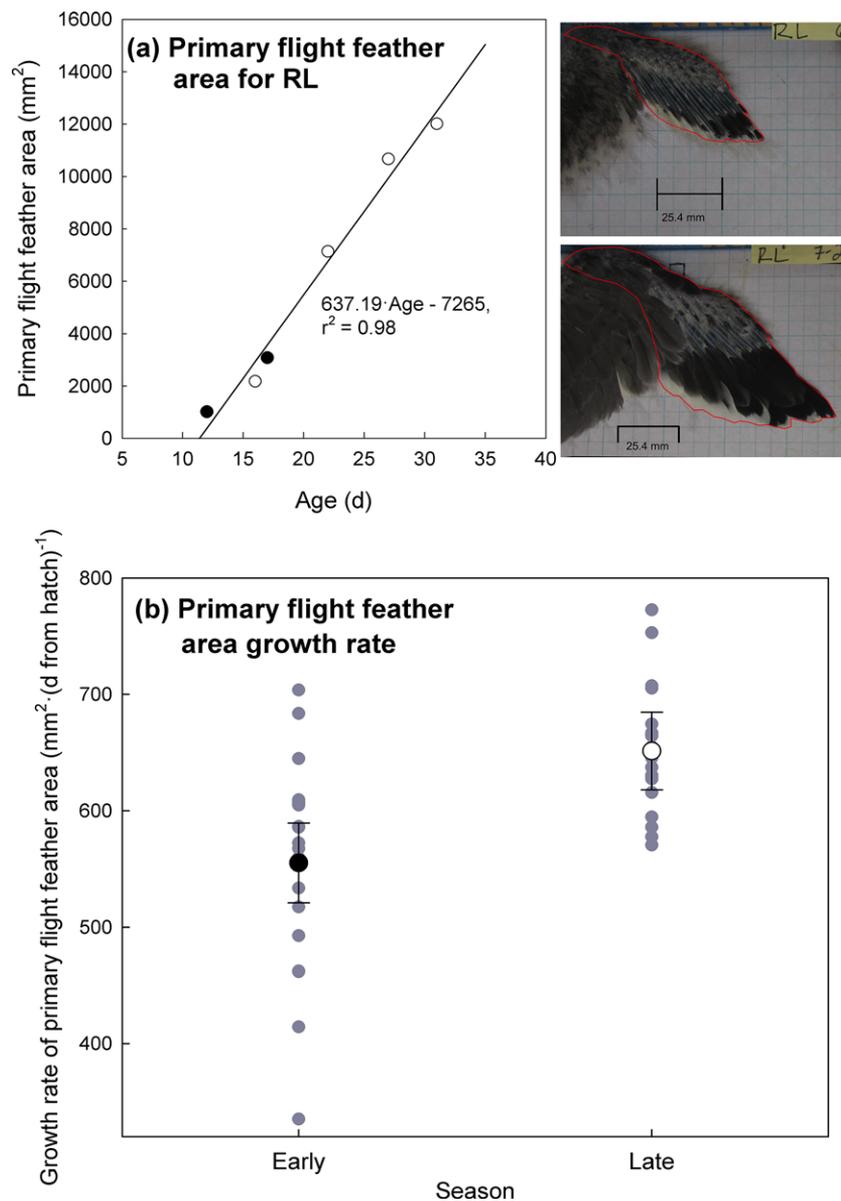
chicks from early- and late-season eggs. Median mass after age 35 days of chicks from early-season eggs ( $243.23 \pm 4.044$  g) was not significantly different from the median mass of chicks from late-season eggs ( $237.13 \pm 3.942$  g), with less than 4% of the variation explained by season ( $F_{1,37} = 1.167$ ,  $P = 0.287$ ,  $r^2 = 0.031$ ) (Fig. 5a). Similarly, less than 1% of the variation in median tarsus length after age 35 days was explained by season ( $F_{1,37} = 0.163$ ,  $P = 0.689$ ,  $r^2 = 0.004$ ), as median tarsus length after age 35 days did not differ between chicks from early- ( $43.82 \pm 0.331$  mm) and late-season eggs ( $43.64 \pm 0.322$  mm) (Fig. 5b).

The rate of increase in primary flight feather area with age differed between chicks from early- and late-season eggs. Early

versus late season explained 30% of the variation in the rate of primary flight feather growth ( $F_{1,37} = 16.144$ ,  $P < 0.001$ ,  $r^2 = 0.304$ ) from ages 10–30 days posthatching, as chicks hatched from early-season eggs accumulated primary flight feather area more slowly as they aged ( $555.15 \pm 17.116$  mm<sup>2</sup>·(day from hatch)<sup>-1</sup>) than chicks hatched from late-season eggs ( $651.24 \pm 16.682$  mm<sup>2</sup>·(day from hatch)<sup>-1</sup>) (Fig. 6).

## DISCUSSION

Results from our common-garden experiment indicate there is an early versus late seasonal effect on posthatching growth of Franklin's gull chicks. Chicks from early-season eggs grew differently from chicks from late-season eggs, but did not differ in their size at the age at which they fledged (Fig. 5). Differ-



**Figure 6.** Development of the wing estimated from the increase in area occupied by the primary flight feathers. Growth rate of the primary flight feather area for chicks age 10–30 days posthatch was determined (a) by the slope of the regression line for primary flight feather area estimated from digital images and age (inset images show the outlined primary flight feather area for an individual bird [RL] at ages 12 and 19 days, respectively, corresponding to the filled circles in the graph), and (b) significantly slower in chicks from early-season eggs than for chicks from late-season eggs ( $F_{1,37} = 16.144$ ,  $P < 0.001$ ,  $r^2 = 0.304$ ). Symbols as in Figure 2.

ences in chick growth were manifested in two distinct ways. First, chicks from early-season eggs overshot their asymptotic (fledging) mass, whereas late-season chicks did not (Figs. 1 and 3). Second, chicks from early-season eggs exhibited slower growth in mass and wing area than late-season chicks (Figs. 2

and 5), but had faster skeletal growth rates (Fig. 2). Surprisingly the faster growth rates in body mass of chicks from late-season eggs were not a function of increased daily food consumption; in fact, late-season chicks consumed less food per day in the first week after hatching than early-season chicks (Fig. 3). Pho-

toperiod and prehatching effects in eggs influence embryonic growth (Clark and Reed, 2012), and here we show that early versus late season but not photoperiod continue to affect growth through the juvenile period. Collectively, these data suggest that both pre- and posthatching growth are programmed at laying and lead to seasonal patterns in offspring growth.

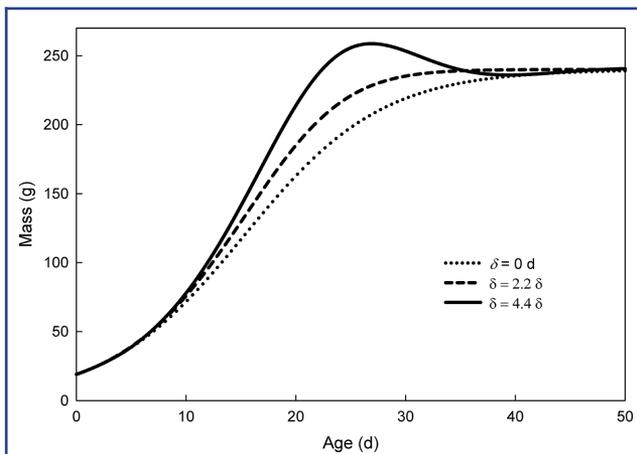
We propose two hypotheses to explain the mechanisms driving the observed early versus late seasonal differences in growth rate. One hypothesis is that there is a genetic component to the seasonal variation in growth rates. Additive genetic variance for the timing of breeding has been measured in a number of species (van der Jeugd and McCleery, 2002; Teplitsky et al., 2010; Kim et al., 2012; Gienapp et al., 2013, but see (Liedvogel et al., 2012). If growth rates and timing of breeding are heritable and natural selection favors early-season birds that produce slow growing offspring and late-season birds that produce rapidly growing and maturing chicks, the growth patterns we observed could evolve and be maintained through assortative mating based on timing of breeding. Growth rates are flexible and influenced by environments (e.g., food, nutrients, vitamins, temperature). However, growth rates also have heritable components and respond to selection as shown in a variety of domestic species. Heritability of growth rate has not been well documented in free-living species but is necessary to understand evolutionary contexts of growth. A second hypothesis (but not mutually exclusive to the genetic hypothesis) is that differences in early versus late seasonal growth patterns reflect changing maternal investments in eggs that allow plastic responses to the timing of breeding.

Reproductive investments in offspring often decline as the breeding season progresses. Most studies focus on clutch size as the measure of investment, and seasonal declines in clutch size are considered the result of changes in predation risk or food availability that make later hatching offspring less likely to recruit (Brown and Brown, '99; Cooper et al., 2005; Evans et al., 2009; Boulton et al., 2011). Seasonal variation in egg size has received less study (Arnold, '92; Encabo et al., 2001), but the general hypothesis is that egg size declines as the season progresses. As with clutch size, diminished investment in size or egg constituents is assumed to correspond to a reduced likelihood of recruitment by later hatching chicks. Among other measures of avian reproductive investment, maternally derived egg constituents (particularly hormones) have received the most attention, and these egg components are known to affect offspring growth (Schwabl, '96b; Lipar et al., '99; Lipar and Ketterson, 2000). These constituents also can exhibit a seasonal pattern. Testosterone levels in yolk are reported to decline with season in several species of birds (Schwabl, '96a; Pilz et al., 2003; Gil et al., 2006; Tobler et al., 2007; also see Müller et al., 2004). Female canaries exposed to longer day lengths produce eggs with lower levels of yolk testosterone than females exposed to shorter day length (Schwabl, '96a). Likewise plasma levels of thyroid hormones vary with photoperiod (Sharp, 2005; Nakao,

2009) and yolk thyroid hormones mirror maternal plasma levels (McNabb and Wilson, '97). The thyroid hormones and testosterone are of particular interest because they affect embryonic metabolism and growth (McNabb and Wilson, '97; Lipar and Ketterson, 2000). The mechanism by which maternal egg environments program growth is not clear at this time. Our study provides the first controlled experiment to determine the effects of the timing of breeding on posthatching chick growth. Our findings suggest that the relative contributions of genetic and maternal environments on seasonal patterns of growth in free-living species warrant further study.

An overshoot and decline to asymptotic mass soon after fledging has been observed in several other birds (Morbey et al., '99; Mauck and Ricklefs, 2005; Wright et al., 2006; Riou and Hamer, 2010; Sprague and Breuner, 2010), but has not been reported in gulls (Laridae). Hypotheses to explain the pattern of mass loss near fledging focus primarily on stored energy built as a buffering mechanism against (1) periods of fasting that arise due to variability in food resources or ability to forage or (2) the transition to independence with an accompanying decline in parental provisioning (Riou and Hamer, 2010). Recent studies have shown that chick mass loss coincides with changes in plasma hormone concentrations (e.g., corticosterone) and the onset of primary flight feather growth (Kozłowski et al., 2010; Sprague and Breuner, 2010), and may be regulated intrinsically by chick physiology (Kozłowski et al., 2010). In Franklin's gull, chicks achieve flight capability and parental feeding ceases at approximately 45 days after hatching (Burger, '72; Burger and Gochfeld, 2009). We observed peak masses at approximately 28 days after hatching (Fig. 4), which is consistent with hypotheses related to either fasting or reductions in parental care except chicks in our experiment neither fasted nor received reduced food ration. However, we also show that chick mass loss is related to the timing of egg laying, which is consistent with hypotheses of intrinsic regulation by physiological mechanisms of the chick (Kozłowski et al., 2010; Sprague and Breuner, 2010). Furthermore, we hypothesize that these physiological mechanisms are established through dynamics that occur at the time eggs are laid (i.e., maternal investments to eggs or genotype differences) and differ with the timing of laying.

The loss in mass we observed did not coincide with primary flight feather growth. In Franklin's gull, primary flight feather growth begins approximately 1 week after hatching, and chicks from early- and late-season eggs exhibit substantial feather growth prior to 28 days from hatch (Fig. 6) when mass peaks. This is in contrast to pelagic birds in which the mass loss begins with primary flight feather growth (Kozłowski et al., 2010). However, chicks from early-season eggs had significantly slower primary flight feather growth than chicks from late-season chicks (Fig. 6), and therefore completed wing feather development at older ages.



**Figure 7.** Asymptotic growth in mass simulated by a logistic differential equation in which the negative feedback response is delayed according to time  $\delta$ . A longer delay in the response to negative feedback corresponds to a greater peak in mass above the long-term, asymptotic mass. Curves correspond to the model  $\frac{dM}{dt} = 0.28 M(t) \left(1 - \frac{M(t-\delta)}{230}\right)$ , where  $M(t)$  is mass at age  $t$ .

We hypothesize that the slower accumulation of mass prior to age 28 days from hatch in early-season chicks facilitates a slower rate of primary flight feather growth and wing maturation compared to late-season chicks. Body mass is a measure of both size and energy storage, whereas skeletal length only measures size. We did not observe differences in tarsus length (i.e., size exclusively) between early- and late-hatched chicks (Figs. 1 and 5), so the contrast in peak mass between early- and late-season chicks (Fig. 4) may represent differences in energy storage or energy use. Energy reserves may permit a longer period of development for feathers or additional energy used to repair tissue damage from their rapid growth phase, but these hypotheses are yet to be evaluated.

Theoretical models of determinate growth in vertebrates assume a mechanism incorporating negative feedback. Mathematical models (e.g., the logistic equation) have been extensively developed to represent continuous, determinate somatic growth (Ricklefs, '68, '69; Edelman-Keshet, '88). In most models of growth, the effects of negative feedback occur instantaneously, resulting in patterns of growth in which size increases with age to an upper limit but does not increase above that limit (MacDonald, '78; Edelman-Keshet, '88). This contrasts with what we observed for mass in early-season chicks (Fig. 1a). Delay-differential equation models incorporate a delay term ( $\delta$ ) in the negative feedback response and can yield dynamics in which size increases to a peak before declining to an asymptotic level (MacDonald, '78; Edelman-Keshet, '88), with the characteristics of the peak related to the delay term ( $\delta$ ) as shown in Figure 7.

We propose this as a theoretical, mechanistic model to characterize growth in body mass of Franklin's gull, and that the timing of laying (i.e., season) programs the physiological sensitivity to negative feedback in chick growth in body mass. That is, chicks from early-season eggs have a delayed negative feedback on mass accumulation (i.e.  $\delta$  is negatively related to timing of reproduction) compared to chicks from late-season eggs.

Collectively our data show a pattern of slower growth in body mass and wing feathers in early-season chicks. Indeed, this pattern was previously observed even at the embryonic stage (Clark and Reed, 2012). In migratory birds, offspring produced late in the breeding season will have less time to complete development in preparation for migration than offspring produced early in the season. Rapid growth in flight feathers is presumably advantageous for the chicks of migratory birds. However, if there is a tradeoff between growth rate and tissue quality or repair mechanisms, this could explain the pattern of development we observed. We predict that measures of feather quality (e.g., fault bars, tensile strength) and developmental stress (e.g., oxidative tissue damage) are negatively correlated with growth rates of Franklin's gull chicks.

The intrinsic growth and developmental trajectories of late-season offspring may mitigate parent-offspring conflicts. Our data indicate that late-season chicks produced mass more efficiently than early-season chicks because they achieve faster mass growth rate even though they consumed less food per day. Franklin's gull adults leave the breeding site after either successful completion or nest failure and move to other wetlands before migrating in late October and early November (Burger and Gochfeld, 2009). Late-season parents are under tighter time constraints than early-season parents because they must balance the costs of rearing their current offspring with recovery from the breeding season, feather molt, preparation for migration, and future breeding attempts. The rapid and efficient development of late-season chicks would further reduce demands on parents breeding late in the season.

Growth is a complex trait and seasonal variation in growth is often interpreted in the context of seasonal variation in food availability, parental care, or other factors extrinsic to offspring. Our data suggest that the intrinsic way in which chicks are growing in early- versus late-season nests is programmed prior to hatching in Franklin's gull. Whether or not these differences in growth rate are adaptive remains to be evaluated, but our data indicate that offspring are responding to cues of season present at the time eggs are produced.

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## ETHICAL APPROVAL

All applicable institutional and national guidelines for the care and use of animals were followed (NDSU IACUC protocol A10067).

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