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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

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 variations. 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

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.

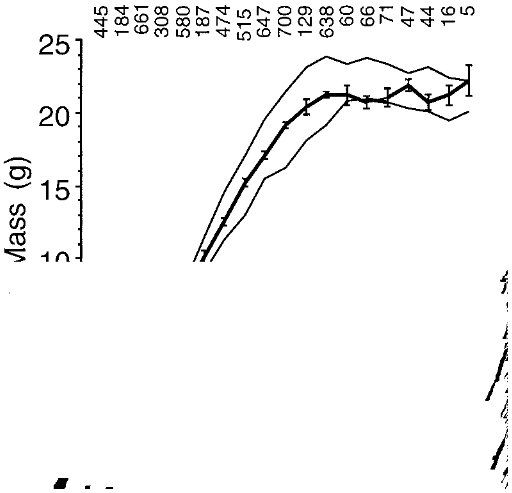

FIG. 1. Change in mass during growth of nestling Tree Swallows. Bold line represents mean mass (62 SE) of nestlings from Ithaca, New York during the period 1990–1993. Thin lines show the 10th and 90th percentiles of mean masses for nestling Tree Swallows from 13 other locations across North America. 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.

RESULTS

The growth of nestling Tree Swallows exhib-

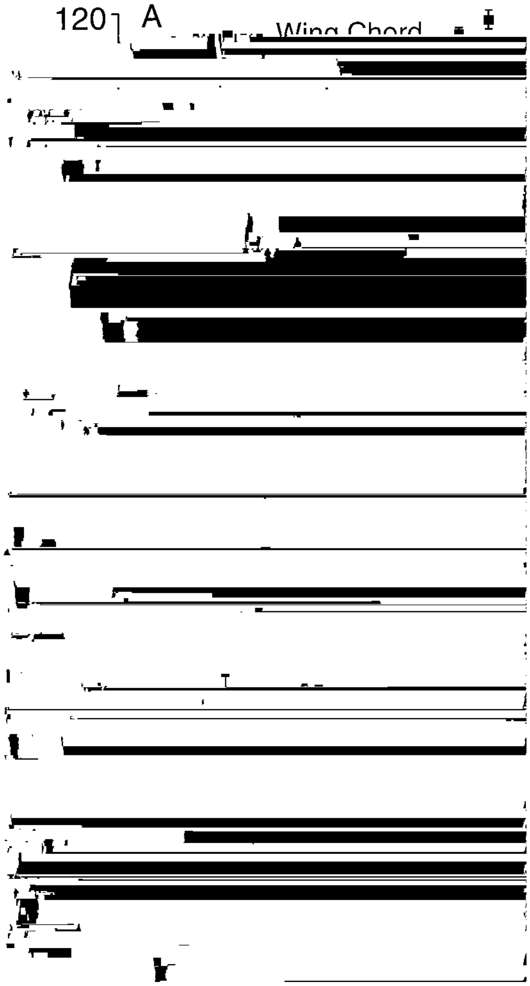

FIG. 2. Growth of wing and flight feathers (2A), and manus and tarsus (2B) of nestling Tree Swallows. Analogous data for fledglings (''Fledge'') and adults are also provided. Mean 6

either average daily mean temperature (*t* 5 20.19, *Z* 5 0.80, *n* 5 11, *P* 5 0.42) or the average daily high temperature (*t* 5 20.35, *Z* 5 1.51, *n* 5 11, *P* 5 0.13). There was no difference in *K* between sites classified as uplands (0.52 6 0.05, *n* 5 5) and those near water (0.50 6 0.05; Mann-Whitney *U*-test, *Z* 5 0.60, *n* 5 9, *P* 5 0.55). The average clutch size in a population was not correlated with nestling growth rate constants (*t* 5 20.16, *Z* 5 0.75, *n* 5 13, *P* 5 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 (*t* 5 20.17, *Z* 5 0.91, *n* 5 16, *P* 5 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 6 0.03; single brood 0.46 6 0.02; *Z* 5 0.36, *n* 5 13, *P* 5 0.72). There was a slight tendency for species with larger clutch sizes to grow faster but that was not significant (*t* 5 0.48, *Z* 5 1.85, *n* 5 16, *P* 5 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 6 0.01, significantly higher than the mean of 0.429 6 0.02 for 16 species of Hirundinidae (*Z* 5 3.03, *P* 5 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 6 0.04) than do non-Hirundines (0.87 6 0.02; *U*-test, *Z* 5 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 (χ^2 5 12.4, df 5 1, *n* 5 1,641, *P* , 0.001), as were those with longer wings (χ^2 5 6.55, df 5 1, *n* 5 1,233, *P* 5 0.011), and tarsi (χ^2 5 5.5, df 5 1, *n* 5 215, *P* 5 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 5 9.5 6 0.3 g, experimental nestlings 5 9.0 6 0.3 g; Wilcoxon test, *Z* 5 1.02, *P* 5 0.31). Brood size of the two groups did not differ (control 5 5.3 6 0.2, experimental 5 5.4 6 0.2; Wilcoxon test, *Z* 5 1.01, *P* 5 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 6 0.1 g per nestling during day 6 (8% of their starting mass), whereas control broods gained an average of 1.9 6 0.3 g per nestling (20% of their starting mass) during the same period (Wilcoxon test, *Z* 5 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 5 32.8 6 1.1 mm, control 5 36.0 6 0.7 mm, Wilcoxon test, *Z* 5 2.94, *P* 5 0.003) and day 12 (experimental 5 32.8 6 1.1 mm, control 5 36.0 6 0.7 mm, Wilcoxon test, *Z* 5 3.69, *P* 5 0.007). Tarsus length of day 12 experimental nestlings (36.0 6 0.7 mm) was significantly shorter than controls (36.0 6 0.7 mm Wilcoxon test, *Z* 5 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* 5 0.85, *n* 5 18, *P* 5 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.

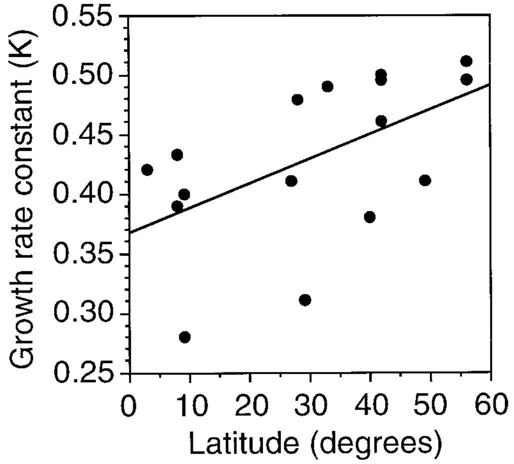

FIG. 4. Growth rates of nestlings of 16 species of Hirundinidae in relation to latitude. Growth rates increased significantly with distance from the equator; *n* 5 16, *t* 5 0.43, *Z* 5 2.33, *P* 5 0.020. Sources of data given in Table 1. Line fit using least squares regression provided for illustration.

Kendall rank correlation;*t* 5 0.35, *Z* 5 2.02, *n* 5 18, *P* 5 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 6 0.8 mm, *n* 5 9), 10 (26.6 6 1.2 mm, *n* 5 17), and 12 (37.4 6 1.8 mm, *n* 5 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-

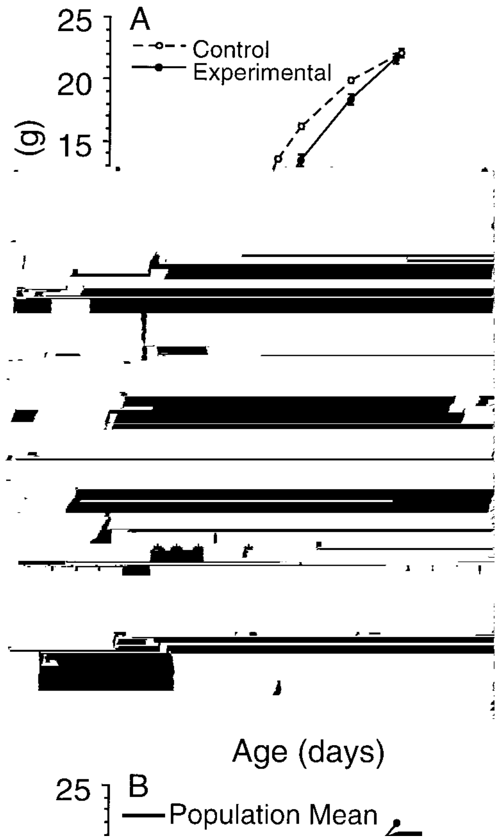

FIG. 5. Effects of experimental (A) and natural (B) short-term food deprivation on subsequent growth of nestling Tree Swallows. Effects of experimental growth reduction on day 6 persisted until day 12 (A). Lines for each category based on mean mass of nestlings within broods 6 SE. Mass of deprived nests (*n* 5 18 broods) and control nests (*n* 518 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 ''*.''

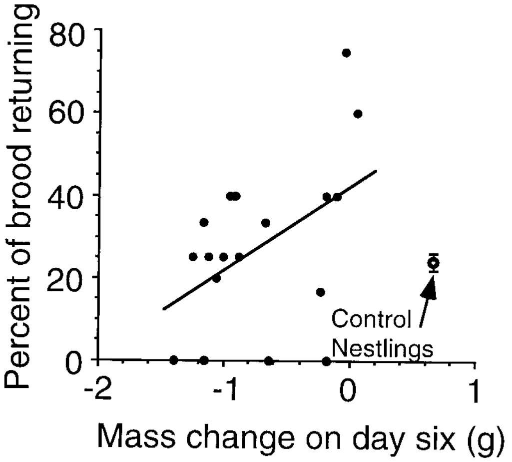

FIG. 6. Effects of experimental food deprivation on the proportion of a brood recaptured in the following year. Mass change during the experiment is based on the mean change in mass for all nestlings in a brood. Return rates of experimental and control broods (6 SE) did not differ, but among experimental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

ence 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

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

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