Day length, reproductive effort, and the avian latitudinal clutch size gradient

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Abstract. Explaining latitudinal patterns in life history traits remains a challenge for ecologists and evolutionary biologists. One such prominent pattern is the latitudinal gradient in clutch size in birds: the number of eggs laid in a reproductive bout increases with latitude in many species. One intuitive hypothesis proposes that the longer days at high latitudes during the breeding season allow parents to spend more time foraging each day, which results in greater total food delivery to the brood each day, and hence more offspring produced. This day length hypothesis is virtually untested, although it was proposed nearly 100 years ago. We developed a conceptual framework for distinguishing between the day length hypothesis and the widely accepted alternative hypothesis that attributes the latitudinal gradient in clutch size to increased per capita food resources at higher latitudes. Using this framework to contrast components of reproductive effort and life history patterns in a mid- and high-latitude Tree Swallow (*Tachycineta bicolor*) population provided clear evidence for the day length hypothesis, but little evidence for the alternative. Our findings suggest that the length of an animal's workday may be an important, but unappreciated, component of reproductive effort.

Key words: Ashmole's hypothesis; avian ecology; clutch size; day length; Lack's rule; latitudinal gradient; life history; Tachycineta bicolor; *Tree Swallow.*

INTRODUCTION

Early research on avian clutch size, the number of eggs laid in a reproductive bout, played a pivotal role both in developing modern life history theory and in clarifying thought about group vs. natural selection as a driver of adaptation (Lack 1947, Williams 1966). Life history theory pioneer David Lack was fascinated by one particularly enigmatic pattern, a near ubiquitous latitudinal gradient in avian clutch size, which reputedly motivated his thoughts about clutch size as adaptation. In a wide diversity of taxa in both hemispheres, clutch size increases with latitude, and this pattern is observed in both intraspecific and interspecific comparisons. The pattern of the latitudinal gradient in clutch size is striking for its generality across bird taxa, but is also present in many other taxa, including lizards (Forsman and Shine 1995), fish (Fleming and Gross 1990), mammals (Lord 1960), and turtles (Iverson et al. 1993). Although this major life history pattern has been recognized for over a century, its underlying ecological and evolutionary drivers are very poorly understood and remain contentious.

Several hypotheses for the latitudinal gradient in clutch size in birds have been proposed, indicating key roles for latitudinal gradients in nest predation (Skutch 1949, Martin et al. 2000), adult mortality (Ghalambor

and Martin 2001), and food resources relative to population density (Ashmole [1963]; now referred to as Ashmole's hypothesis). A recent comparative analysis suggests that although nest predation rates predict clutch size variation within regions (Martin et al. 2000), they do not appear to explain latitudinal patterns. The demographic data needed for a strong test of the adult mortality hypothesis are currently lacking, but an indirect test based on behavioral covariates of survival provides indirect support (Ghalambor and Martin 2001). Ashmole's hypothesis has received perhaps the widest support (Jetz et al. 2008, Griebeler 2010), but most of the evidence is based on large-scale comparative analyses that assess indirect proxies of food availability such as primary productivity and annual temperature variation. When distinguishing among these major hypotheses, it is important to note that Ashmole's hypothesis suggests both a general pattern—greater per capita food availability at higher latitudes—and a specific explanation for why the general pattern occurs: breeding populations are smaller at higher latitudes. Moreover, most of these studies examined interspecific clutch size patterns rather than differences across populations of the same species. Because both natural selection and the trade-offs that drive selection occur within, rather than across, species (Gustafson and Sutherland 1988), analysis of intraspecific patterns is needed for fully convincing support.

Surprisingly, one obvious hypothesis for the latitudinal gradient in clutch size has been largely ignored: the

day length hypothesis. Most birds feed their offspring, and given that food is often a key, proximate factor limiting clutch size, the latitudinal gradient in clutch size could be explained, in part, by the gradient in usable daylight during the breeding season (Hesse 1922, Lack 1947). Specifically, the longer days at high latitudes may allow parents to forage for more hours per day, gather more food per day for their young, and thereby support larger clutches. Despite its intuitive appeal, this hypothesis has received scant attention. After Lack suggested that, based on incomplete verbal reasoning, "some factor in addition to daylength must be concerned" (Lack 1968:167), it has been subject to only two empirical studies in 60 years (Hussell 1972, Sanz 1999). Both of these studies failed to find support for the day length hypothesis, but because they provide somewhat incomplete tests (as we will discuss), their negative results are not fully compelling.

By partitioning components of the total food parents deliver to their nest, we developed a conceptual framework that makes it feasible to disentangle the relative importance of day length and environmental food availability (Ashmole's hypothesis) as explanations for differences among avian populations in average reproductive output. We then used this framework to conduct a direct, quantitative test of both the day length and food availability hypotheses by comparing components of food delivery to offspring by Tree Swallows in two populations separated by 25 degrees of latitude. This contrast revealed that day length, but not general food availability, predicts the difference between the two populations in reproductive output, and thus suggests that day length should no longer be ignored as an important contributor to the latitudinal gradient in clutch size. Moreover, differences among populations in available day length have important implications for how we assess physiological processes such as growth; these need to be scaled to the organism's workday and not human clock time.

METHODS

Study system

We performed a comparative study of two populations of Tree Swallows breeding on private property adjacent to Elkhorn Slough National Estuarine Research Reserve on the central coast of California (36°91′ N, 121°45′ W) and on private land (Long Lake) near Wrangell-St. Elias National Park in eastern Alaska (61°22′ N, 143°18′ W). Tree Swallows are cavity-nesting, diurnal, aerial insectivores that forage almost continuously during daylight hours for the duration of the chick-rearing period (Rose 2009).

The California population consists of >80 pairs of Tree Swallows. They breed around brackish and freshwater ponds in nest boxes that were established in the late 1990s by the property owner. Habitat surrounding the boxes is mixed coastal chaparral and rangeland for cattle and horses. The Alaska population regularly consists of ~30 pairs of Tree Swallows breeding in 75 boxes established in 1991 on the margin of a freshwater lake four miles (~6.4 km) long. Habitat surrounding the boxes includes an open, mowed lawn and landing strip bordered by mixed forests of white spruce (*Picea glauca*), aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and black spruce (*Picea mariana*).

In each population we followed the nesting behavior and success of up to 47 pairs of birds each year for two breeding seasons, 2006 ($N = 47$ pairs for California, $N = 25$ pairs for Alaska) and 2007 ($N = 40$ pairs for California, $N = 29$ pairs for Alaska). Sample sizes are variable depending on the test performed and the year. Due to our inability to precisely age all chicks in 2006, results pertaining to chick growth and brood mass are based on data from 2007 only. Diet sampling was conducted in 2007. All other results are based on combined data from both 2006 and 2007.

Conceptual framework for partitioning effects of day length and food availability

The two hypotheses that we tested are both based on the total food supply brought to nests by parents, but because they differ in how this total food supply is obtained, they can be distinguished. According to the food availability hypothesis, there is more food available per individual at higher latitudes and, consequently, birds are predicted to feed their chicks at a higher rate (more food per hour). In contrast, the day length hypothesis predicts that the higher total food delivered to nests at high latitudes results from parents foraging more hours per day for their offspring, not that they provision at a higher hourly rate or bring back more food per visit. We developed a simple quantitative framework to distinguish the importance of these two critical predictions, and we describe how parents in each population might translate increased day length or resources into eggs and chicks, based on distinct components of parental effort. The day length and food availability hypotheses are not mutually exclusive, and our framework can be used to determine their relative importance. Moreover, although our framework enables a test of the general assumption of Ashmole's hypothesis—that there is more food per individual at higher latitudes—it does not address the specific population density mechanisms proposed by Ashmole. In other words, we use "Ashmole's hypothesis" to refer broadly to any mechanisms that could account for more food in the environment per individual at high latitudes. Thus, our study assesses whether food per individual varies with latitude, but not why it might differ.

We assume that Lack's optimal clutch size theory applies to the two study populations so that the total mass of chicks raised to fledging by a given pair of birds in each population is a function of the total mass of food delivered to chicks (Lack 1947). We focus on total brood mass, rather than the more traditional clutch size, because two factors indicate that food supply should

correlate with the total mass of offspring produced, not just clutch size. First, theory indicates that selection should act to optimize both the quantity (clutch size) and quality (individual mass) of offspring alive at the end of parental dependence (Smith and Fretwell 1974, Lloyd 1987). Second, many species, including Tree Swallows, show latitudinal gradients in both body size and nestling growth rates (McCarty 2001, Ashton 2002, Kilpatrick 2002). Our conceptual framework therefore focuses on understanding the factors that can explain differences between populations in both clutch size and average brood mass.

For any single pair of birds, we assume that their total reproductive output (total mass of chicks produced) is proportional to the total amount of food that the parents provide the brood over the nestling period. Considerable work on the energetics of growth in birds supports this assumption (e.g., Drent and Daan 1980). Where populations differ in the length of the nestling period, this time difference will have to be considered. However, in our study the time needed for parents to feed chicks to 90% of their maximum mass did not differ between populations (Appendix A), so we could ignore the length of the nestling period and focus on the total amount of food brought to the nest on an average day. We thus break down the total amount of food delivered to chicks in each population into three measurable components: the number of hours spent provisioning per day; the average number of provisioning visits (loads) per hour; and the average amount of food brought to the nest per visit (load size). Expressing this relationship as the ratios of the two populations (AK, Alaska; CA California) highlights three critical comparisons needed to differentiate between the day length and food availability hypotheses:

$$\frac{\text{AK brood mass}}{\text{CA brood mass}} \propto \frac{\text{AK load size}}{\text{CA load size}} \times \frac{\text{AK loads/h}}{\text{CA loads/h}}$$

$$\times \frac{\text{AK hours/d feeding chicks}}{\text{CA hours/d feeding chicks}}. \quad (1)$$

Thus, if the amount of daylight available for feeding chicks is the main factor limiting reproductive output, then the ratio of the average number of hours that birds in the two populations spend feeding their chicks each day should reflect the ratio of their reproductive output. In contrast, if greater food availability is the primary explanation, resource abundance limits clutch size or brood mass, and the ratios of load size and/or number of loads per hour between populations should singly or together equal the observed ratio in reproductive outputs. Alternatively, both hypotheses may partially explain the pattern in reproductive effort, such that the product of all three ratios equals that of reproductive output. If this product does not correspond to that of reproductive output, then alternatives to both the day length and the food availability hypotheses should be considered.

Egg and chick measurements

In both populations, nests were checked daily during the laying period. Near to hatching, nests were checked by mid-morning and then several times throughout the day in order to measure chicks as close to hatching as possible. Chicks were marked on the feet with indelible ink to allow identification of individuals prior to banding on day 12. Hatch day was considered to be day 1 of chick development, and all chicks were measured on day 1, 3, 6, 9, 12, and 15. Because automatic perch recorders needed to be transported to Alaska for use in that population before the California population had fledged, we had to use two different methods for determining fledging date. In California, a field assistant examined nests daily through the nest hole with a fiber-optic scope. Fledging was considered to have occurred either when a nest was empty the day after it contained a full brood, in the absence of signs of predation, or when less than half of the brood was found in a nest for two consecutive checks, and observations confirmed that adults were no longer feeding the chicks. Fledging for the Alaska population was determined by analyzing data from automatic perch recorders. As verified by visual checks, the fledging of one or more chicks was accompanied by a dramatic decline in the frequency of parental visitation to the nest, as measured by the perch recorders. Fledging date was, therefore, assigned to the date when visitations to the nest dropped by at least half in the absence of sign of predation.

Duration and rate of chick feeding

To accurately quantify the feeding rates and duration of the active period for pairs in both populations, we designed an automatic perch recorder (APR) device (see Plate 1). This is an inexpensive, battery-powered device that allows for the collection of long-term and accurate data on hourly rates of nest visitation, the duration of a pair's workday, and the total number of visits the pair makes to its nests throughout the nestling period. Essentially, this device is an easily tripped switch, attached to a perch that parents must touch when entering the nest box, attached to an event-recording data logger (for details on the design, functioning, and verification of accuracy of the device, see Rose 2009). McCarty (2002) showed that 95–98% of parental visits to Tree Swallow nests result in food delivery to chicks, thus allowing reliable translation of rates of nest visitation into rates that describe the number of times chicks are fed.

Load size

To determine the quantity of food that birds bring to their chicks each time they visit the nest, we modified a nest box trap designed by Quinney (1985; see Plate 1). This trap allowed us to capture birds with boluses of insects in their beaks as they returned to feed their chicks. When we were ready to capture birds, we set the Quinney trap after observing the departure of a parent. We then

hid next to the nest box underneath a camouflage tarp or in a fabric blind placed close to the box the previous evening. When a field assistant alerted us that one member of the pair had re-entered the box, we sprang up and reached into the box to grab the parent bird. We then quickly used forceps to remove the insect bolus, usually a discreet ball of insects held together with saliva. We preserved the boluses in 70% ethanol. We later dried them for 24 hours in a 60°C oven and weighed them on an electronic balance accurate to 10^{-6} g. We collected diet samples from at least one parent at each nest ($N = 21$ nests in Alaska, $N = 24$ nests in California). We trapped parents before noon on chick development day 6/7, 9/10, and 12/13. We only included samples in our analysis from birds that we were able to capture at least twice, giving us 50 samples from each population.

Fitting chick growth curves

Because logistic growth curves accurately describe chick growth in Tree Swallows (Zach and Mayoh 1982), we used an iterative, least-squares procedure in MAT-LAB to fit logistic growth curves for each nest to Ricklefs' equation:

$$M(x) = \frac{M(\infty)}{1 + \left[\dfrac{M(\infty) - M(0)}{M(0)}\right] e^{-Kx}} \qquad (2)$$

where x is the nestling age, $M(x)$ is chick mass at age x, $M(\infty)$ is the asymptotic or fledging mass, $M(0)$ is the mass at hatching, and K is the growth rate constant of the equation with units of 1/time (Ricklefs 1983). An average curve was fit for each nest, using measurements for all chicks in that nest. Comparisons of chick growth rates across populations were made using K values for all nests. Similarly, we compared the populations' brood masses at fledging using nest specific values of $M(\infty)$.

Measuring day length

One problem with past work on the day length hypothesis has been defining the duration of a day in a biologically relevant, non-arbitrary way. This is especially critical when considering subarctic and arctic areas, where large parts of the usable day (that is, with adequate illumination for diurnal animals to be active) occur when the sun is below the horizon. We compared measures of the active periods of swallows, as measured by the APR devices, with different standardized definitions for day length that included sunrise to sunset, and the periods between either civil dawn and twilight, nautical dawn and twilight, or astronomical dawn and twilight. We determined that, for both populations, the most accurate measure of usable daylight includes civil twilight (see Appendix B: Fig. B1): a measure not defined by sunrise and sunset, but by "when the center of the Sun is geometrically 6 degrees below the horizon . . . and illumination is sufficient, under good weather conditions, for terrestrial objects to be clearly distinguished" (U.S. Navy 2007). Civil twilight begins in the morning before

sunrise but sometime after complete darkness ends, and it ends in the evening after sunset but prior to the onset of complete darkness. Our measure of useable daylight, therefore, is the number of hours between when civil twilight begins in the morning and ends at night.

Statistical analyses

All statistical analyses were performed using either MATLAB version 7.9.0.529 (2009; MathWorks, Natick, Massachusetts, USA) or JMP version 9.0.2 (2011; SAS Institute, Cary, North Carolina, USA). In order to make population-level comparisons of variables that we measured on individual pairs of birds, we used nested mixed-model ANOVAs in JMP to compare variation across populations in the chick-feeding rates, duration of workday, and load size. To meet the assumptions of normality and homoscedasticity of residuals, we performed a natural log transformation on all response variables used in the ANOVAs (chick-feeding rate, duration, and load size). Log transformation of load size successfully normalized the data, and log-transforming chick-feeding rate and duration improved the normality of the data more than other transformations. Because ANOVA tests are robust to some nonnormality when sample sizes are large and close to balanced (Quinn and Keough 2002), we proceeded with using the log-transformed data for chick-feeding rate and duration. In these models, response variables (chick-feeding rate, duration, and load size) were treated as fixed effects with the pair included as a random variable in all models. In order to avoid problems of pseudoreplication, we nested pairs within each population, treating them as nominal variables. We examined the possible effect of chick age on our response variables by evaluating it as a continuous variable in all of our models. Descriptive statistics provided in text, figure legends, and tables were computed using untransformed data. All percentage differences in rates were calculated as the percentage increase from California to Alaska.

RESULTS

The latitudinal gradient in clutch size has been well documented for Tree Swallows in North America (Dunn et al. 2000). In our study, average clutch size across the two-year study was 9.4% greater in Alaska than in California (two-sample t test, $t_{118} = 3.27$, $P < 0.001$), with a greater difference in 2006 (15.5%) than in 2007 (3.4%; Fig. 1A, Table 1). The Alaskan swallow population not only raised more chicks, but also had chicks that were 25.9% larger at fledging, on average, than those of their California counterparts (Figs. 1B and 2A, Table 2). This resulted in Alaskan nests producing 32.9% greater total brood mass per nest (two-sample t test, $t_{47} = 5.44$, $P < 0.001$); Table 2).

Birds in Alaska had more available daylight than California birds and, as predicted by the day length hypothesis, they used this additional daylight to spend more hours foraging each day. Comparing available
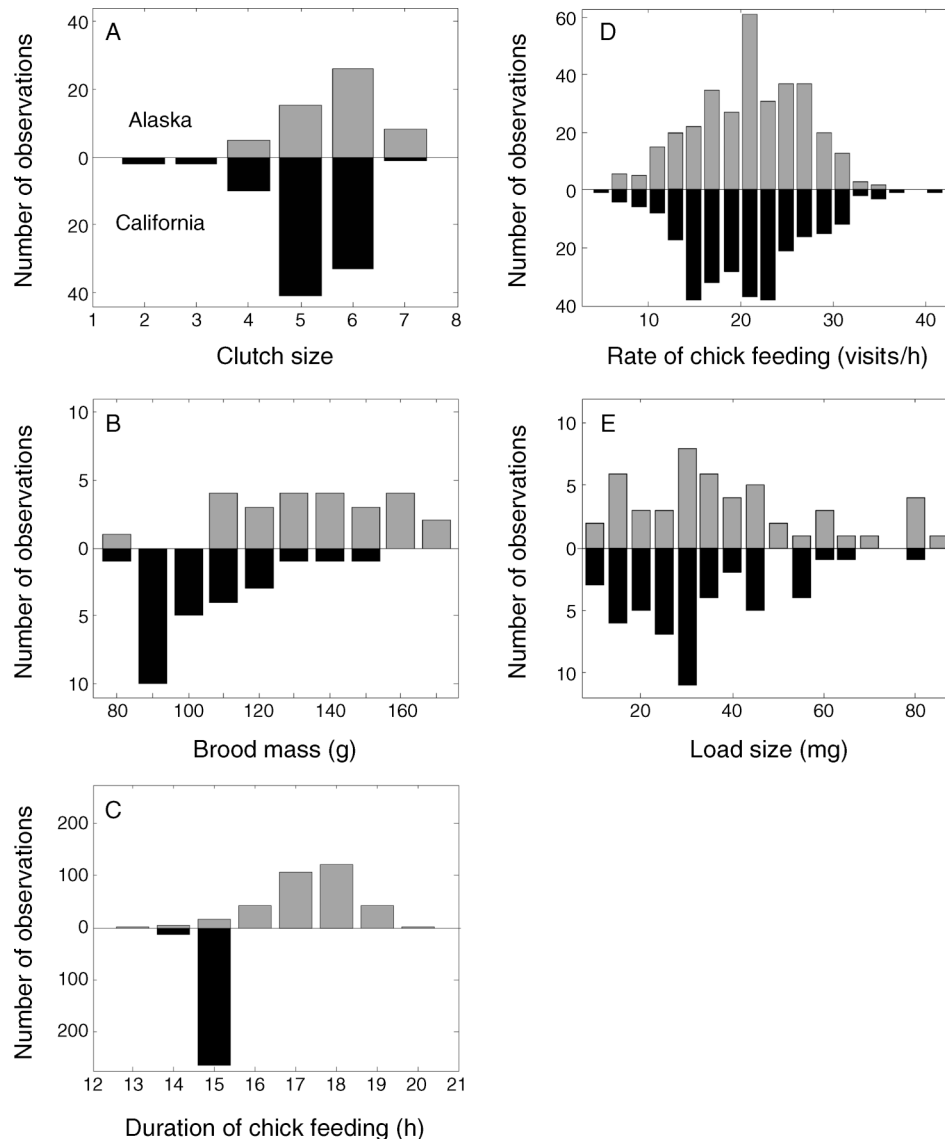
FIG. 1. Foraging durations, but not resource differences, correspond to differences in brood mass between Alaska (AK) and California (CA) populations of Tree Swallows. Histograms of (A) clutch size (AK, $N = 54$ pairs; CA, $N = 87$ pairs); (B) total brood mass at fledging (AK, $N = 25$ nests; CA, $N = 26$ nests); (C) daily duration of chick feeding for 36 AK and 40 CA pairs across 334 AK and 280 CA breeding days; (D) average hourly rate at which chicks were fed for 36 AK and 40 CA pairs; and (E) the mass of insects delivered to broods of chicks in a single load by pairs in each population (AK, $N = 21$ pairs; CA, $N = 24$ pairs) (number of insect boluses obtained in each population: AK, $N = 50$; CA, $N = 50$).

daylight hours in the two populations revealed that birds in Alaska had 52.4% more hours of useable daylight than California birds (contrast based on cumulative available daylight summed across the 21-day average chick rearing period; Appendix C: Fig. C1). Birds in Alaska used this additional light to spend an average of 16.0% more time per day feeding chicks than did birds in California (17.4 h/d in Alaska, 15.0 h/d in California; Fig. 1C and Table 2; nested mixed-model ANOVA for population, $F_{1,50} = 293.31$, $P < 0.0001$). The nested mixed-model ANOVA also revealed a significant relationship of daily duration of chick feeding to chick age

TABLE 1. Clutch size and fledging success (percentage of eggs that yield a fledgling).

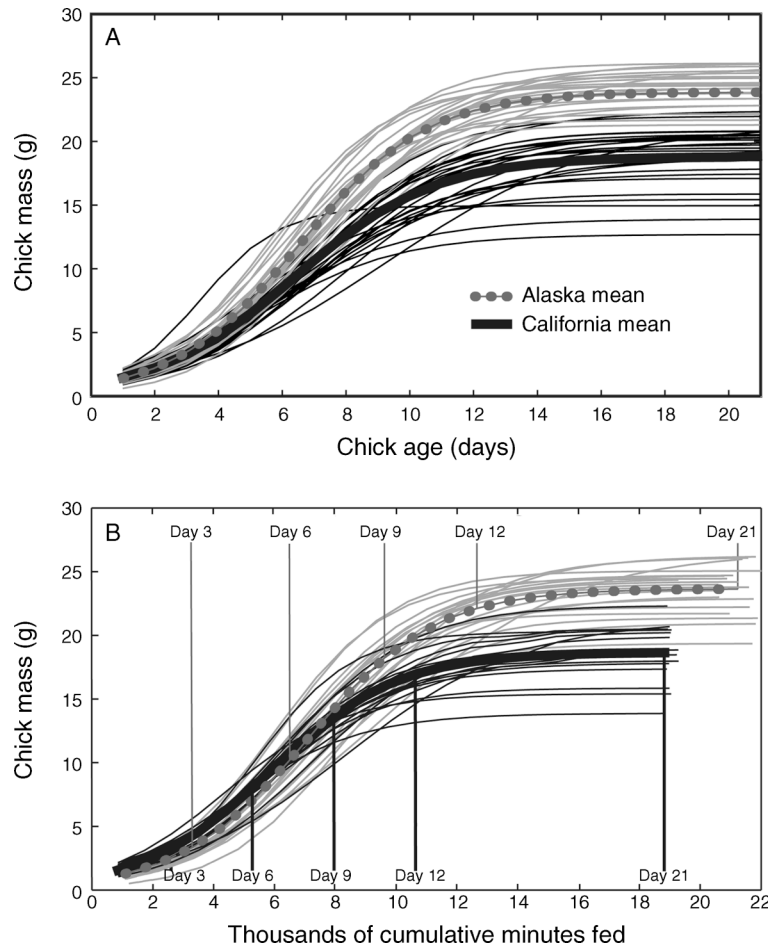| Year and population	No. nests	Clutch size (no. eggs)		Fledging success (%)
		Mean	Range	
2006				
Alaska	25	5.80	4–7	81.42
California	47	5.02	2–6	81.87
2007				
Alaska	29	5.59	4–7	93.12
California	40	5.40	4–7	90.53

Fig. 2. Correcting for feeding visits equalizes Tree Swallow chick growth rates in Alaska and California, as shown by logistic growth curves for Alaska (gray lines) and California (black lines) nests fit to average chick mass for each nest in each population in 2007. Panel (A) shows the relationship of chick growth to age in days from hatching to fledging. Panel (B) corrects for the fact that birds in Alaska are fed more in the same number of days than birds in California by showing the relationship of chick growth to the cumulative minutes they are fed from hatching to fledging. Thick gray dotted and black lines represent mean growth curves for Alaska and California, respectively.

($F_{1, 771} = 65.95$, $P < 0.0001$; increase in log-transformed workday length with chick age = 0.004 ± 0.0005, mean $\pm$ SE).

Contrary to the predictions of the food availability hypothesis and the general prediction of Ashmole's hypothesis that there would be greater per capita food availability at higher latitudes, birds in Alaska did not

bring food to their nests at a higher hourly rate than California birds, nor did they bring larger load sizes per visit. The rate at which birds fed their chicks did not differ significantly between populations in either year (Fig. 1D, Table 2, and Appendix D: Fig. D1; nested mixed-model ANOVA for population, $F_{1,50} = 1.23$, $P = 0.27$; effect of population on log-transformed chick-

TABLE 2. Variation in chick growth rates and measurements between years.

Year and population	Asymptotic individual chick mass (g)	Asymptotic chick mass averaged by nest (g)†	Daily chick-feeding duration (h)	Feeding rate per nest per minute
2006				
Alaska	24.25 (21.96, 26.24)	23.63 (19.17, 25.50)	17.4 (15.80, 19.10)	0.36 (0.24, 0.48)
California	20.56 (17.64, 22.79)	20.65 (17.51, 22.76)	14.98 (14.68, 15.25)	0.33 (0.20, 0.47)
2007				
Alaska	23.72 (21.02, 26.78)	23.88 (21.11, 26.03)	16.76 (14.86, 18.43)	0.35 (0.21, 0.48)
California	18.88 (13.71, 22.31)	18.80 (14.67, 21.62)	15.03 (14.63, 15.40)	0.35 (0.22, 0.52)

Notes: Data presented are means, with their 10% and 90% quantiles in parentheses. Data are not normally distributed.
† Data presented are population means of the average mass of chicks at fledging produced by each nest.

PLATE 1. Male Tree Swallow carrying an insect bolus at his nest entrance. Visible in this photograph are the perch and switch apparatus of the automatic perch recorder (data logger not visible) and a disarmed "Quinney" trap (Quinney and Ankney 1985). A color version of this photograph is available in Appendix E. Photo credit: Daniel Doak.

feeding rate (number of times chicks are fed/min) = -0.028 ± 0.025, mean $\pm$ SE), although there was the expected effect of age on chick-feeding rate within population (for age, $F_{1, 755} = 116.0$, $P < 0.0001$; effect of age on log-transformed chick-feeding rate = 0.025 ± 0.002, mean $\pm$ SE; Appendix D: Fig. D1). Similarly, the amount of food brought to nests on a given trip did not differ significantly between populations either (Fig. 1E), Neither the mean nor the distribution of the dry mass of insect boluses delivered to chicks differed significantly (two-sample K-S test, $P = 0.20$; nested mixed-model ANOVA for population, $F_{1,44} = 2.97$, $P = 0.09$). There was, however, a small but significant effect of chick age on load size (for age, $F_{1,85} = 4.30$, $P = 0.04$; effect of age on log-transformed load size (mg) = 0.042 ± 0.020, mean $\pm$ SE).

One additional factor, prey quality, could contribute to geographic variation in brood mass, but was not included in our conceptual framework. Prey quality can affect offspring growth rates (Boag 1987), so we compared chick growth rates between the two populations as an indirect test for an effect of prey quality. When compared by the standard measure of growth rate (mass gain per day), chicks in Alaska grew faster than those in California (Fig. 2A; two-sample t test with unequal variances, $t = 5.4$, $P < 0.001$, df = 46; for Alaska, final mean brood mass = 124.9 ± 4.41 g, mean $\pm$ SE; for California, 94.05 ± 3.57 g). However, Alaska chicks were fed for more hours each day and therefore received more total food per day. Given this, the question now becomes whether they grew faster than expected for the same amount of food received. Because load sizes and hourly feeding rates did not differ between populations, we could compare growth rates per unit time fed by examining chick mass as a function of cumulative total amount of time chicks were fed across the nestling

period. When growth is scaled to cumulative feeding time, the slopes of the two population mean growth curves are nearly identical during most of the active growth phase between hatching and day 9 (Fig. 2B). This suggests that there is no difference between populations in average prey quality. Thus, the population-level differences in apparent chick growth rates (i.e., when measured per day rather than per unit time fed) appear to be driven entirely by longer chick-feeding days. Chicks in Alaska are larger at day 9 than chicks in California because they have been fed more times in total.

DISCUSSION

Our conceptual framework and field research enabled us to examine the relative contribution of resource availability vs. day length as proximate drivers of a latitudinal gradient in reproductive investment. We found that differences in resource availability cannot explain differences in reproductive output between the Alaska and California Tree Swallow populations, and thus we find no support for the general assumption behind Ashmole's hypothesis. In contrast, the amount of time spent feeding chicks each day in the two populations did differ in direction and magnitude in parallel to reproductive output, suggesting that the day length hypothesis can explain some of the observed population differences in both clutch size and brood mass. In addition, our findings suggest that studies of avian life history evolution may need to pay more attention to the length of the parental workday, regardless of its relation with day length.

Our populations differed strikingly in final brood mass, and we wanted to understand how much of that difference was due to clutch size vs. chick size effects. The ratio of brood mass in Alaska to brood mass in California is generated by two components: the 1.09 ratio of clutch sizes and the 1.26 ratio of chick mass at fledging. Together these predict a ratio in brood masses of $1.09 \times 1.26 = 1.38$. However, because not all eggs hatch into chicks that survive to fledging, this reduces the observed brood mass ratio to 1.33. Because brood size and chick mass ratios multiply to yield the total effect on brood mass, it is simplest to express their relative importance on an additive log-ratio scale such that the natural log of the brood mass ratios equals the sum of the natural logs of brood size and chick mass ratios. Using this scaling, we can compare each component as a proportion of the total brood mass. With this approach, population differences in chick mass account for 81% of the observed difference in brood mass, and differences in brood size account for the remaining 19%. Because fledging success rates are similar in our two populations (Table 1), the effects of brood size are roughly equivalent to those of clutch size. In other words, as previously stated, birds in Alaska produce 33% more mass of chicks than birds in California, and 81% of this difference is attributable to
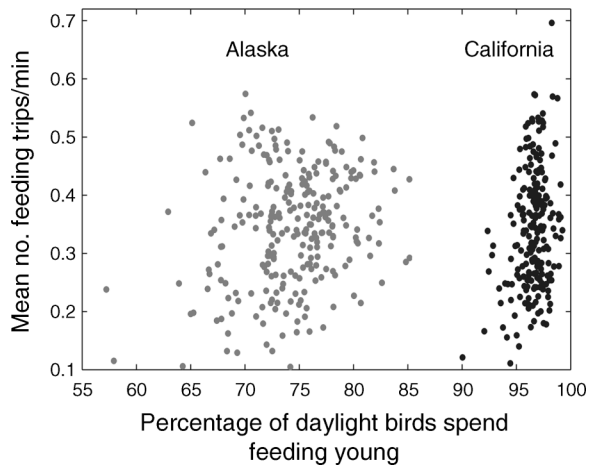

FIG. 3. Daylight strongly limits activity periods for Tree Swallows in California but not Alaska. Pairs in California use, on average, 96.3% of their available daylight to feed chicks, whereas birds in Alaska use an average of only 74.2%. Data points represent the daily duration of foraging for individual pairs within each population sampled repeatedly across the nestling period: $N = 36$ Alaskan pairs (gray) sampled across 334 breeding days; $N = 40$ Californian pairs (black) sampled across 280 breeding days.

differences in chick size, rather than chick (or egg) number.

Although the difference between populations in day length utilization explains half or more of the variation in either clutch size or brood mass, day length per se cannot be the sole factor driving the latitudinal gradient in clutch size. The two populations differ strikingly in the amount of available daylight they use: on average, California birds used 96.7% of their available daylight compared to 71.0% for Alaskan birds (Fig. 3 and Appendix B: Fig. B1). Moreover, Alaska birds not only used a much lower proportion of available daylight hours, but individuals also showed greater variation in the duration of their active period, and no bird ever used the full 24 hours of daylight available to them. Taken together, these patterns suggest that although day length sets the limit to reproductive effort in the California population, it does not do so in the Alaska population. In the population with essentially unlimited light, trade-offs with factors other than day length also appear to play a role in limiting reproductive effort. Perhaps above some threshold level, longer workdays incur adult survival costs that counterbalance the benefits gained by increased food for young (Gustafson and Sutherland 1988, Stearns 1992). Thus, although we did not directly test predation-based hypotheses for the observed latitudinal gradient in reproductive effort (Skutch 1949), our study does not exclude an important role for adult mortality patterns in shaping life history evolution, particularly within populations. The factors that drive life history evolution within populations are not always the same ones that explain differences between populations (Martin et al. 2000). Our aim was to explain the

difference in clutch size and brood mass between populations, a difference that appears to be mainly explained by day length. However, adult mortality patterns may be essential for understanding the patterns of investment within populations and, in particular, it could explain why birds in Alaska do not work even longer days than they do, because they are clearly not limited by day length.

The observation that swallows in the two study populations differ in the fraction of the available daylight used (Fig. 3) is also germane to the history of the day length hypothesis. Support for the day length hypothesis diminished after its proposal by Hesse in 1922 and Lack in 1947. This dismissal was not based on empirical study, but rather on flawed assumptions. As noted by Hussell (1985), Lack (1968) assumed that if day length were the sole explanation for the latitudinal gradient in clutch size, then the proportionate increase in clutch size with latitude should equal the proportionate increase in available light. The fact that these proportions differed for several species played a role in his conclusion that day length alone inadequately explains the latitudinal gradient in clutch size. Because David Lack was an influential figure in the development of life history theory in general (Ricklefs 2000), his dismissal of the day length hypothesis in favor of explanations pertaining to resource abundance and the density-dependent regulation of populations was likely the reason that the hypothesis has since received little attention. Our findings show why we should not expect a 1:1 correspondence between clutch size and available day length, counter to Lack's assumption. First, when birds do not use all of the available day length, as is the case for the Alaska population, the proportionate increases in clutch size with latitude are not expected to match the increases in day length. Second, when offspring size and growth rates also change with latitude, again we do not expect clutch size to increase in linear proportion with day length across latitudes. Perhaps most important, the logic used to reject the day length hypothesis required the assumption that it is the only factor that explains the latitudinal gradient in clutch size, rather than one of several contributing factors.

The two studies since Lack both tested for the predicted linearity in the relationship of day length to clutch size and did not consider the idea that day length may vary across latitudes in its strength as a predictor of the latitudinal gradient (Hussell 1972, Sanz 1999). Hussell (1972) concluded that day length was not an important driver of the latitudinal gradient because clutch size continues to increase above the Arctic Circle for both Lapland Longspurs (*Calcarius lapponicus*) and Snow Buntings (*Plectrophenax nivalis*). Above the Arctic Circle, breeding-season day length is a uniform 24 hours across latitudes, and hence cannot explain clutch size patterns. He also demonstrated that the duration of the active period remained constant above the Arctic Circle.

Although Hussell's findings rule out a role for day length over the latitude he assessed, they do not rule out day length generally.

In the second direct test of the day length hypothesis, Sanz (1999) made an important contribution by considering the length of the workday as an important metric of reproductive effort, and he showed that this variable was a strong predictor of geographic variation in clutch size. However, Sanz found that the length of the workday was not related to the amount of daylight, nor was clutch size itself. We propose two reasons why Sanz did not find a relationship between day length and clutch size. One reason may be that Sanz tested only for a linear relationship between day length and clutch size, and our own data suggest that the relationship may be quadratic. Second, Sanz used the interval between sunrise and sunset as a measure of day length rather than including civil twilight. The problem of using this approach is highlighted by a paradoxical observation that can be seen in Sanz's data: at some latitudes, the measured duration of the working day exceeds the amount of daylight available (Sanz 1999: Appendix). It is possible that if these data were recalculated to include civil twilight in the measurement of day length, clutch size might correlate with day length for Sanz's study populations. Regardless of the limitations of these two studies, negative results from a small sample of studies is not sufficient to reject a hypothesis as a factor for all birds.

Our study is based on the assumption that Lack's hypothesis applies to Tree Swallows, namely, that clutch size is ultimately determined by the food available for nestlings. Alternatively, energy and nutrients for egg production could also constrain clutch size and produce a latitudinal gradient in clutch size because northern populations have longer days to forage during the laying period than do southern populations. Several previous studies found that measures of food availability correlate with both timing of breeding and clutch size (Hussell and Quinney 1985, Winkler and Allen 1996, Dunn et al. 2011), but there is too little information to determine whether food availability during laying directly limits clutch size. Food supplementation studies in a wide variety of species suggest that although food availability can influence timing of breeding, for most species it does not tend to affect clutch size (reviewed by Meijer et al. 1990). Such experiments have not yet been done in Tree Swallows (and they would be very difficult), but based on energetic considerations, Hussell and Quinney (1985) suggest that clutch size in Tree Swallows is unlikely to be determined by food availability during laying, except in extreme situations where food levels are unusually low.

Our work showed that birds in the two study populations differed in the length of time spent each day foraging for their chicks. This result raised an important, unappreciated issue about the significance of geographic variation in growth rates: is the more rapid growth in Alaska chicks due simply to the increased

amount of time they are fed each day, or are the chicks fed a higher quality diet? We did not directly assess prey quality, but our comparisons strongly suggest that the more rapid growth in Alaska can be explained entirely by the number of times chicks are fed each day and, hence, by the effects of day length. Comparisons with the standard metric of growth (grams/day) revealed that chicks grew faster in Alaska, but when we then compared growth in terms of cumulative amount of time fed rather than age, the growth curves of the two populations overlapped completely, at least for the early period of growth. The growth curves eventually diverged because chicks in Alaska reach a higher final body size than chicks in California. These observations highlight an overlooked problem in many areas of environmental physiology: the application of clock time to biological processes such as growth may obscure the mechanisms driving processes that occur in physiological time. Accordingly, it would be worth revisiting early reports of latitudinal gradients in growth rates (McCarty 2001, Kilpatrick 2002) to determine whether the patterns are driven by differences in day length, or other factors.

In birds, the latitudinal gradient in clutch size is only one of a much larger suite of geographic patterns in reproductive effort and allocation. For many species, clutch size tends to be greater in the center of continental land masses (Klomp 1970) and is smaller on islands than on the mainland (Cody 1966, Covas 2012). The day length hypothesis has the potential to explain aspects of these patterns as well; populations in the middle of continents and mainland populations all breed later in the season than their counterparts and therefore experience longer days during their nestling period. Our results suggest that these and other broad-scale life history patterns may be explained in part by day length, rather than requiring explanations based on complex ecological interactions.

Our study provides the first evidence that latitudinal differences in day length underlie a latitudinal gradient in reproductive output in a bird. Moreover, for the two populations we compared, day length was the main factor that explained population differences in the total amount of food provided to offspring per day. We found no evidence that environmental differences in food availability played a role, counter to a widely accepted hypothesis for the latitudinal gradient in clutch size. We cannot extrapolate from our study that day length contributes to the latitudinal gradient in clutch size in birds generally, but our findings indicate that day length should no longer be ignored in studies of latitudinal gradients in clutch size and other life history traits. Our study also highlights the benefits of conducting an integrative analysis of all life history traits that connect to food provisioning rates, not just clutch size. Given that multiple life history traits often covary with latitude, it may not make sense to try to separate the effects of food provisioning on isolated life history traits. Indeed, we suggest that the attempt to test day length effects narrowly on clutch size patterns, while ignoring covarying traits like offspring growth rates and size, may have contributed to the early, and premature, dismissal of day length as a factor influencing life history patterns.

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Supplemental Material

Appendix A

Methods for determining timing of chick growth and fledging (*Ecological Archives* E094-118-A1).

Appendix B

Workday duration compared to day length (*Ecological Archives* E094-118-A2).

Appendix C

Comparison of available daylight for Tree Swallows in Alaska and California (*Ecological Archives* E094-118-A3).

Appendix D

Chick-feeding rate increases with age in both Alaska and California populations (*Ecological Archives* E094-118-A4).

Appendix E

A color version of Plate 1 (*Ecological Archives* E094-118-A5).

Appendix A: Timing of Chick Growth and Fledging

Our data for directly comparing the time to fledging in the two populations are imperfect as a result of using different methods for assessing fledging in each population (see Duration and Rate of Chick Feeding in Materials and Methods). Additionally, assigning fledging dates to tree swallow nests is problematic because of pronounced fledging asynchrony and the observation that fledglings may leave the nest and later return to it. Therefore, instead of directly comparing time to fledging in the two populations, we compared the length of time that was needed for adults to feed chicks to 90% of their maximum mass. To do this we used the nest specific brood mass growth equations described in the main text (see Fitting Chick Growth Curves in Materials and Methods). The mean time periods were nearly identical in the two populations (mean CA= 11.74 days, mean AK= 11.13 days; t=1.76, P=0.09, d.f. =49). After approximately 12 days, chicks in both populations gain very little mass (figure 2A). Substantial energy is no doubt needed for maturation (e.g. feather growth) and maintenance costs after 12 days, but quantifying these requirements is far more difficult and less certain than measuring gain in mass, and was beyond the scope of this study.

Appendix B: Workday duration compared to day length
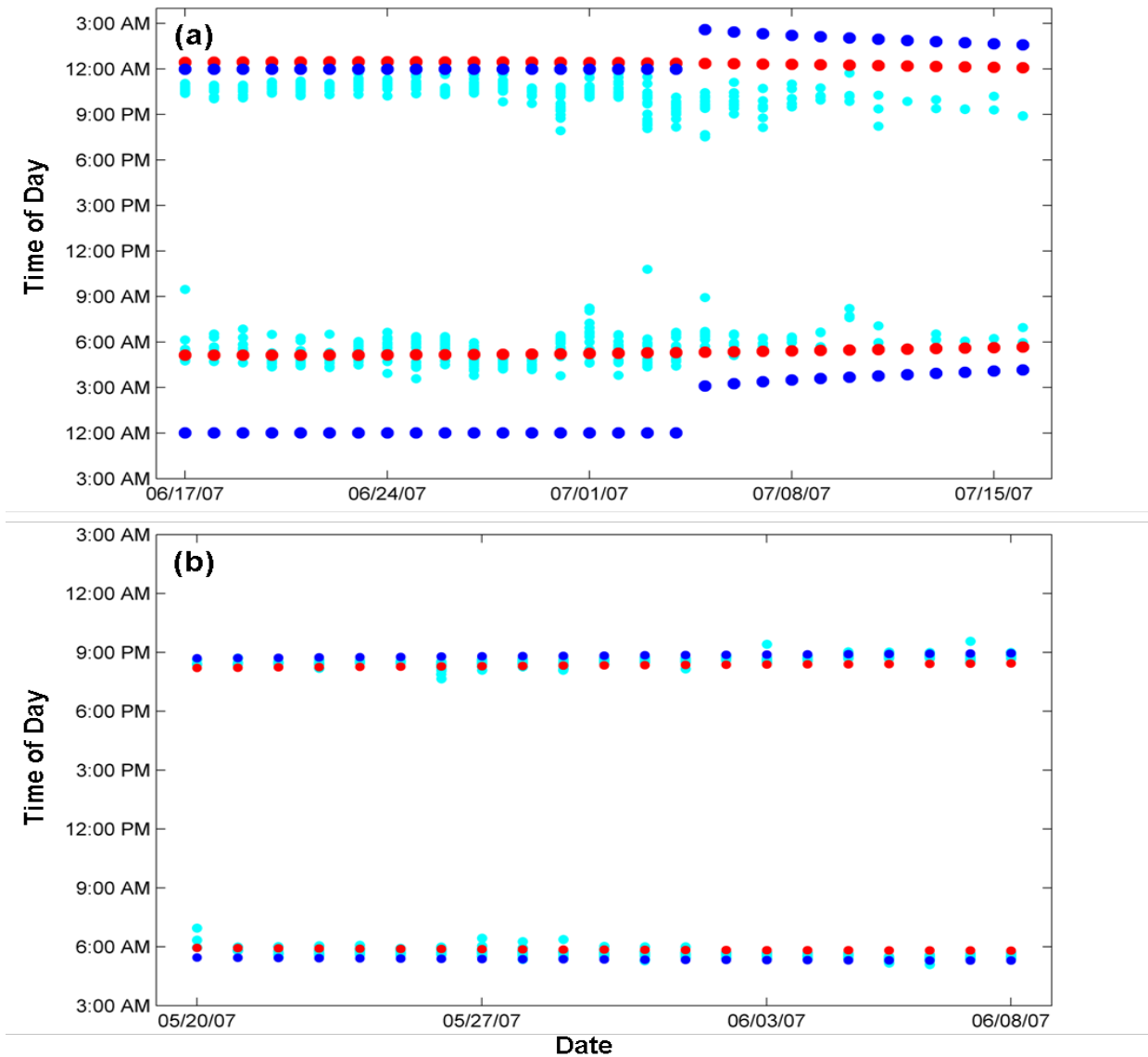

Fig. B1. Duration of active periods of pairs in Alaska (panel A) and California (panel B) compared to the duration of daylight. The beginning and end of active periods for individual pairs across the nesting season are plotted in light blue dots, sunrise and sunset in red dots and civil dawn and twilight are in dark blue dots. Birds in Alaska have 24 hours of civil twilight prior to July 4th, and they use this time to feed chicks well before sunrise. Birds in California are mostly confined in their active periods feeding chicks at the start of civil dawn and ending at civil twilight.

Appendix C: Tree swallows in Alaska have more available daylight than the California population
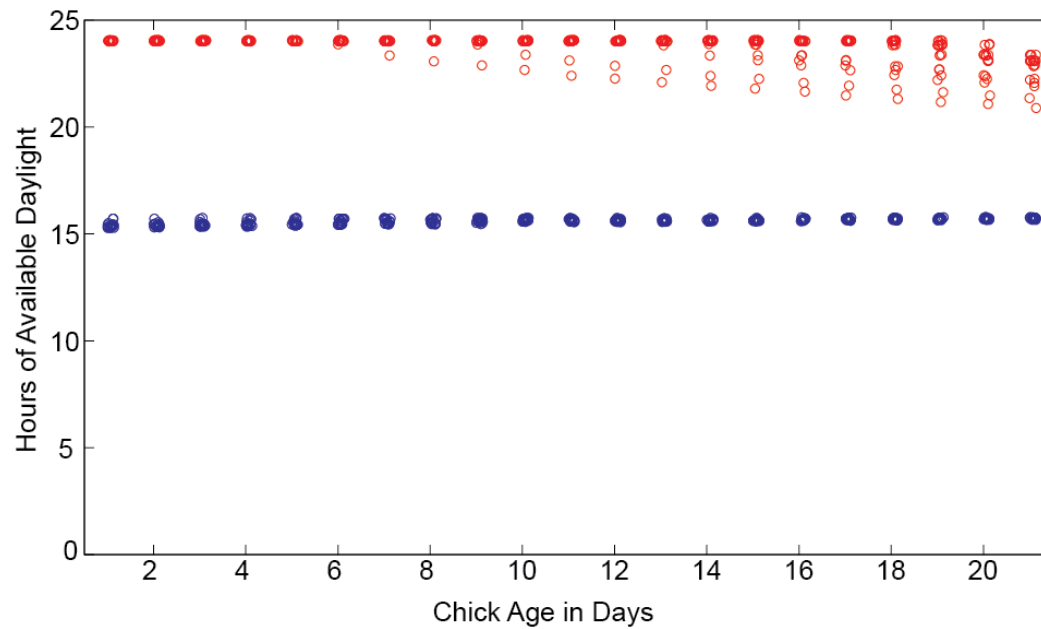

Fig. C1. Tree swallows in our Alaska population experienced 52.4% more hours of daylight during the nestling period than birds in our California population. Red and blue circles indicate the number of hours of light available to each pair on every day of their chicks' development in Alaska and California, respectively. Circles are jittered in order to show overlapping data. Variation in available day length for a given chick age in Alaska is caused mostly by variation in the date of clutch initiation. While there is also variation in the timing of clutch initiation in California, there is less variation in how day length changes across the nestling period, and this results in the consistency in the hours of available day length shown here.

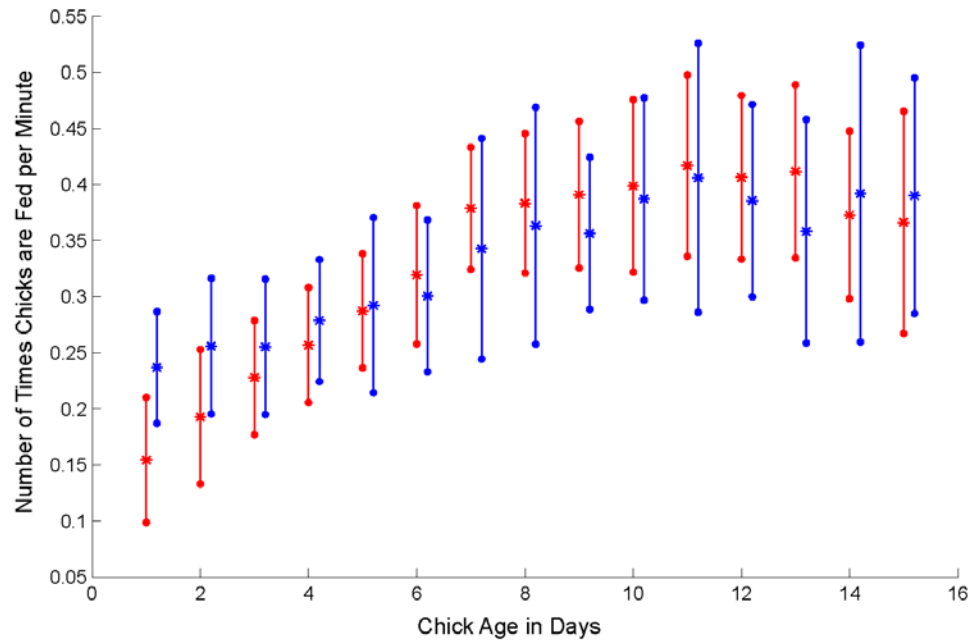**Appendix D: Chick feeding rate increases with age in both populations**

Fig. D1.The mean rate of chick feeding versus chick age in days for Alaska (red stars) and California (blue stars) and their standard deviations (lines). Chick feeding increases with chick age and is not significantly different between populations other than on days 1 and 2 of chick development.