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# VARIATION IN GROWTH OF NESTLING TREE SWALLOWS ACROSS MULTIPLE TEMPORAL AND SPATIAL SCALES

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ABSTRACT.—Differences within a species in rates of growth of nestlings can be used as indicators of the quality of parental care, environmental conditions, and future success of offspring, whereas comparisons among different species may reflect a history of different ecological conditions or life-history strategies. The presesnt study examines the patterns of variation in growth in nestling Tree Swallows (*Tachycineta bicolor*) from across the species' range and compares Tree Swallows to other species. Growth of Tree Swallows was typical of other species in the family Hirundinidae. As a family, the Hirundinidae have slower growth than typical for passerines. Growth rate of species of Hirundinidae was not correlated with adult body mass or average brood size. Contrary to predictions, species that are double-brooded did not have higher growth rates, but swallow species living at higher latitudes did have higher growth rates than tropical species. Substantial variation in growth rates was observed among populations of Tree Swallows, yet the amount of variation observed between breeding colonies only a few kilometers apart, or from the same colony in different years, was as great as that seen in populations separated by hundreds of kilometers. Within a population, differences in growth among years were correlated with temperature and food supply when nestlings were being raised. No correlation between climate and growth was seen when comparing different populations. Differences between populations were not explained by local habitat, nor were large-scale geographic patterns evident. I used both experimental and observational evidence to evaluate the implications of short-term reduction in growth for subsequent growth and survival. Nestlings were slow to recover from even very short periods of delayed growth that occur early in the nestling phase. Return of nestlings with experimentally or naturally induced delayed growth was reduced, which suggests that short interruptions in growth may have long term effects on postfledging survival, even though mass at fledging is not affected. *Received 9 August 1999, accepted 16 September 2000.*

NESTLINGS OF ALTRICIAL BIRDS exhibit substantial variation in growth rates both within and among species. Variation within a species is often used as an indicator of variability in parental care, environmental conditions, or nestling quality. Growth rates of nestlings influence length of time offspring are dependent on their parents, their energy requirements and rate of food delivery required of the parents, and length of time they are exposed to nest predators (Lack 1968, Bosque and Bosque 1995, Halupka 1998). Variation among species is typically seen as a result of variation in life-history strategies. Altricial birds are among the fastest growing vertebrates (Case 1978), with most small passerines attaining full adult mass within 10 to 20 days of hatching. High rates of energy intake are necessary to sustain that rapid growth. In a broader context, those energy demands, coupled with physiological constraints on growth, accentuate the trade-offs that exist between maximizing growth and attempting to optimize other aspects of life histories (Lack 1968, Ricklefs 1984, Ricklefs and Starck 1998, Starck and Ricklefs 1998b).

Within a species, nestlings with below-average growth or size at fledging generally suffer from reduced postfledging survival (Gebhardt-Henrich and Richner 1998). Reduced growth may also have a long-term effect on fitness, even when it does not appear to result in lower postfledging survival, by decreasing the ability to obtain a breeding territory or mate or by lowering subsequent fecundity (Gustafsson and Sutherland 1988, Richner 1992, Richner et al. 1989, Lozano 1994). Although it is clear that growth is a good indicator of future success, factors that determine variation in size and mass are not as well understood.

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Previous studies have generally not differentiated between growth reductions that are due to chronic food shortages or that are caused by poor parental care and those caused by short-term fluctuations in food supply within a season. Several groups of birds with food supplies that are subject to short-term fluctuations, such as seabirds (Hawksley 1957, Dunn 1975, Konarzewski and Taylor 1989) and aerial insectivores (Koskimies 1950, Lack and Lack 1951, Bryant 1978, Wrege and Emlen 1991), are observed to undergo periods of interrupted growth and development under adverse conditions, resuming normal growth once conditions improve. The long-term effects of those temporary growth reductions have seldom been explored, but if starvation interferes with critical developmental stages, permanent changes could result. Previous studies have found that nestlings subject to short-term shortages of food eventually attain full body mass (Wiggins 1990b, Negro et al. 1994), making it unclear whether such reductions in growth have a long-term effect on postfledging survival if survival depends solely on body size.

In contrast to the view that intraspecific variation is due to effects of the environment, variation among species is often viewed as the adaptive outcome of different selection pressures. Predation rates, food availability, number of breeding attempts per year, and level of competition among siblings are all thought to influence interspecific differences in growth (Lack 1968, Bosque and Bosque 1995, Halupka 1998). Even though the sources of intraspecific and interspecific variation in growth are ultimately the same, the two types of variation have seldom been considered together.

The present study employed two approaches to address the question of the ecological significance of variation in growth rates of Tree Swallows (*Tachycineta bicolor*) and variation among the species in the Hirundinidae. First, I described both the inter- and intraspecific variation in growth. Variation in growth among different species and among different groups of Tree Swallows was compared to factors that might contribute to variation, such as climate, life history (clutch size and number of broods per season), habitat, food supply, and geographic location. The absolute degree of variation among related species provides insight into the degree of plasticity possible on an evolutionary time scale, whereas differences in life history among related species may indicate how growth responds to changes in the relative demands placed on developing nestlings. Second, I examined the significance of short-term periods of reduced feeding on growth and the possible long-term effects of those reductions. Although the importance of chronic food shortages is well known, relatively little attention has been paid to short-term fluctuations in resources and their effect on subsequent aspects of an individual's biology. I present observational and experimental evidence to examine the importance of short-term reductions in growth.

## METHODS

Tree Swallows breeding in nest boxes were studied at the Cornell University Experimental Ponds Facility (42°30′N 76°27′W), near Ithaca, New York. This facility consists of two breeding sites located approximately 2 km apart. Unit One supported approximately 55 to 75 pairs of breeding Tree Swallows, and Unit Two had between 10 and 23 pairs. Insect abundance was measured daily using suction traps running during daylight hours, and high temperature was recorded daily. These sites and methods for sampling insects are described in detail in McCarty and Winkler (1999a, b). All values are reported as means ± SE.

Nestlings of all ages were weighed to the nearest 0.1 g during the 1990–1993 breeding seasons using either Pesola spring scales or a portable Ohaus electronic balance. In addition, nestlings were measured on day 10 only in 1989, and those data are included in analyses of return rates. Swallows breeding at those sites are monitored closely for the exact date of hatching to determine nestling age. All nestling ages are given as hatch day equal to nestling day 1. Lengths of flattened and straightened wing chord (hereafter ''wing length''), the 9th (outermost) primary, and 6th (outermost) rectrix feather were measured to the nearest 0.5 mm using a ruler with a wing and feather stop. Length of the manus was calculated from difference between wing and 9th primary length. Length of the tarsometatarsus (henceforth ''tarsus'') was measured to the nearest 0.1 mm using dial calipers. Nestling Tree Swallows typically fledge on day 21; disturbing nestlings after day 15 may cause premature fledging, so sample sizes for older nestlings are small and come primarily from nestlings removed for other studies.

Growth curves were fitted to mass data and growth rate constants were calculated for nestlings from Ithaca in each year and at both breeding locations. Nestlings at Ithaca were measured at more than one age, but not every day, providing a mixed longitudinal sample (Ricklefs 1983). Logistic growth curves are suitable for Tree Swallows (Zach and Mayoh 1982) and curves were fitted to mean masses for each population using an iterative, least-squares procedure (non-lin module of SYSTAT; Wilkinson et al. 1992) and equation:

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

where $x$ is the nestling age, $M(x)$ is body mass at age $x$, $M(0)$ is the initial mass, $M(\infty)$ is the asymptotic body mass, and $K$ is the growth rate constant (Ricklefs 1983).

*Variability in Tree Swallow growth rates.*—Growth rates of nestling Tree Swallows from Ithaca were compared to published data on the growth of Tree Swallows from other sites throughout North America. For all data sets, logistic growth-rate constants were calculated for the mean population growth using equation 1. For consistency, that equation was used even when the authors of the original papers present a value for $K$. That eliminates variation owing to differences in the method used to calculate $K$ (Starck and Ricklefs 1998a).

When not given in the original paper, latitude and longitude of the breeding sites were estimated from site descriptions. When possible, other study sites were classified as being either near water or as dry uplands, and mean clutch size for the population was determined on the basis of descriptions in the original papers. Climate data summaries for the period 1961–1990 were obtained from regional climate databases for locations where Tree Swallow growth had been measured. The average temperature and average daily high temperature for the month of June provided by those summaries were used as indicators of breeding season climate. Data for comparisons of climate among individual years at the Ithaca site were based on data collected on site (see McCarty and Winkler 1999b for details). Those variables were compared to variation in growth-rate constants using nonparametric Kendall rank correlation (Conover 1980).

*Comparison with other species.*—Interspecific variation in growth among the Hirundinidae was examined using published descriptions of growth. For each species in the family Hirundinidae with an available growth curve, the mean mass of nestlings at each age was used to estimate the growth-rate constant using equation 1. Information on adult body mass, life history (clutch size and number of broods per season), and location studied (latitude) was collected from published sources. Those variables were compared to the growth constants using nonparametric Kendall rank correlation or Mann-Whitney tests (Conover 1980).

Growth of species in the Hirundinidae was compared to other species of passerines. Ricklefs (1968a) provides growth constants and ratio of asymptotic mass to adult mass for small and medium-sized passerines (<100 g). Those data were used to compare members of the other families of passerines to the data on the Hirundinidae described above using nonparametric Mann-Whitney tests (Conover 1980).

*Postfledging survival.*—All nestlings in the Ithaca population were banded prior to fledging. Adult swallows were captured in mist nets prior to breeding or at their nest boxes during breeding. Return rates of birds banded as nestlings are used as an estimate of survival by providing a sample of those nestlings that survive to one year. Because nestling mass and wing were measured at different ages in different years (between days 8 and 12), measurements were standardized by subtracting the mean value for each year from each individual's mass or wing length and then dividing by the standard deviation for that year, to produce a mean of 0 and standard deviation of 1 for each year's measurements. Data from 1989 to 1993 were then pooled and effects of standardized mass, wing length, and tarsus length on the probability of an individual being captured as an adult were analyzed using logistic regression (Hosmer and Lemeshow 1989).

*Effects of short-term fasting.*—A fasting experiment was conducted to determine the importance of short-term reductions in growth to the subsequent growth of nestlings. Nests available on days when experiments were conducted were paired to balance the experimental groups for nestling age, brood size, and pre-treatment nestling mass. Nests were also paired by age of female parent so nests of second-year (brown) females were compared to nests of other second-year females. Within those pairs, nests were randomly assigned to either control or treatment groups. Initial mass was measured on day 5 and the morning of the start of the experiment (day 6). On the morning of day 6, nestlings were weighed between 0630 and 0730 Eastern Standard Time (EST), and all nestlings from the experimental broods were removed and were fasted until the evening of the same day. One or two nestlings from a nonexperimental nest were placed in the treatment nests to keep the parents from abandoning while their chicks were gone. Nestlings in control broods were weighed and returned to the nest. Experimental broods were placed in controlled temperature chambers under an incandescent lamp. As part of a separate experiment, nestlings were held at either 20 or 30°C. The absolute mass of the two groups did not differ by day 7 (30°C = 10.7 ± 0.7 g, 20°C = 10. 4 ± 0.6 g, $U$-test, $Z < 0.01$, $P > 0.99$), so I pooled temperature treatments into a single experimental group. Treatment nestlings were returned to the nest between 1730 and 1845 EST.

Control and treatment nestlings were weighed at the time the treatment broods were returned to their nests. Experimental nestlings differed from controls both in being deprived of food and in being subject to possible stress induced by simply being separated from their nest and parents for several hours. However, because nestlings of that age group are too young to show any fear response and settled into experimental nests in an apparently normal manner, that difference is probably of minor significance for differences in growth.

Nestlings in control and treatment nests were weighed between 1300 and 1800 EST on nestling days 7, 8, 10, and 12. Paired nests were weighed within one hour of each other. Wing length of all nestlings was measured on days 10 and 12, and the tarsus was measured on day 12. Masses and wing lengths were not measured on day 12 at four nests that were disturbed by other researcher activities on that day. Tarsus length was still measured on day 12 for those nests, because adult tarsus length is obtained before day 12 (see below). For statistical analyses, each brood was treated as an experimental unit and the mean masses (or other measurements) for the chicks within broods were compared using paired Wilcoxon signed-rank tests (Conover 1980). The proportion of the broods in each group that were recaptured in subsequent years are compared using the Wilcoxon test to explore long-term effects of fasting on survival. In addition, the relationship between mass change of the experimental group and proportion of the brood subsequently recaptured is examined using Kendall rank correlation.

The experimental results are also compared to a sample of nestlings that underwent a natural period of weather-related fasting, resulting in reduced growth. A wet, cool period in 1992 resulted in the deaths of all nestlings in the population, except for four broods that hatched during the adverse conditions. The growth of those nestlings after conditions improved is compared to the population mean using one-group sign tests (Conover 1980). The number of nestlings from those four nests returning in subsequent years is compared to the number returning from nests that hatched immediately after the period of adverse weather using Fisher's exact test.

## RESULTS

The growth of nestling Tree Swallows exhibited the classic sigmoidal curve found in other passerines (Fig. 1). Nestlings typically reached adult mass of approximately 20 g around day 10 or 11, approximately half way through the 21-day nestling period. Nestlings continued to increase their mass for one to three days, reaching a peak mass of around 22 g. During the period of this study, the heaviest nestling reached 27.6 g. Fitting the data from Ithaca to a logistic growth curve gave a growth rate constant, $K = 0.50$, and an asymptotic mass of 21.7 g.

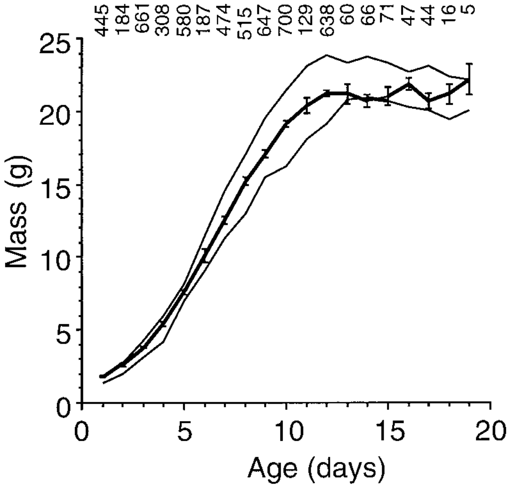

FIG. 1. Change in mass during growth of nestling Tree Swallows. Bold line represents mean mass (±2 SE) of nestlings from Ithaca, New York during the period 1990–1993. Thin lines show the 10th and 90th percentiles of mean masses for nestling Tree Swallows from 13 other locations across North America. Sample sizes (number of nestlings) for Ithaca data are given across the top of the figure. Data for other sites from: Paynter 1954; Sheppard 1977; Marsh 1980; Zach and Mayoh 1982, 1986; Wiggins 1990b; Pijanowski 1991; Fabro 1993; Nichols et al. 1995; Teather 1996; Secord and McCarty 1997; Ramstack et al. 1998.

Growth of the structural features wing length and flight feathers was more linear than the increase in mass (Fig. 2A). Flight feathers (primaries and rectrices) first emerged on day 7. Growth of the wing length and flight feathers continued throughout the nestling period, with growth being completed some time after fledging (Fig. 2A). The bony structures, tarsus and manus length, were the first to reach adult size (Fig. 2B). Tarsus reached the adult length of 12 mm between day 8 and 9, whereas manus length reached its adult length of 25 to 26 mm by day 9 (Fig. 2B).

*Variability in Tree Swallow growth rates.*—Within the Ithaca population, nestling growth rates varied with breeding location and year. Between the two Ithaca breeding sites, growth was consistently higher at Unit Two (Fig. 3A),

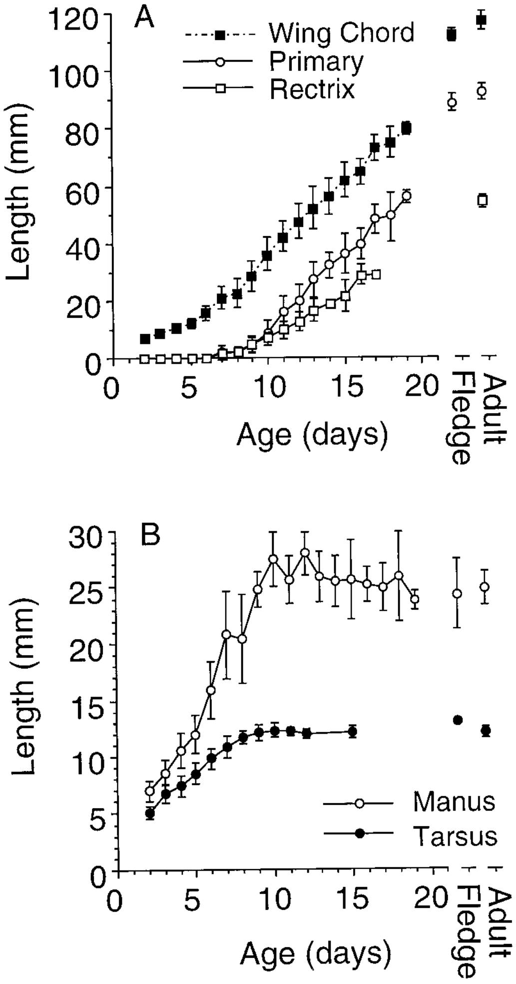

FIG. 2. Growth of wing and flight feathers (2A), and manus and tarsus (2B) of nestling Tree Swallows. Analogous data for fledglings ("Fledge") and adults are also provided. Mean ± SE given for each age: Sample sizes for each age vary from 10 to >600 individuals.

with $K$ for Unit One = 0.49, and $K$ for Unit Two = 0.53. Temporal variation also contributed to the overall variability in growth rates. Growth varied among years at the Ithaca site (Fig. 3B), with $K$ varying from 0.49 in 1992 to 0.56 in 1991. Although sample size is small (four years), growth-rate constants were positively correlated with mean high temperature during the breeding season (Kendall rank correlation; $\tau = 1.00$, $Z = 2.04$, $n = 4$, $P = 0.042$) and with mean insect abundance over the breeding season ($\tau = 1.00$, $Z = 2.04$, $n = 4$, $P = 0.042$).

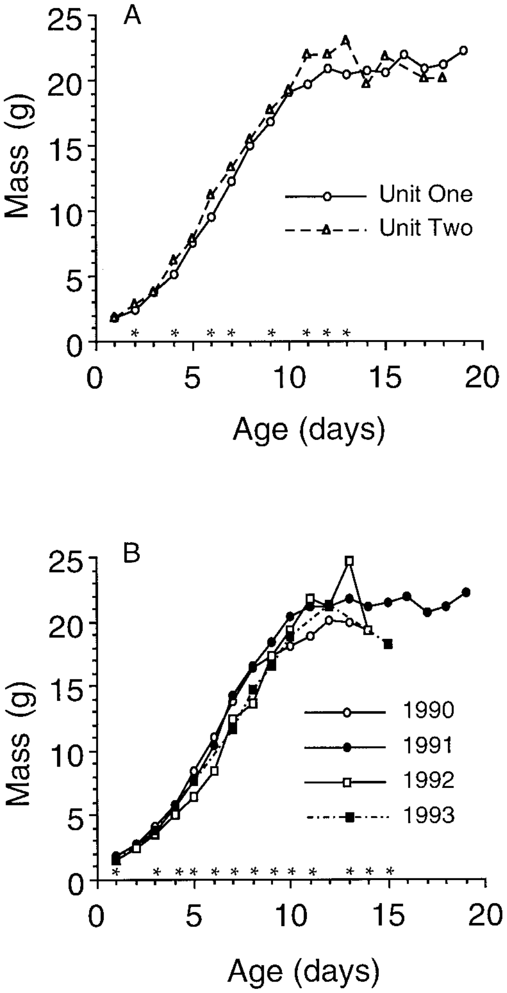

FIG. 3. Variation in nestling growth rates at Ithaca among years and between sites. For each age, nestling mass was compared using ANOVA and "*" indicates that the differences between sites (A) and among years (B) are significant after application of a sequential Bonferroni adjustment (Rice 1989). Error bars omitted for clarity.

Among studies conducted across the Tree Swallow's range, values for the growth-rate constants varied between $K = 0.41$ (Pijanowski 1991) to $K = 0.59$ (Zach and Mayoh 1982), with an average $K$ for the 15 sites of 0.50 ± 0.01. Nestling growth-rate constants were not correlated with the latitude or longitude of the nesting site (Kendall rank correlation, latitude $\tau = -0.04$, $Z = 0.21$, $n = 15$, $P = 0.83$, longitude $\tau = -0.22$, $Z = 1.16$, $n = 15$, $P = 0.25$). Growth-rate constants from those sites were not correlated with either average daily mean temperature ($\tau = -0.19$, $Z = 0.80$, $n = 11$, $P = 0.42$) or the average daily high temperature ($\tau = -0.35$, $Z = 1.51$, $n = 11$, $P = 0.13$). There was no difference in $K$ between sites classified as uplands (0.52 ± 0.05, $n = 5$) and those near water (0.50 ± 0.05; Mann-Whitney $U$-test, $Z = 0.60$, $n = 9$, $P = 0.55$). The average clutch size in a population was not correlated with nestling growth rate constants ($\tau = -0.16$, $Z = 0.75$, $n = 13$, $P = 0.45$).

*Comparison with other species.*—Growth of nestling Tree Swallows was within the range of variability seen in the family Hirundinidae (Table 1). Among swallow species, there was no correlation between adult body mass and nestling growth rate ($\tau = -0.17$, $Z = 0.91$, $n = 16$, $P = 0.36$). Species known to regularly lay two broods per season (Turner and Rose 1989) did not have growth rates different from single-brooded species (double brood 0.43 ± 0.03; single brood 0.46 ± 0.02; $Z = 0.36$, $n = 13$, $P = 0.72$). There was a slight tendency for species with larger clutch sizes to grow faster but that was not significant ($\tau = 0.48$, $Z = 1.85$, $n = 16$, $P = 0.06$) and confounded by the increase in clutch size with latitude. Growth rates of swallows did vary with latitude, with species breeding closer to the equator having slower growth (Fig. 4).

Ricklefs (1968a) provides growth constants for 63 species of small and medium-size passerines (excluding Hirundinidae and species with adult mass over 100 g) from 14 families or subfamilies. The average $K$ for those passerines is 0.501 ± 0.01, significantly higher than the mean of 0.429 ± 0.02 for 16 species of Hirundinidae ($Z = 3.03$, $P = 0.003$). Ricklefs (1968a) also provides the ratios of asymptotic mass to adult mass for 58 species of small and medium-size passerines (excluding Hirundinidae and species with adult mass over 100 g). The Hirundinidae in Table 1 had a significantly higher ratio (1.15 ± 0.04) than do non-Hirundines (0.87 ± 0.02; $U$-test, $Z = 5.28$, $P < 0.001$).

*Postfledging survival.*—For the Ithaca population as a whole, nestling growth was significantly related to the probability that a nestling would be recaptured, either as a spring migrant or a breeding individual. Logistic regression on the pooled data for 1989–1993 shows that heavier nestlings were more likely to return ($\chi^2 = 12.4$, df = 1, $n = 1{,}641$, $P < 0.001$), as were those with longer wings ($\chi^2 = 6.55$, df = 1, $n = 1{,}233$, $P = 0.011$), and tarsi ($\chi^2 = 5.5$, df = 1, $n = 215$, $P = 0.019$).

*Effects of short-term fasting.*—An experimental group of nestlings were fasted for 10 to 12 h on day 6 (Fig. 5A). Mass of nestlings in control and treatment broods did not differ at the beginning of the experiment (control nestlings = 9.5 ± 0.3 g, experimental nestlings = 9.0 ± 0.3 g; Wilcoxon test, $Z = 1.02$, $P = 0.31$). Brood size of the two groups did not differ (control = 5.3 ± 0.2, experimental = 5.4 ± 0.2; Wilcoxon test, $Z = 1.01$, $P = 0.31$), and was well within the typical brood size of 5 to 6 nestlings of this and other Tree Swallow populations (Robertson et al. 1992, McCarty and Secord 1999).

Experimental nestlings lost an average of 0.7 ± 0.1 g per nestling during day 6 (8% of their starting mass), whereas control broods gained an average of 1.9 ± 0.3 g per nestling (20% of their starting mass) during the same period (Wilcoxon test, $Z = 3.59$, $P < 0.001$). Nestlings in the experimental broods remained significantly lighter through day 10 (Fig. 5A). On day 12, the two groups no longer showed significant differences though the trend towards heavier nestlings in the control group remained (Fig. 5A). The experimental treatment also resulted in a difference in structural size. Wing chord was smaller in experimental broods on both day 10 (experimental = 32.8 ± 1.1 mm, control = 36.0 ± 0.7 mm, Wilcoxon test, $Z = 2.94$, $P = 0.003$) and day 12 (experimental = 32.8 ± 1.1 mm, control = 36.0 ± 0.7 mm, Wilcoxon test, $Z = 3.69$, $P = 0.007$). Tarsus length of day 12 experimental nestlings (36.0 ± 0.7 mm) was significantly shorter than controls (36.0 ± 0.7 mm Wilcoxon test, $Z = 3.35$, $P < 0.001$). All nestlings in both experimental and control broods survived to fledging.

Given the observed relationship between growth and the probability of being recaptured as an adult in this population (above), one would predict that nestlings with artificially reduced growth rates would return at a lower rate than unmanipulated nestlings. Sample size is small, but there was no significant difference in return rates of nestlings from experimental and control broods (Fig. 6; $Z = 0.85$, $n = 18$, $P = 0.39$). However, among the experimental nestlings there was a significant relationship between the amount of mass lost during the manipulation and the proportion of the brood recaptured the following year (Fig. 6;

TABLE 1. Comparison of the growth rates of swallows and martins, family Hirundinidae. Fledging and adult wing is wing chord in millimeters. Nesting period in days, masses in grams. Data from tables and figures in original papers. *K* is the growth constant of the logistic growth curve calculated using Equation 1 or taken directly from the original paper if insufficient data were available.

| Species | Mass at hatching | Fledging mass | Fledging wing | Adult mass | Adult wing | Nestling period | *K* | Source |
|---|---|---|---|---|---|---|---|---|
| *Tachycineta bicolor* | 1.8 | 22.2 | 79.6 | 20.1 | 117.4 | 21 | 0.49–0.56 | 1, 2, 3 |
| *Tachycineta albilinea* | 1.6 | 13.2 | 59 | 13.9 | 96.1 | 23–27 | 0.43 | 1, 4 |
| *Tachycineta thalassina* | 1.7 | 17.0 |  | 15 | 118.4 | 23 | 0.41 | 1, 2, 5 |
| *Tachycineta cyaneoviridis* | 1.9 | 16.5 | 76.5 | 17.5 | 112.3 | 23 | 0.41 | 1, 6 |
| *Progne tapera* | 4 | 35 |  | 36.1 | 127 | 28 | 0.28 | 1, 7 |
| *Progne subis* | 4.0 | 47–51 |  | 56 | 118.4 | 27–31 | 0.38–0.40 | 1, 2, 8, 9, 10 |
| *Progne chalybea* | 3 | 36 |  | 41.5 | 131.1 | 25–28 | 0.40 | 1, 7 |
| *Notiochelidon cyanoleuca* |  |  |  | 10.5 | 94.2 | 26 | 0.39 | 1, 4 |
| *Stelgidopteryx serripennis* | 1.5 | 15.0 | 84 | 15.9 | 107 | 18–21 | 0.46 | 1, 2, 11 |
| *Riparia riparia* | 1.5 | 15.8 |  | 13.5 | 107 | 22 | 0.41–0.58 | 1, 12 |
| *Hirundo rustica* | 1.9 | 18.6 | 91 | 18.9 | 123.1 | 18–23 | 0.46–0.56 | 1, 2, 13 |
| *Hirundo tahitica* | 1.8 | 14.6 | 76 | 14.1 | 102 | 19–21 | 0.42 | 14 |
| *Petrochelidon spilodera* | 1.1 | 29.1 | 92 | 20.6 | 111 | 24–25 | 0.311 | 1, 15 |
| *Petrochelidon pyrrhonota* | 1.5–2.2 | 21 |  | 21.6 | 109 | 23–24 | 0.43–0.55 | 1, 2, 16, 17 |
| *Petrochelidon ariel* | 1.3 | 11.8 | 75 | 11.2 | 91.9 | 23 | 0.48 | 1, 18 |
| *Delichon urbica* | 1.7 | 17.7 | 98–101 | 18.3 | 111 | 27 | 0.50 | 19, 20, 21, 22 |

1 = Turner and Rose 1989; 2 = Ricklefs 1968a; 3 = McCarty this study; 4 = Ricklefs 1976; 5 = Edson 1943; 6 = Allen 1996; 7 = Turner 1984; 8 = Ricklefs 1968b; 9 = Allen and Nice 1952; 10 = Hill 1994; 11 = Lunk 1962; 12 = Petersen 1955; 13 = Jones 1987; 14 = Bryant and Hails 1983; 15 = Earlé 1986; 16 = Stoner 1945; 17 = Chapman and George 1991; 18 = Tarburton 1991; 19 = O'Connor 1977a; 20 = Bryant and Gardiner 1979; 21 = Prinzinger and Siedle 1988; 22 = Bryant 1975.

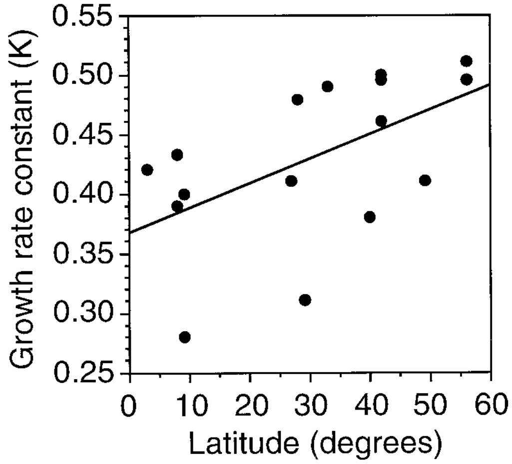

FIG. 4. Growth rates of nestlings of 16 species of Hirundinidae in relation to latitude. Growth rates increased significantly with distance from the equator; $n = 16$, $\tau = 0.43$, $Z = 2.33$, $P = 0.020$. Sources of data given in Table 1. Line fit using least squares regression provided for illustration.

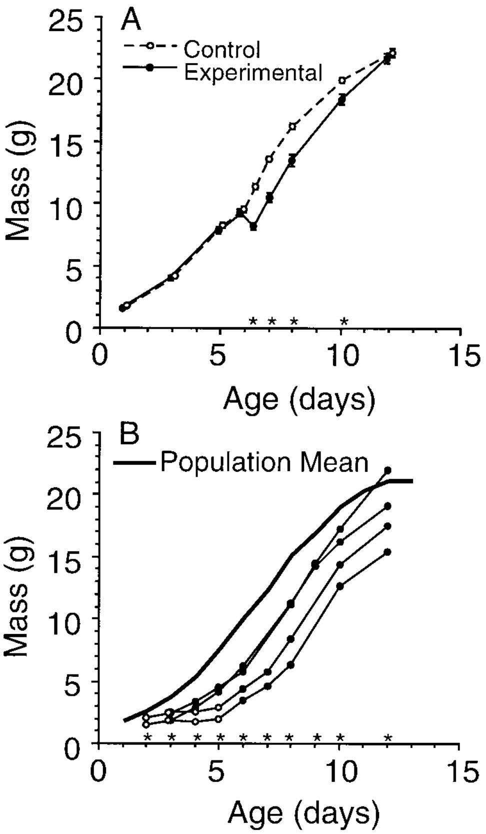

FIG. 5. Effects of experimental (A) and natural (B) short-term food deprivation on subsequent growth of nestling Tree Swallows. Effects of experimental growth reduction on day 6 persisted until day 12 (A). Lines for each category based on mean mass of nestlings within broods ± SE. Mass of deprived nests ($n = 18$ broods) and control nests ($n = 18$ broods) compared using paired Wilcoxon sign rank tests for each age. Ages where differences remain significant after application of a sequential Bonferroni adjustment to $P$-values (Rice 1989) are indicated by "*." Growth of nestling Tree Swallows during and after a naturally occurring period of adverse environmental conditions was retarded (B). The bold line represents normal growth based on Figure 1. Circles joined by thin lines represent the mean mass of nestlings in four broods hatched during periods of adverse weather. Open circles represent mean mass during the period adverse weather was occurring; closed circles show mass after weather conditions returned to normal. Mass at each age is compared to the population mean using one sample sign tests. $P$-values that remain significant after application of a sequential Bonferroni adjustment are indicated by "*."

Kendall rank correlation; $\tau = 0.35$, $Z = 2.02$, $n = 18$, $P = 0.043$).

Patterns of reduced growth similar to those observed in the fasting experiments can be seen in cases of natural starvation due to inclement weather. During a four-day period of low temperatures, rain, and reduced availability of insects beginning on 19 June 1992, most adult Tree Swallows stopped feeding their nestlings. Although all nestlings older than 3 days at the beginning of this period died after three or four days (McCarty 1995), some nestlings that hatched at the beginning of the period survived. Those nestlings failed to grow or develop through that period, and, once feeding resumed on 23 June, they remained several days behind their normal growth trajectory (Fig. 5B). Wing length at days 8 (14.4 ± 0.8 mm, $n = 9$), 10 (26.6 ± 1.2 mm, $n = 17$), and 12 (37.4 ± 1.8 mm, $n = 17$) were also significantly shorter than the population mean (one group sign tests, $P < 0.001$ for each day). Although those nestlings fledged successfully, the reduced growth experienced resulted in a long-term effect on those nestlings. Nestlings from the five nests that hatched during the period of adverse weather were less likely to be recaptured (1 of 23 nestlings) than nestlings that fledged from the three nests that hatched in the week im-

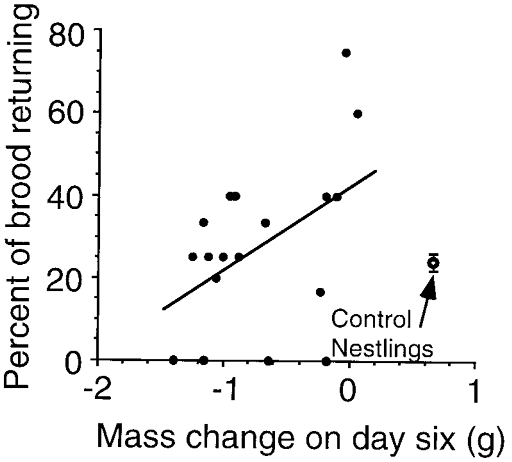

FIG. 6. Effects of experimental food deprivation on the proportion of a brood recaptured in the following year. Mass change during the experiment is based on the mean change in mass for all nestlings in a brood. Return rates of experimental and control broods (±SE) did not differ, but among experimental nestlings there was a correlation between the amount of mass lost during the experiment and the proportion of the brood returning.

mediately following the adverse weather (6 of 15 nestlings; Fisher's exact test, $P = 0.009$).

## DISCUSSION

*Variability in Tree Swallow growth rates.*—Growth of nestling Tree Swallows at Ithaca varied with breeding location and year (Fig. 3). The two breeding sites at Ithaca are separated by only 2 km and are in very similar habitats (McCarty and Winkler 1999a, b). The consistent differences in growth between those two sites are not a function of clutch size (McCarty and Winkler 1999b) or food availability, because insect abundance is similar at the two sites (McCarty 1995). Rather, the basis for the differences between the two Ithaca sites probably lies in differences in density of breeding birds. The density of nest boxes and hence, density of breeders, is 3 to 6 times higher at Unit One, and parents at that site must forage further from their nests, possibly because of interference among foragers (McCarty and Winkler 1999a). Higher densities of breeding pairs reduces nestling nutrition in some passerines (Wiklund and Andersson 1994), but other swallows, notably Cliff Swallows (*Petrochelidon pyrrhonota*), have increased success at larger colonies (Brown and Brown 1996). The difference may lie, in part, in a more even distribution of the insects Tree Swallows eat, eliminating the dependence of Tree Swallows on colony-mates for finding food. Tree Swallows usually forage within sight of the nest site, in contrast to Cliff Swallows where individuals may fly an average of 500 to 700 m from the nest to forage (Brown and Brown 1996, McCarty and Winkler 1999a).

Some differences in growth among years in the Ithaca population are probably related to variation in weather and food supply during nestling rearing. Previous work shows that short-term temporal variation in temperature and food supply, on the scale of 48 h, affects nestling growth (McCarty and Winkler 1999b). The food supply of Tree Swallows is correlated with temperature on a short-time scale (McCarty and Winkler 1999b) and that translates into a relationship between mean temperature and food supply across an entire breeding season. At Ithaca, the lowest growth rate occurred in 1992, a year when most nestlings died during a period of poor weather in mid-June and when both temperature and food supply were below normal; higher growth rates occurred in warmer years with higher abundances of insects.

Across North America, substantial variation in growth among different populations of Tree Swallows was found, but none of the factors examined that differ among those sites explain that variation. The lack of a correlation between growth-rate constant and either latitude or longitude suggests that broad-scale patterns in climate across North America are not responsible for the variation (but see Dunn et al. 2000). Although this and previous studies show that temperature and food supply have important effects on growth on a short-time scale and in a single location, those effects cannot be extrapolated to effects that occur on larger scales. Although changes in climate over time have effects on timing of laying in Tree Swallows (Dunn and Winkler 1999), differences in climate at different sites do not influence growth. Likewise, though breeding sites near water may have larger and more reliable food supplies (Quinney and Ankney 1985, Dunn and Hannon 1992), there was no consistent difference in growth between nestlings at sites near water and those at upland sites.

The lack of a correlation between average clutch size for a population and its growth rate supports results of analyses that have examined effects of brood size on growth rates within populations of Tree Swallows (Zach and Mayoh 1982, Wheelwright et al. 1991, McCarty and Winkler 1999b). It is not surprising that natural brood size has little effect on growth rates. It is likely that decisions about the number of offspring to produce are heavily influenced by differences in individuals' abilities to raise young successfully. Because rapid growth is such an important determinant of future success, adjustments in clutch size and brood size will tend to minimize differences in growth rates both within and among populations. The effects of brood size on growth are more likely to be seen in experiments where individuals are forced to raise additional young. However. the effects of even enlarged brood size on growth in Tree Swallows has been difficult to document (DeSteven 1980, Wiggins 1990a, Wheelwright et al. 1991).

Like other passerines, mass and size of bone and feather structures changes rapidly in Tree Swallows (Figs. 1 and 2). Both bone structures measured in Ithaca Tree Swallows—tarsus and manus—reached adult length by day 9. Rapid development of tarsus has been described as a possible adaptation for intrabrood competition during begging (O'Connor 1984), and rapid lengthening of the wing bones may be necessary to provide time for sufficient calcification before fledging (Carrier and Leon 1990, Carrier and Auriemma 1992) or may be a prerequisite for flight feather development.

Tree Swallows fly immediately upon exiting the nest for the first time. However, the 9th primary feathers reach only 60–70% of adult length prior to fledging, and full adult length of primaries may not be attained until the first or even second prebasic molt (Robertson et al. 1992), a pattern seen in many passerines (Alatalo et al. 1984). This is a surprising result for a species so dependent on flight for obtaining food and where selection on flight efficiency would be expected to be strong, though shorter wings may reflect a tradeoff between increased maneuverability at the expense of flight speed (Alatalo et al. 1984)

*Comparison with other species of swallows.*—Given the similarity in ecology among species of swallows, it is interesting to note the degree of variability seen in growth rates among the Hirundinidae (Table 1). The overall ecological and morphological similarity among species make the swallows an appropriate family for interspecific comparisons of growth. Differences in life history that do exist among species are not correlated with variation in nestling growth. Although it has been suggested that species that do not attempt to rear more than one brood per season should have lower growth rates than double-brooded species (Ricklefs 1984), the data for swallows do not support that hypothesis: single-brooded species have growth rates similar to those of regularly double-brooded species. Likewise, whereas brood size changes with latitude, number of offspring raised does not appear to have an effect of growth rate.

Swallows do support the general pattern of slow growth in tropical species (Fig. 4; Ricklefs 1968a, 1976). The Hirundinidae provide a robust example of that pattern both because several genera contain both temperate and tropical representatives and because of the overall ecological similarity among species. Additional data will be needed to interpret possible factors leading to that pattern in swallows, but it seems likely that the pattern of peak availability and degree of variation in the supply of aerial insects may be an important contributing factor in that relationship. That is in contrast to the intraspecific comparison among Tree Swallow populations where no correlation with latitude exists. The simplest explanation for that difference is that the latitudinal range covered by the interspecific comparison (approximately 53° latitude) is far greater than the variability among Tree Swallow populations that have been studied (8° latitude).

As a group, the Hirundinidae have lower growth rates than other passerines (this study) and they also have longer nestling periods than other passerines of similar size (McCarty 1995). Differences between Hirundinidae and other passerines are also reflected in the significantly higher ratio of the asymptotic mass of nestlings to adult mass in swallows. The ratio of 1.15 in the Hirundinidae indicates that swallows tend to reach and even exceed adult mass prior to fledging, whereas the other passerines (ratio = 0.87) fledge at an earlier developmental stage.

Several aspects of the ecology of swallows, including their relatively large brood sizes, susceptibility to short-term fluctuation in food supply, relatively safe nest sites, or the necessity of greater development before fledging could influence patterns of growth rates. If swallows do have safer nest sites, their slow growth would tend to support the trade-off between growth and mortality proposed by Lack (1968), who suggested that predation risk selected for faster growth, whereas starvation risk selected for slower growth. The effects on growth of the susceptibility of swallows to food shortages are difficult to predict. Although slower growth may decrease maximum energy demands (Lack 1968, Case 1978), rapid growth might limit the duration of the vulnerable (Lack 1968, Winkler 1993).

*Postfledging survival.*—The lower probability of recapture in nestling Tree Swallows with below average growth of mass, wing length, or tarsus length, is typical of other species of passerines (Gustafsson and Sutherland 1988, Tinbergen and Boerlijst 1990, Gebhardt-Henrich and van Noordwijk 1991, Gebhardt-Henrich and Richner 1998). Subsequent recapture of nestlings as adults is frequently used as an indicator of postfledging survival. Because not all surviving nestlings are recaptured, that assumes that all nestlings have an equal probability of dispersing. As is the case for most small passerines, not enough is known about natal dispersal of Tree Swallows to evaluate that assumption. Given the difficulty that cavity nesters such as Tree Swallows have in securing breeding sites (Robertson et al. 1992), it seems that the ability to secure a nest cavity at the natal site, and thus be recaptured, would be advantageous.

The relationship between nestling growth and subsequent recapture appears to be a causal one (Tinbergen and Boerlijst 1990), but the mechanism behind the relationship remains unclear. Perrins (1965) attributed the relation between nestling size and survival in Great Tits (*Parsus major*) to the higher energy reserves available to the heavier young birds. That interpretation has been challenged by Garnett (1981) who calculated that differences in fat reserves were probably not able to significantly influence survival. The lack of a relationship between fat stores of individual nestling Tree Swallows and either their total body mass or the size of structural features such as wing or tarsus length (McCarty 1995) suggests that increased energy stores are not primarily responsible for the differences in recapture seen here. Garnett (1981) proposed that body size acting through dominance and social interactions may be responsible for differences in postfledging survival. That effect is seen in Carrion Crows (*Corvus corone*; Richner et al. 1989, Richner 1992) and may occur in Tree Swallows (Lozano 1994).

*Effects of short-term fasting.*—The fasting experiment indicates that short-term reductions in growth have long-term effects on the subsequent size (as measured by tarsus length) and mass of nestling Tree Swallows (Fig. 5A). An analogous pattern is seen associated with natural growth reductions caused by inclement weather (Fig. 5B). Compensatory growth is not observed after either experimental or natural periods of short-term growth. Nestlings having short periods of fasting do eventually reach normal mass but only after a longer period of growth. The delayed growth seen in those nestlings emphasizes the importance that just a few hours or days of delayed growth can have effects comparable to the cumulative effects of chronic food shortage throughout the nestling period.

The conclusions of this study differ from those of Wiggins (1990b), who found no long-term effects of reduced nestling growth in Tree Swallows (see also Wheelwright and Dorsey 1991). Wiggins produced differences in growth by removing one or two nestlings from each brood for periods of 4 h between days 5 and 8, and then compared the growth of these ''deprived'' nestlings to their siblings who had not been removed. Deprived nestlings grew slower but there were no apparent differences between groups by day 15. The manipulation used by Wiggins is analogous to conditions under which a single nestling finds itself at a competitive disadvantage relative to its siblings for a portion of the nestling period. The manipulation used in the present study is meant to mimic the conditions experienced by nestlings during periods of poor environmental conditions; the entire brood experiences a food shortage for an extended period, and when conditions return to normal the parents must then contend with an entire brood of deprived nestlings. In Wiggins' (1990b) experiment, parents have more opportunity to compensate for the reduced condition of the deprived nestling because its siblings are in good condition. The failure of nestlings in either experiment to show any compensatory increase in growth rates emphasizes the constraints owing to the already high rates of growth in nestling passerines (Lepczyk et al. 1998, Ricklefs et al. 1998)

The ability to temporarily interrupt growth and development during periods of poor weather has been cited as a possible adaptation to short-term fluctuations in food supply faced by aerial insectivores (O'Connor 1977b, Emlen et al. 1991). Both the experimental and naturally occurring periods of nutritional stress clearly show that occurs in Tree Swallows (Fig. 5). However, reduced growth and interrupted development during periods of low food abundance have also been reported in species other than aerial insectivores (Dickerson and McCance 1960, Ricklefs and Peters 1979, Price 1985, Schew and Ricklefs 1998). Further investigations of that phenomenon need to discriminate between two possibilities: (1) that the ability to interrupt growth is a special adaptation of aerial insectivores for surviving periods of low food availability, or (2) that interruption in growth is an unavoidable byproduct of low body temperatures and low food intake in ''normal'' passerines. Given the long nestling period and potential for temporary reductions in food supply, it is not surprising that interrupted growth is most often observed in aerial insectivores; it remains to be tested whether interrupted growth in species subject to severe short-term fluctuations in food abundance are special adaptations to an unpredictable food supply.

Given the relationship between growth and postfledging survival in this population, those effects on growth may in turn translate into significant effects on fitness. Although sample sizes in this experiment were small and there was not a difference between the starved and control groups, the significant relationship between mass lost and probability of return within the starved group (Fig. 6) suggests that intensity of short-term reductions in growth may influence postfledging survival. The existence of a long-term cost of short-term growth reductions is supported by experimental evidence from other species (Tinbergen and Boerlijst 1990) as well as the low return rates of nestling Tree Swallows with delayed growth caused by inclement weather.

Those results emphasize the importance of the interplay between both temporal and spatial variation in understanding variation in nestling growth in Tree Swallows. There is increasing interest in using growth as an indicator of environmental conditions, especially in Tree Swallows (Quinney et al. 1986, Blancher and McNicol 1988, St. Louis and Barlow 1993, McCarty and Secord 1999). To successfully interpret environmental effects on growth, it will be critical to recognize the magnitude of variation that can occur on small temporal and spatial scales. Complex interactions among variables are likely to produce differences in growth rates, and past events can have long lasting effects on growth that might mask effects of specific environmental stresses.

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