

GEOGRAPHIC VARIATION IN THE TRADE-OFF BETWEEN NESTLING GROWTH RATE AND BODY CONDITION IN THE TREE SWALLOW

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Abstract. Nestlings can exhibit considerable variation in developmental patterns both within and among locations due to differences in environmental conditions and parental investment. I investigated trade-offs between nestling growth rate and residual body mass (body condition) at three locations across the range of the Tree Swallow (*Tachycineta bicolor*). Nestlings at the northern extreme of the range in Alaska had slower growth rates, lower body mass, and higher residual body mass than nestlings in New York and Tennessee. High insect availability was correlated with increased growth rates of nestlings in New York and Tennessee, but not in Alaska. Conversely, nestlings in Alaska showed increased residual body mass with high insect availability, but nestlings in New York and Tennessee did not. The trade-off between growth rate and residual body mass varied among sites, with fast-growing nestlings in Tennessee maintaining a higher residual body mass than those in Alaska. These results suggest that factors affecting offspring growth and condition vary among sites, leading to geographical differences in offspring development trajectories.

Key words: *body condition, developmental trade-offs, environmental variation, food availability, geographic variation, nestling growth, Tachycineta.*

Variación Geográfica del Costo-Beneficio entre la Tasa de Crecimiento de Polluelos y la Condición Corporal en *Tachycineta bicolor*

Resumen. Los patrones de desarrollo de los polluelos en el nido pueden presentar una variación considerable tanto entre como dentro de localidades debido a diferencias en las condiciones ambientales y en la inversión parental. Investigué el costo-beneficio entre la tasa de crecimiento de polluelos y el peso corporal residual (condición corporal) en tres localidades a lo largo del rango de distribución de *Tachycineta bicolor*. Los polluelos, en el extremo norte de distribución en Alaska, tuvieron tasas de crecimiento más lentas, menor peso corporal y un peso corporal residual mayor que los polluelos en Nueva York y Tennessee. La alta disponibilidad de insectos se correlacionó con el aumento de la tasa de crecimiento en Nueva York y Tennessee, pero no en Alaska. De modo contrario, los polluelos en Alaska exhibieron un peso corporal residual mayor con una disponibilidad mayor de insectos, pero los polluelos en Nueva York y Tennessee no presentaron esta relación. El costo-beneficio entre la tasa de crecimiento y el peso corporal residual varió entre localidades. Los polluelos en Tennessee, con una tasa de crecimiento mayor, mantuvieron un peso corporal residual mayor que los polluelos en Alaska. Estos resultados sugieren que los factores que afectan al crecimiento y a la condición de la progenie varían entre localidades, originando diferencias geográficas en las trayectorias del desarrollo de la progenie.

INTRODUCTION

The developmental trajectory of altricial nestlings can influence their likelihood of survival (Hochachka and Smith 1991, Starck and Ricklefs 1998). In many species there are counteracting pressures on growth rate, with strong selection for rapid growth to fledge as

early as possible (Winkler and Allen 1996, Monrós et al. 2002), while at the same time larger fledglings, which may require longer developmental periods, have a higher probability of survival (Tinbergen and Boerlijst 1990, Hochachka and Smith 1991). For example, growth rate affects the length of the dependent period, which can influence exposure to predation and the level of parental care (Lack 1968, Bosque and Bosque 1995). Longer developmental periods can be associated with greater physiological development, greater flight ability, and higher fledging condition, all of which

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can increase survival rates (Ricklefs 1984, 1992, Lindén et al. 1992). Growth rate therefore becomes a balance between the benefit of long developmental periods and competing life-history demands, particularly increased predation risk and migratory needs (Martin and Li 1992).

Under most conditions, allocating resources to growth reduces resource stores, so high growth rates should correspond to reduced body reserves. Excess body reserves can provide a buffer against starvation during periods of low food availability or high thermoregulatory demand, and many studies of birds have shown that body condition (an index of body mass corrected for structural size) is a good predictor of fledgling survival (Perrins 1964, Hochachka and Smith 1991, Lindén et al. 1992, Adriaensen et al. 1998). In this study, I examine geographic variation in the trade-off between growth rate and residual body mass (body condition) in the Tree Swallow (*Tachycineta bicolor*) by examining nestling development at three widely separated sites across the breeding range.

Variation in nestling growth rate may be a function of habitat quality (Tremblay et al. 2003), aridity (Tieleman et al. 2004), and latitude (Ricklefs 1976, Wikelski et al. 2003), and may vary with body size (Remeš and Martin 2002). In a prior study examining geographic variation of growth in Tree Swallows, McCarty (2001) found no latitudinal trend in growth rate among populations, but his study did not examine residual body mass and its relationship with growth rate and did not assess swallows at the extremes of their range. Here, I build upon McCarty (2001) by examining geographic variation in nestling growth rate and residual body mass of Tree Swallows along a latitudinal gradient. I compared swallows at the southern extreme of their range (Tennessee) to those at the northern extreme (Alaska) and those toward the center of their distribution (New York); sites would be expected to differ in many critical factors that can influence nestling growth rates, including predation risk, length of the breeding season, and the mean and variation in food supply.

First, I tested the prediction that by adding sites at the extremes of the range, I would observe a latitudinal gradient in nestling growth. In particular, due to the shorter breeding season and longer daylight hours, I

predicted that nestlings in Alaska would show more rapid growth than nestlings in New York, which in turn would grow faster than nestlings in Tennessee. The main purpose of the study was to test for trade-offs between growth rate and residual body mass (body condition). Therefore, if nestlings in Alaska grow more rapidly, they would also be expected to show lower residual body mass than nestlings in other sites.

When assessing geographic variation, it is important to consider that variation in growth rates can reflect short-term environmental fluctuations and not necessarily variation in selective pressures (McCarty and Winkler 1999b, McCarty 2001). Accordingly, I included as covariates three important factors that could cause variation in growth among sites: insect availability, parental feeding rates, and temperature.

METHODS

Tree Swallows are common, cavity-nesting migrants that breed across North America (Robertson et al. 1992). I studied Tree Swallows breeding in nest boxes erected for their use from May to July 2000 in Tompkins County, New York (centered around 42°29'N, 76°27'W); from April to July 2001 in Loudon, Anderson, and Knox Counties, Tennessee (centered around 35°53'N, 84°18'W); and from May to July 2002 near Fairbanks, Alaska (centered around 64°49'N, 147°52'W).

Nests were checked daily during nest-building, egg-laying, and close to hatching to determine date of clutch initiation, clutch size, and exact day of hatching. On days 4, 6, 10, 12 of the nestling period (hatch = day 1), nestlings were marked individually using colored nail polish applied to claws for nestlings younger than 10 days and metal U.S. Fish and Wildlife Service bands after 10 days of age. Although some growth occurs after day 12, a subsample of data showed no difference in size hierarchies or growth rates in the period up to day 12 ($n = 244$) compared to days 12–16 ($n = 42$), thus most nests were not visited after day 12 to minimize the risk of premature fledging. During each visit, the following measurements were recorded for each nestling: body mass (± 0.05 g) using a portable Ohaus digital balance, flattened left wing length (9th outermost primary) using a ruler with a wing stop (± 0.5 mm), and

head-bill length and tarsometatarsus (hereafter tarsus) length using dial calipers (± 0.1 mm). The same observer measured all nestlings in Alaska and Tennessee; two additional individuals measured nestlings in New York, however there was high interobserver repeatability ($F_{46,47} = 2.45$, $P = 0.001$; repeatability = 0.86). In addition, the wing and body feathers of each nestling were examined for ectoparasites (e.g., feather lice, blowfly larvae). A total of 224 nestlings were included in this study (Alaska: 57 nestlings in 15 nests; New York: 107 nestlings in 25 nests; Tennessee: 60 nestlings in 16 nests). The incidence of ectoparasite infection was low (5 of 224 nestlings), so ectoparasite measurements were not included in analyses.

At each site, insect availability was estimated using two 2 m aerial insect samplers powered by a Robbins and Myers (Dayton, Ohio) 1650 RPM 0.08 HP motor (12.5 m sec^{-2} ; McCarty and Winkler 1999a). These samplers collect aerial insects and allow quantification of relative insect abundance on a daily basis. Insect samplers were placed within 10 m of water at locations where electrical power was available and were run from 07:00 to 17:00 in New York and Tennessee and 07:00 to 22:00 in Alaska; insect availability data were corrected to account for time differences among sites. After removing seeds and other debris, packed insect volume (mm^3) was measured by centrifuging samples at 5000 rpm for 75 min.

Video cameras were used to record parental visitation rates during three 60-min periods between days 8 and 11 for each breeding pair; observations were stratified over daylight hours. Females were marked with a small dot of correction fluid on the back to differentiate the sexes in video observations. For each observation, cameras were set with timers to begin recording 15 min after set-up to minimize the effect of disturbance on provisioning behavior. In addition, to determine the length of daylight hours over which Tree Swallows fed young, cameras were left overnight on timers to record feeding observations for 15-min intervals every hour for two hours before and after sunset and sunrise. A data logger (Hobo, Onset Corp., Bourne, Massachusetts) was placed in two unoccupied nest boxes at each site to obtain temperature inside nest boxes. Average daily temperature and wind speed were obtained from the National Weather Service.

STATISTICAL ANALYSES

Tree Swallow growth for all body measures is well approximated with logistic growth curves (Zach and Mayoh 1982, McCarty 2001, Dawson et al. 2005), so growth rates were calculated using logistic growth curves following the procedure outlined in McCarty (2001). The fit of the logistic model to the data was assessed by examining the linearity of the derivative of the fitted equations (Zar 1999). Growth rate from day 4 to day 12 was calculated as the growth rate constant K of a logistic growth function (Starck and Ricklefs 1998) for three nestling measures: 9th primary wing feather, tarsus, and head-bill length measurements. Because nestling measures are highly correlated, values of K were combined in a principal components analysis for some analyses. The first principal component (PC1) had high positive loadings of all three growth rates and explained 89% of the variation. Residual body mass of nestlings on day 12 was calculated as the residual of a regression of body mass against head-bill size, a structural measure of body size ($F_{1,222} = 8.9$, $\beta = 0.67$, $R^2 = 0.54$, $P = 0.003$). The number of daily feeding visits for each nest was calculated by multiplying the average number of feeding visits observed during feeding observations by the time between sunrise and sunset from day 8 to day 11.

Because breeding dates differ slightly from year to year, clutch initiation date was standardized to a mean = 0 for each site; values <0 reflect individuals breeding before the mean breeding date for each site, values >0 after the mean breeding date. Nestling growth and residual body mass were compared among sites using a mixed model analysis of variance (PROC MIXED; Littell et al. 1996) with nest as a random effect. This design avoids pseudo-replication and allows for comparison among individual nestlings because covariation among nest mates is controlled as a random effect (Littell et al. 1996). In addition, each model contained the following fixed effects: breeding site, standardized clutch initiation date, clutch size, number of daily feeding visits, insect availability during the period of nestling growth, average daily temperature during the period of nestling growth, average daily nest box temperature during the period of nestling growth, and average daily wind speed. All two-way interaction terms were initially included in

TABLE 1. Comparison of body size, growth rate, and residual body mass among nestling Tree Swallows at three breeding sites. I measured 57 nestlings in Alaska, 107 in New York, and 60 in Tennessee. For each variable, raw data are listed on the first line and least-square means on the second. Growth rate (PC1) is the first principal component of a principal components analysis containing head-bill, tarsus, and 9th primary wing feather growth. Residual body mass is the residual of a regression with head-bill length as the independent variable and body mass as the dependent variable for nestlings at day 12. *P*-values are from a main effect of breeding site in a mixed-model ANOVA (see text for more detail). Superscripts refer to differences among sites for each variable at *P* < 0.05.

	Alaska	New York	Tennessee	<i>P</i> -value
	Mean ± SE	Mean ± SE	Mean ± SE	
Tarsus length (mm)	11.3 ± 0.5	12.0 ± 0.5	11.8 ± 0.5	0.01
Head-bill length (mm)	11.4 ^a ± 0.5	12.0 ^b ± 0.5	11.9 ^b ± 0.6	0.01
	23.5 ± 1.0	24.6 ± 0.9	23.4 ± 0.8	
9th primary feather length (mm)	23.9 ^a ± 1.0	24.6 ^b ± 1.0	23.7 ^b ± 0.9	0.01
	43.3 ± 2.2	44.7 ± 1.0	44.1 ± 1.5	
Body mass (g)	42.3 ^a ± 2.1	45.6 ^b ± 1.1	45.0 ^b ± 1.4	0.02
	22.8 ± 0.9	21.6 ± 0.3	21.0 ± 0.7	
Growth rate (PC1)	22.4 ^a ± 1.0	21.7 ^b ± 0.7	21.2 ^b ± 0.7	0.001
	-0.55 ± 0.14	0.56 ± 0.16	0.11 ± 0.15	
Residual body mass day 12	-0.43 ^a ± 0.18	0.57 ^b ± 0.17	0.07 ^b ± 0.16	0.01
	2.63 ± 0.41	-0.21 ± 0.21	-0.73 ± 0.46	
	2.68 ^a ± 0.50	-0.25 ^b ± 0.49	-0.76 ^b ± 0.51	

each model and then removed sequentially by highest *P*-value for those interactions with *P* > 0.20. Means ± SE are reported.

RESULTS

FACTORS AFFECTING BODY MASS AND MORPHOLOGY

Nestlings in Alaska maintained higher body mass on day 12 than nestlings in New York or Tennessee (site: $F_{2,197} = 5.2, P = 0.02$; Table 1). Nestlings from larger clutches also tended to maintain higher body mass ($F_{1,197} = 5.4, P = 0.02$). In addition, as insect availability increased, nestling body mass increased ($F_{1,197} = 15.4, P < 0.001$). There was no significant effect on body mass of clutch initiation date, parental feeding rate, temperature, or wind speed (all $F < 1.5, all P > 0.55$). Nestlings in Alaska had shorter tarsi, head-bill lengths, and wing feather lengths than nestlings in New York or Tennessee (tarsus: $F_{2,197} = 5.8, P = 0.01$; head-bill: $F_{2,197} = 6.7, P = 0.01$; wing: $F_{2,197} = 6.2, P = 0.01$; Table 1). There was no significant effect on tarsus, head-bill, or wing length of clutch initiation date, parental feeding rate, temperature, or wind speed (all $F < 1.2, all P > 0.6$).

FACTORS AFFECTING GROWTH RATE

There were differences among sites in nestling growth rate, with nestlings in New York and

Tennessee growing faster than nestlings in Alaska ($F_{2,197} = 21.7, P < 0.001$; Table 1). As insect availability increased, nestling growth rate also increased ($F_{1,197} = 7.2, P = 0.01$), but the effect of insects on growth varied by site, with growth rate increasing with insect availability in New York and Tennessee but not in Alaska (PC1: $F_{2,197} = 8.4, P < 0.001$; Fig. 1). This trend of site-level differences in the effect of insect availability on growth also held true when individual body measures were examined (head-bill: $F_{2,197} = 5.9, P = 0.003$; 9th primary wing feather: $F_{2,197} = 7.4, P = 0.001$; tarsus: $F_{2,197} = 9.2, P = 0.003$; Fig. 1). There was no significant effect on growth rate of clutch initiation date, clutch size, parental feeding rate, temperature, or wind speed (all $F > 1.1, all P > 0.65$).

FACTORS AFFECTING BODY CONDITION

Nestlings in Alaska had higher residual body mass than nestlings in either New York or Tennessee ($F_{2,196} = 4.5, P = 0.01$; Table 1). Insect availability affected residual body mass only in Alaska, where increasing insect availability led to higher residual body mass (insects: $F_{1,196} = 5.1, P = 0.01$; interaction: $F_{2,196} = 7.8, P = 0.001$; Fig. 2). In addition, insect availability affected absolute body mass differently among sites. In New York and Tennessee, increasing insect availability led to increased

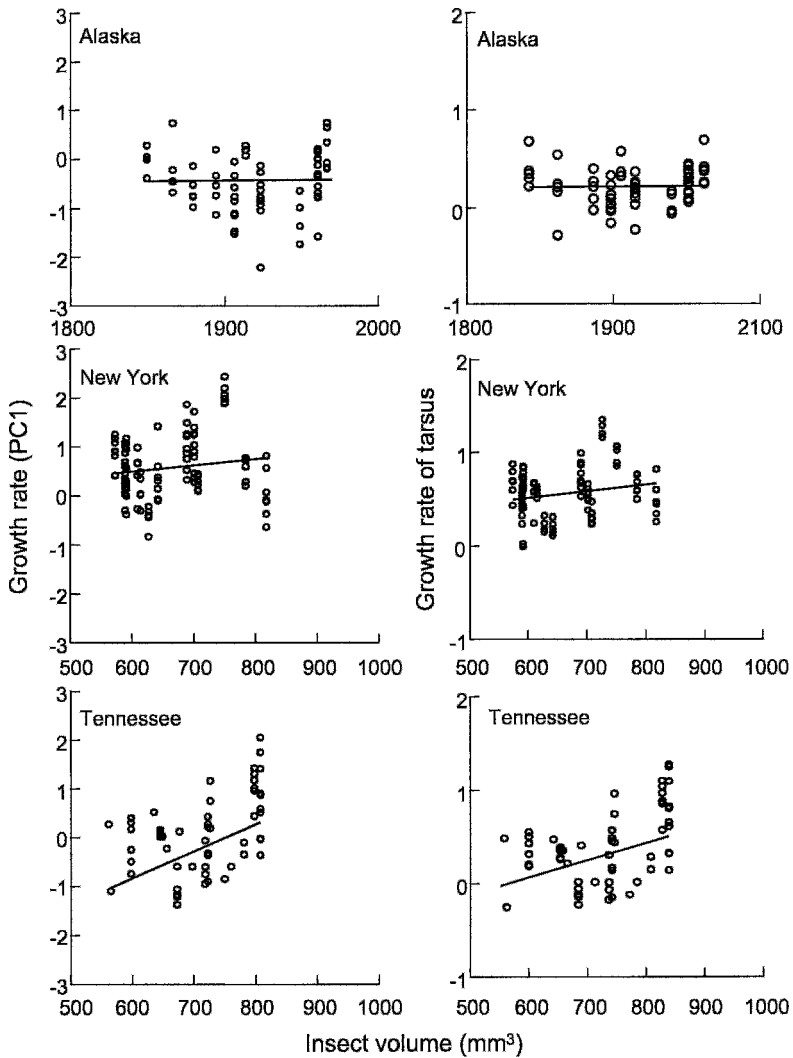


FIGURE 1. Nestling Tree Swallow growth rate in relation to insect availability at three breeding sites in the United States. Growth rate (PC1) is the first principal component of a principal components analysis containing head-bill, tarsus, and 9th primary wing feather growth. Growth rate of tarsus is the slope of a logistic function for each individual. Note that the x axis for Alaska is a different scale than for New York and Tennessee.

body mass, but there was no relationship in Alaska (insects: $F_{1,196} = 7.4, P = 0.007$; interaction: $F_{2,196} = 9.2, P < 0.001$; Fig. 2). Residual body mass was correlated with composite growth rate ($F_{1,196} = 8.9, P < 0.001$), but the relationship varied widely among sites (interaction: $F_{3,196} = 11.0, P < 0.001$; Fig. 3). In Tennessee, fast-growing nestlings also maintained high residual body mass ($F_{1,51} = 11.3, \beta = 0.81, R^2 = 0.57, P = 0.001$), while in Alaska, nestlings with high residual body mass

grew slowly ($F_{1,49} = 6.6, \beta = -0.78, R^2 = 0.21, P = 0.01$). There was no relationship between residual body mass and growth rate in New York ($P = 0.45$). When body measures were compared separately to absolute body mass, nestlings in Alaska showed a similar pattern of decreasing body mass with increasing growth rate for all three body measures (tarsus $F_{1,49} = 12.4, \beta = -1.03, R^2 = 0.46, P = 0.001$; head-bill: $F_{1,49} = 7.2, \beta = -0.98, R^2 = 0.31, P = 0.01$; 9th primary wing feather: $F_{1,49} = 5.7, \beta =$

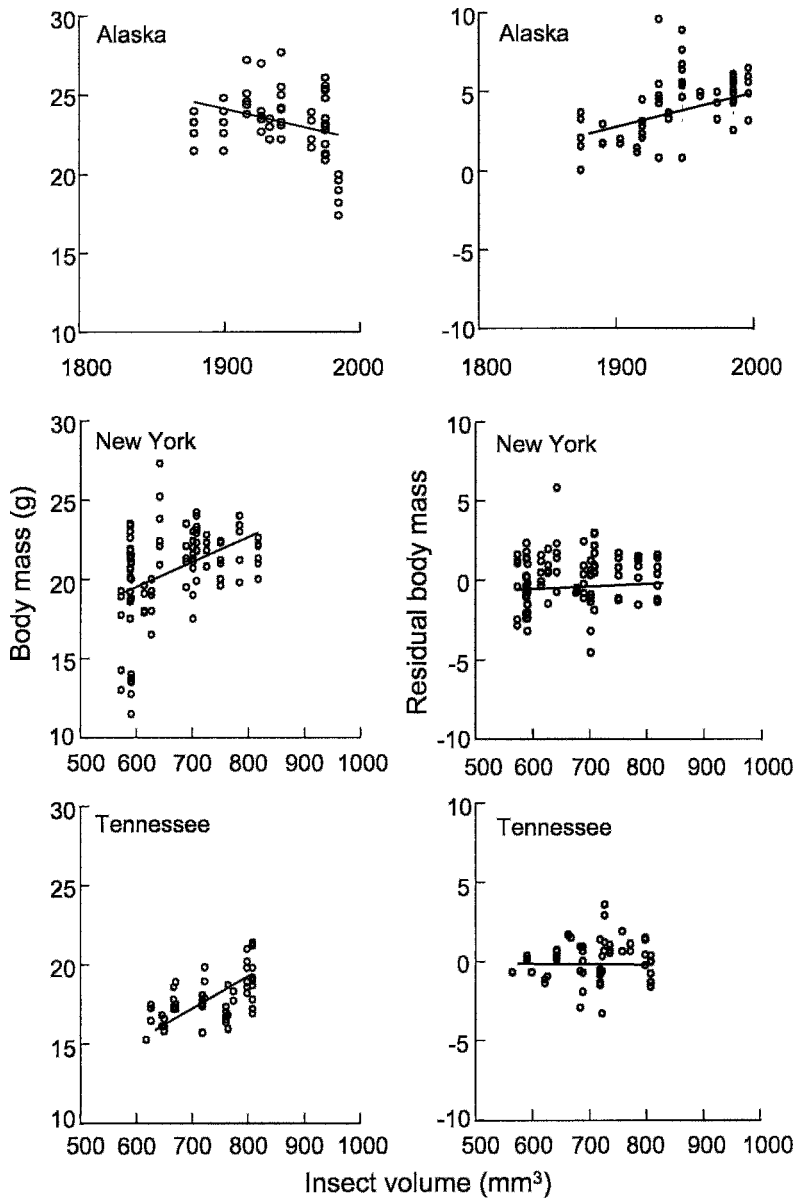


FIGURE 2. Relationship between insect availability and absolute and residual body mass at three breeding sites of the Tree Swallow. Residual body mass is the residual of a regression with head-bill length as the independent variable and body mass as the dependent variable for nestlings at day 12. Note that the x axis for Alaska is a different scale than for New York and Tennessee.

-0.74, $R^2 = 0.24$, $P = 0.02$; Fig. 4). In Tennessee, increased growth rates of head-bill length and 9th primary wing feather, but not tarsus, were associated with increased body mass (tarsus: $F_{1,51} = 0.5$, $\beta = 0.11$, $R^2 = 0.06$, $P = 0.45$; head-bill: $F_{1,51} = 0.9$, $\beta = 0.88$, $R^2 = 0.34$, $P = 0.01$; 9th primary wing feather: $F_{1,51}$

$= 6.3$, $\beta = 0.69$, $R^2 = 0.26$, $P = 0.01$; Fig. 4). In New York, there was no relationship between growth rate of tarsus or head-bill length with body mass, but increasing feather growth was correlated with increasing body mass (tarsus: $F_{1,102} = 0.31$, $\beta = 0.01$, $R^2 = 0.04$, $P = 0.56$; head-bill: $F_{1,102} = 0.28$, $\beta = -0.02$, $R^2 = 0.01$,

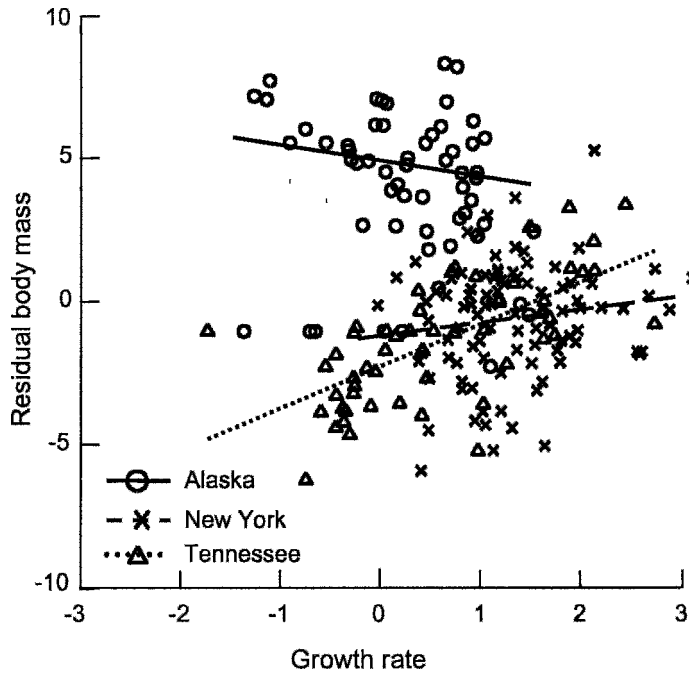


FIGURE 3. Relationship between growth rate and residual body mass for nestling Tree Swallows at three breeding sites in the United States. Growth rate (PC1) is the first principal component of a principal components analysis containing head-bill, tarsus, and 9th primary wing feather growth. Residual body mass is the residual of a regression with head-bill length as the independent variable and body mass as the dependent variable for nestlings at day 12.

$P = 0.65$; 9th primary wing feather: $F_{1,102} = 6.4$, $\beta = 0.59$, $R^2 = 0.22$, $P = 0.01$; Fig. 4). There was no significant effect of clutch initiation date, clutch size, parental feeding rate, temperature, or wind speed on growth rate (all $F < 1.1$, all $P > 0.65$).

INSECT AVAILABILITY AND FORAGING VISITS

Insect availability showed considerable daily variation at all three sites, but overall prey availability showed an increasing linear trend as the breeding season progressed, with no differences in the rate of increase among sites (standardized ordinal date vs. packed insect volume [mm^3]: $\beta = 4.4$, $F_{2,203} = 4.9$, $P = 0.009$, $R^2 = 0.21$, site-level difference in slope: $F_{2,203} = 1.1$, $P = 0.35$). Food availability differed among sites, with more food available in Alaska (AK) than in New York (NY) or Tennessee (TN; site-level difference in abundance: $F_{2,203} = 16.2$, $P < 0.001$; pairwise comparisons: AK vs. NY, $P = 0.01$; AK vs. TN, $P = 0.001$; NY vs. TN, $P = 0.18$; mean volume of insects collected

[mm^3] per 8-hr period: AK, 1886 ± 81 ; NY, 647 ± 39 ; TN, 616 ± 34). Tree Swallows fed nestlings from sunrise to sunset at all three sites (feeding visits per chick per day: Alaska, 79.9 ± 7.7 ; New York, 73.0 ± 7.8 ; Tennessee, 52.3 ± 8.4).

DISCUSSION

The relationship between nestling growth rate and body mass (both residual and absolute) differed among sites, however in the opposite direction from that predicted. Nestlings in Alaska were predicted to grow quickly and thus have low residual body mass, but instead I observed the opposite: high body mass and slow growth relative to other sites. This was due to nestlings in Alaska having smaller structural measures (tarsus, head-bill, and wing lengths) and higher body mass than nestlings at other sites. Differences in developmental trajectories among sites appeared to be determined, in part, by different sensitivities to food availability. Growth rates in both New York and Tennessee were affected by insect availability—chicks

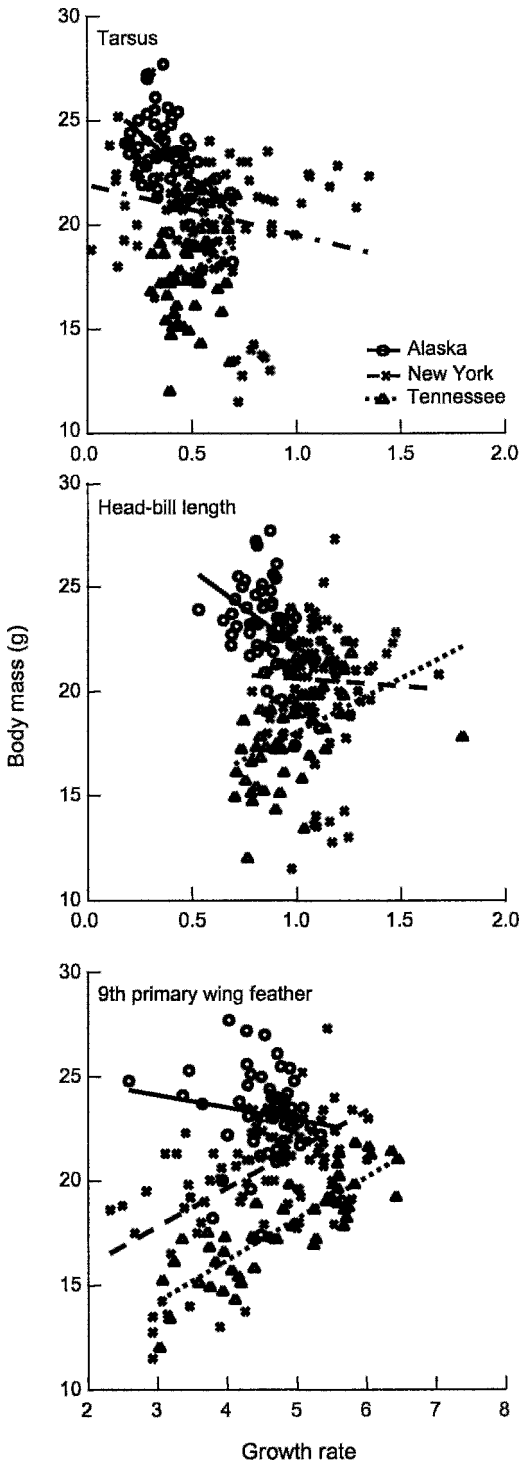


FIGURE 4. Relationship between growth rate and absolute body mass of nestling Tree Swallows at three breeding sites in the United States. Growth

developing during periods of high availability tended to grow faster—but there was no relationship between insects and growth rate in Alaska. Instead, nestlings in Alaska showed increased residual body mass as food supplies increased, while nestlings in New York and Tennessee did not. However, nestlings in New York and Tennessee increased absolute body mass with increasing food availability, while nestlings in Alaska did not. This suggests different priorities for resource allocation among sites, with nestlings in Alaska allocating resources to maintaining body reserves, and nestlings in New York and Tennessee dividing resources to grow in body size and body mass at similar rates.

Nestlings in Alaska may maintain high residual body mass because Tree Swallows are sensitive to periods of cold weather; however, temperatures during the nestling period in interior Alaska were no different than temperatures in New York (Alaska: $16.2 \pm 0.7^\circ\text{C}$, New York: $16.8 \pm 0.8^\circ\text{C}$, $t_{82} = 1.3$, $P = 0.2$). Alternatively, differences in migratory pressures may drive the need for high resource stores in Alaska. In Alaska, the breeding season is short and most individuals begin migratory movements within days after fledging (DRA, unpubl. data); thus, it may be critical to store sufficient fat for an ocean or mountain crossing on migratory journeys south. However, this is speculative, as little is known about the exact migratory paths and history of Tree Swallows in Alaska. At a minimum, though, swallows from Alaska likely travel longer distances to wintering grounds than do swallows from New York or Tennessee.

I found varied results when testing for a trade-off between growth rate and residual body mass, suggesting that consequences of different investment strategies vary by site. In Alaska, individuals with high residual body mass showed lower growth rates. However, in Tennessee, individuals with rapid growth also had high residual body mass, while in New York there was no link between growth and condition. These site-level differences may have

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rates for individual body measures are the slopes of a logistic function modeling growth for each individual.

arisen because of the polarization in morphology in Alaska, where nestlings had small structural size and high body mass. Nestlings in Alaska that allocated resources to increasing body mass tended to grow slowly. This result is particularly surprising given that insect supplies were highest in Alaska, suggesting different responses of offspring and parents to food than in other sites. Conversely, in Tennessee, nestlings that were efficient at rapid growth were also efficient at maintaining high residual body mass. Interestingly, these differences were not due to differences in the number of food deliveries by parents, as there was no role of feeding visits in explaining these relationships, despite feeding visits in Tree Swallows tending to reflect food deliveries (McCarty 2002). Differences among sites may reflect differences in diet quality (Johnston 1993, Dawson and Bidwell 2005); the next step in this line of inquiry would be to compare quality of prey among sites. In addition, differences among nestlings may result from aspects of physiological quality or environmental conditions (Burness et al. 2000, Dawson et al. 2005). This suggests that a cross-fostering experiment such as those conducted in other vertebrate groups (Niewiarowski and Roosenburg 1993) would be helpful by breaking the link between parental quality and offspring conditions.

The results reported in this study suggest that factors affecting nestling development may differ in the far northern extreme of the range of Tree Swallows. McCarty (2001) found no geographic variation in nestling growth rate; nestlings from New York and Tennessee fit this pattern, but nestlings from Alaska did not. The possibility exists that the results reported here represent idiosyncratic site-level effects and not true geographic differences, especially given the single year of work at each site. However, multiple covariates were included in all models including food resources, feeding visits, and environmental conditions (e.g., nest box temperature, ambient temperature, and wind speed). The greater food supplies in Alaska should have led to positive, not negative, correlations between growth and resource stores. Furthermore, the sites differed most in nestling *response* to food supplies, suggesting that differences reported among sites might not be due simply to differences in food levels, as found in many previous studies (Zach and

Mayoh 1982, Quinney et al. 1986, McCarty and Winkler 1999a, McCarty 2001), but rather to differences in how nestlings allocate resources.

Other factors that could underlie site-level differences include differences in egg mass. Eggs in all nests were weighed before incubation and there was no difference in mean egg mass among sites (mass [g]: NY, 1.84 ± 0.01 ; TN, 1.81 ± 0.01 ; AK, 1.86 ± 0.01 ; $F_{2,854} = 0.7$, $P = 0.51$). Another possibility is that nestling growth changes between day 12 (the last day measured) and fledging, as early differences in body size among chicks are often minimized by the time of fledging (Badyaev and Martin 2000, McCarty 2001). This possibly bears more consideration, but is difficult to examine in Tree Swallows as nestlings are prone to premature fledging if disturbed.

What do these results tell us about factors affecting the evolution of growth rates? Without conducting experimental manipulations, it is difficult to determine what processes cause the patterns reported here. While predation rates clearly play a strong role in driving growth in many bird species, as cavity-nesting birds, Tree Swallows would not likely be strongly affected by predation. Thus, factors such as food availability and parental quality should be more important than predation risk, similar to findings from other studies (Tieleman et al. 2004, Tremblay et al. 2005). One site-level difference that merits further examination is variation in flight performance. Tree Swallows are almost exclusively aerial foragers (Robertson et al. 1992), thus patterns of growth relative to body weight are likely more critical than in species less dependent on flight (Redfern 1994, Remeš and Martin 2002). Site-level differences in growth could occur if the suite of insects available at each site require different aspects of flight for prey capture, which would in turn lead to different optimum ratios of body weight to body size. In general, the variation among sites in the relationship between nestling growth and body reserves suggests that site-level effects may drive the optimal development strategy for nestlings.

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