SOURCES OF VARIATION IN GROWTH OF
TREE SWALLOWS

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ABSTRACT.—We studied two populations of Tree Swallows (*Tachycineta bicolor*) that differed primarily in the amount of food available to the breeding birds. We obtained an index of food abundance and performed field experiments to distinguish factors affecting variability in growth of nestlings. The experiments were designed to detect the influence of the location of egg laying, incubation, and nestling rearing, type of parent (natural or foster), and year of breeding on nestling growth. Some broods were transferred between nests and raised by foster parents, and some clutches and broods were transferred between populations. Variables were analyzed in two- and three-way factorial analyses of variance.

The insect biomass index during the nestling period differed about 7-fold between locations, regardless of year of breeding. Nestlings with more food grew and survived better. Type of parent (i.e. natural or foster) or prehatch factors such as location of incubation did not influence growth. The location where nestlings were raised, however, explained as much as 51% of the variation in growth, and genetic variation in offspring and variation in provisioning abilities of parents may have been important components of within-population variation in growth regardless of where parents nested. *Received 11 February 1985, accepted 25 November 1985.*

THE main selective pressures responsible for reproductive performance in nidicolous birds are the availability of food, especially for the young and to a lesser extent for the laying female, and the risk of predation on eggs, young, and parents (Lack 1968). Implicit in Lack's hypothesis is a limitation due to parental foraging ability. Nestling growth or survival has been shown (usually indirectly) to be affected by food supply in several bird species (van Balen 1973; von Bromssen and Jansson 1980; Bryant 1975, 1978a; Crossner 1977; Bryant and Gardiner 1979; Ross 1980; Prince and Ricketts 1981). Reduced availability of food markedly affects parental feeding success in some species (Dunn 1973, Bovino and Burtt 1979, Quinney and Smith 1980), and parents that raise large broods may show reduced survival or body mass compared with those that raise smaller broods (Hussell 1972, Askenmo 1977, Tinbergen 1981).

Previously, the role of food abundance in reproduction often has been obscured because adequate measurements of food supply are difficult to obtain and because of the difficulties

of evaluating factors that also influence reproductive performance such as age of the breeders, timing of breeding, clutch and brood sizes, predation, and weather.

We designed field experiments to test whether differences in food abundance affect nestling growth and survival in populations of Tree Swallows (*Tachycineta bicolor*) at two sites that apparently differed primarily in the amount of food available to the breeding birds. We predicted that growth and survival of nestlings would be superior at the site where food was more abundant. While ultimately we are interested in knowing whether greater food abundance during the breeding season influences Tree Swallow fitness, this question is not easily answered for any animal species in the wild. De Steven (1980) studied the effects of brood enlargement on parental survival in Tree Swallows and found that the return rate of control females that raised normal-size broods was 9% less than for experimentals that raised artificially enlarged broods. However, because more than 200 birds in each category would be required to show that the return rates were statistically different, conclusive data are difficult to obtain. Nevertheless, the weight and size of nestlings have potential significance for their chances of survival (Perrins 1965, 1979) and

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thus, the reproductive fitness of their parents.

Recently, Ricklefs and Peters (1981) and Ricklefs (1984) studied factors affecting intra-populational variability in growth by switching eggs and nestlings among nests of European Starlings (*Sturnus vulgaris*). They concluded that to understand the significance of variation in growth variables, similar experiments must be designed to distinguish differences in factors such as where the eggs are laid and incubated and where the nestlings are reared, by whom the eggs are laid (genetic difference among nestlings), and by whom the nestlings are reared (difference in parental care). Here, we describe results from experiments designed to detect the influence of type of parent (natural or foster) and location of egg laying, incubation, and rearing of nestlings on the growth of young Tree Swallows. We also provide evidence that the breeding sites differed primarily in the abundance of flying insects available to the swallows, and we attribute differences in growth between sites to these differences in food supply.

METHODS

STUDY AREAS AND POPULATIONS

We studied two populations of Tree Swallows, 3.25 km apart, breeding in nest boxes near Port Rowan, Ontario (42°37'N, 80°27'W) in 1980 and 1981 and called them Backus Field and Sewage Lagoon (Quinney and Ankney 1985). Plywood nest boxes (14 × 14 × 33 cm inside, 13 cm thickness, 3.85 cm diameter entrance hole) stood about 1.5 m above ground, attached to metal poles. All poles were fitted with large, metal cone-shaped collars that excluded terrestrial predators, e.g. raccoons (*Procyon lotor*) and fox snakes (*Elaphe vulpina*). Nest boxes were 24 m apart and faced in an easterly direction. Forty-eight nest boxes were arranged in a single row around the perimeter of the two ponds at Sewage Lagoon (north pond: 240 × 90 m, south pond: 240 × 225 m; ponds were 10 m apart). Backus Field had 49 nest boxes with two rows containing 22 and 19 boxes on a strip of uncultivated land planted with small trees, among three cultivated fields, and 8 boxes in similar habitat adjacent to one of the fields. Except for a few pairs of House Wrens (*Troglodytes aedon*) and one pair of Eastern Bluebirds (*Sialia sialis*) at Backus Field, only Tree Swallows have nested in these boxes. Since 1979, all of the nest boxes have been occupied (a minimum of one egg laid) in each breeding season at Sewage Lagoon and greater than 90% at Backus Field. We also used some Tree Swallows that nested at the eastern

tip of the Long Point peninsula (about 50 km southeast of Backus Field) for one of the experiments. This study site has been described by De Steven (1978, 1980). Several studies document the annual rates of return by banded Tree Swallows to nesting areas, and they indicate that genetic exchange among populations is not restricted (Low 1933, Kuerzi 1941, Chapman 1955, Robertson and Gibbs 1982).

Two hundred and seventeen Backus and Lagoon Tree Swallows have been retrapped in the Port Rowan area when breeding, in at least one breeding season following the one in which they were banded as either nestlings or breeding adults. Fifty were retrapped at breeding locations other than the original banding site. Thirty of these 50 Tree Swallows were banded at Sewage Lagoon but retrapped at Backus Field when breeding, 16 were banded at Backus Field but retrapped when breeding at Sewage Lagoon, and the remaining 4 were retrapped while nesting at the eastern tip of the Long Point peninsula. Thus, any differences in breeding performance between Backus Field and Sewage Lagoon are probably phenotypic, not genotypic.

INSECT SAMPLING

Adults captured flying insects and delivered them to their offspring as a bolus of food. We collected samples of boluses and trapped flying insects in two suspended nets placed near the nest boxes at each site (for details see Quinney and Ankney 1985). There was excellent correspondence between the sizes and taxa of insects collected in the nets and those delivered by adult swallows to their nestlings at each site (Quinney and Ankney 1985). Nevertheless, our measurements of food supply probably are not completely consistent between areas because a tall stand of deciduous trees and a generally more heterogenous environment at Backus Field provide shelter for both insects and foraging swallows that is not available at Sewage Lagoon. The nets were opened and closed manually each day and collected insects daily from shortly after dawn until dusk (nestlings are not fed at night). Hourly wind speeds at net height at each site during the period when the nets operated each day were calculated from regression equations based on measurements with hand-held anemometers at the nets and wind speeds recorded at two nearby Environment Canada weather stations at Long Point and Delhi, Ontario. Also, maximum and minimum ambient temperatures were recorded daily at each area.

All insects except dipterans from the net catches and boluses were identified to order; dipterans were classified as either Suborder Nematocera or other dipteran suborders. They were placed by body length into one of six categories: 1–3 mm, 3–5 mm, 5–7 mm, 7–9 mm, 9–11 mm, and 11–13 mm. Fifty to 150 insects from each order or suborder and each size class were used for biomass determinations. These insects were

chosen randomly from net samples obtained in May and June 1980. Insects were dried to constant weight using procedures described elsewhere (Quinney and Ankney 1985). The insect taxa and size categories shown in Table 1 represent 99% and 94% of all insects caught in the nets at Sewage Lagoon and Backus Field, respectively. We assumed that nematocerans >5 mm in length trapped at Backus Field weighed the same as those trapped at Sewage Lagoon.

Two indices of food abundance were calculated for each location each day: number of insects per 100 km wind and insect biomass (mg dry mass) per 100 km wind. For each location, the indices were obtained by summing the total number of insects (or biomass) caught daily in the suspended nets and dividing by the sum of the hourly winds at the two nets. Biomass was calculated by summing over all sizes (taxa), the size (taxon)-specific dry mass times the frequency of the size (taxon) class. Because stationary tow nets similar to those we used are inefficient at low wind speeds (Johnson 1950, Taylor 1962), hourly wind speeds of 0–8 km/h were cubed and divided by 64 before calculating the daily sum of wind. This somewhat arbitrary adjustment was chosen to provide a correction that is in general accordance with Taylor's (1962) measurements of efficiency at wind speeds below 8 km/h. It is based on the assumption that the efficiency of the nets is proportional to the square of the wind speed at speeds of 0–8 km/h and is constant at its maximum value when the wind speed is >8 km/h. Because wind speeds at the suspended nets were usually somewhat lower and insect catches much lower at Backus Field than at Sewage Lagoon, this efficiency correction tends to narrow the differences between the indices for the two sites (Table 2).

FIELD PROCEDURES

Nest boxes were examined every morning during the egg-laying stage. Eggs were numbered with permanent ink and weighed to the nearest 0.05 g with hand-held, 5-g capacity spring scales, usually during the morning that they were laid or as soon after as possible. We rarely visited nests during most of the incubation period to avoid unnecessary disturbance to the breeding birds. Eggs hatched about 13 days after the last egg was laid in clutches of 6 eggs. We revisited nests 12 days after the last egg was laid to look for nestlings and to reweigh the eggs. During hatching, each nest was visited 3 times daily to determine hatch times, to weigh nestlings as soon as possible after hatching, and to mark them individually with permanent ink on various parts of the body. The hatching interval from first to last nestling from a 6-egg clutch when all eggs hatched averaged 29 ± 0.1 h at Sewage Lagoon (n = 17 broods) and 35 ± 0.2 h at Backus Field (n = 9 broods), based on estimated times of hatch of individual young determined as indicated below. However, eggs 1–4 usu-

TABLE 1. Mean dry mass (mg) of insects from net catches. n = number of insects weighed.

Taxon	Length (mm)	Sewage Lagoon Mean mass	n	Backus Field Mean mass	n
Nematocera	1–3	0.05	150	0.09	150
	3–5	0.27	150	0.26	120
	5–7	0.91	115		
	7–9	1.45	150		
	9–11	2.93	90		
	11–13	4.01	10		
Other Diptera	1–3	0.21	65	0.28	68
	3–5			0.44	50
Homoptera	1–3	0.08	50	0.11	50

ally hatched within a few hours of one another, indicating that the female began incubation of her eggs sometime between the laying of the fourth and fifth eggs. We thought that reweighing eggs shortly before they hatched would enable us to match nestlings with the eggs from which they came (particularly eggs 1–4) so that we could compare the growth of first- with last-hatched nestlings in a given brood. We described the condition of each nestling at hatch based on the appearance of the natal down (e.g. wet or dry, matted or fluffy). We used 12-day egg masses together with mass and condition of newly hatched nestlings to estimate hatch time of each young to the nearest 0.25 day. A mean hatch date was calculated for each brood and members of a brood were weighed and measured every evening between 1730 and 2000 EST until the brood averaged 16 days old. Nestlings fledge at about 20 days of age but will leave their nests prematurely if they are handled after 16 days of age (Kuerzi 1941, De Steven 1980). Characteristic marks on nestlings were renewed with permanent ink when necessary until the young were 12 days old, when they were banded with standard U.S. Fish and Wildlife Service bands. Weights to the nearest 0.1 g were taken with hand-held 50-g spring scales, and the length of the outermost (ninth) primary feather was measured with a ruler to the nearest 0.5 mm (on the underside of the wing from insertion on the skin to tip).

During the nestling period, adults were trapped, sexed by the presence of a brood patch or cloacal protuberance, and banded with standard U.S. Fish and Wildlife Service bands if not banded previously. Females were placed in two major age classes, second calendar year (SY) and after second calendar year (ASY), based on plumage differences (Hussell 1983). A few females could not be aged and were called after hatching year (AHY). We did not use SY or AHY females for this study because SY females appear to differ from older females in several reproductive variables (De Steven 1978). We did not know

TABLE 2. Summary of mean daily values ± SE for temperature, wind, and insect trapping.[a]

| | 1980 | | | | 1981 | | | |
| | May | | June | | May | | June | |
	Lagoon	Backus	Lagoon	Backus	Lagoon	Backus	Lagoon	Backus
Temp (°C)	14.4 ± 0.8	13.9 ± 0.8	16.8 ± 0.7	16.1 ± 0.7	12.6 ± 0.9	—	19.3 ± 0.8	19.1 ± 0.7
Wind (km/h)[b]	11.3 ± 0.9	7.0 ± 0.6***[c]	11.4 ± 0.8	7.5 ± 0.5***	9.7 ± 0.6	5.6 ± 0.6*	12.7 ± 0.5	7.9 ± 0.4***
Insect trapping (h)	12.6 ± 0.1	12.5 ± 0.1	13.0 ± 0.2	13.4 ± 0.2	12.7 ± 0.2	12.4 ± 0.1	12.5 ± 0.2	12.9 ± 0.2
Insects trapped	98 ± 19	15 ± 2***	84 ± 10	17 ± 2***	147 ± 21	11 ± 2***	108 ± 15	26 ± 4***
Insects trapped (per 100 km wind)	0.84 ± 0.15	0.21 ± 0.03***	0.62 ± 0.08	0.19 ± 0.03***	1.65 ± 0.23	0.15 ± 0.02***	1.29 ± 0.20	0.44 ± 0.06***
Insect biomass (mg)	47.8 ± 7.8	3.3 ± 0.5***	34.4 ± 6.5	2.9 ± 0.4***	90.9 ± 15.3	1.7 ± 0.3***	46.0 ± 8.2	3.8 ± 0.6***
Insect biomass (mg per 100 km wind)	0.50 ± 0.11	0.04 ± 0.01***	0.27 ± 0.07	0.03 ± 0.01**	0.98 ± 0.22	0.03 ± 0.02***	0.37 ± 0.07	0.04 ± 0.02***

[a] A mininum of 25 days sampled in each month at each site.
[b] Mean daily wind speed at the insect sampling nets calculated for the interval when the nets were operating and adjusted for net efficiency (see Methods).
[c] Asterisks indicate that mean at Backus Field differs significantly from mean at Sewage Lagoon. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

the ages of many males because they were not captured as easily as females and could not be placed in age categories based on plumage characteristics.

EXPERIMENTS

Females that laid 6 eggs (the modal clutch size at both locations) were randomly assigned to categories in the following experiments. The choice was from among clutches completed or hatched (depending on the experiment) on the same day. Nests where fewer than 4 eggs hatched were excluded from the experiments. When more than 4 eggs hatched, broods were maintained at 6 nestlings by introducing young of similar mass from broods not used in the experiments. Thus, all parents raised 6 nestlings. However, in the growth analyses, we used only nestlings that survived to fledging to calculate mean values from the 4–6 young for each brood and excluded those added as replacements for unhatched eggs or dead nestlings.

Experiment 1.—To determine if nestlings raised by foster parents grow differently from those raised by their natural parents, we transferred broods of newly hatched nestlings from their natal nests to be raised by foster parents in the population at the eastern tip of Long Point in 1980 and compared these with broods raised by their natural parents at the same location. We used the Long Point population for Experiment 1 because not enough broods were available to do Experiments 1, 2, and 3 at Backus Field and Sewage Lagoon.

Experiment 2.—To determine if nestling growth was influenced by the location where eggs were laid and incubated, by the location where nestlings were raised, or by the year of breeding (1980 or 1981), we transferred experimental broods of newly hatched nestlings between Backus Field and Sewage Lagoon in 1980 and 1981 and compared these broods with control broods raised at the location where they had hatched. Experimental broods transferred between locations were raised by foster parents. Therefore, in 1980 we also transferred control broods between nests, within locations, so that they too were raised by foster parents. This experiment was repeated in 1981, except that nestlings in control broods were raised by their natural parents because the results of Experiment 1 in 1980 showed no difference in growth between broods raised by foster and natural parents.

Experiment 3.—To determine if the location where eggs were laid or incubated affected nestling growth, newly completed clutches were transferred between Backus Field and Sewage Lagoon in 1981 and compared with groups incubated and raised at the location where they were laid. Also, growth of broods transferred between locations at hatching were compared with broods transferred at clutch completion. This information was necessary because part of Ex-
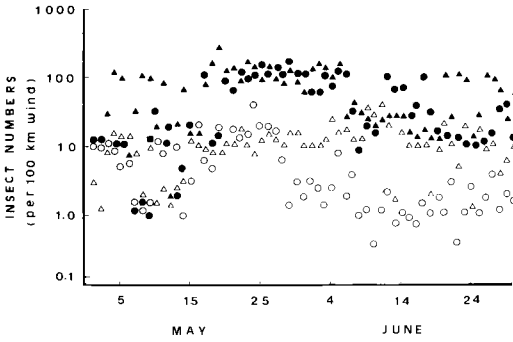
Fig. 1. Index of abundance of flying insects. Mean numbers from two nets at each location. Open symbols represent Backus Field, solid symbols represent Sewage Lagoon, circles represent 1980, triangles represent 1981.

periment 2 did not distinguish the laying period from the incubation period.

The transfer of most broods in all experiments was made on the first day that all eggs had hatched in the nest, but a few transfers were made one day later. When a clutch or brood was removed from its nest to be transferred to another, the nest-box entrance was blocked with a cork for 30 min to prevent the parents from entering an empty nest. Control nests in 1981 were treated in the same manner without removal of young.

We used mean body mass and mean length of the ninth primary of nestlings in a brood when its mean age was 12 days to determine whether the type of parent influenced growth in Experiment 1. We measured 4 variables related to growth of young in Experiments 2 and 3: (1) The rate of change in mean mass of a brood from 1 to 9 days of age, derived from the slope of the linear regression of mean brood mass on mean brood age (estimated to the nearest day). This period included the time to grow from 10 to 90% of maximum mass (after Ricklefs 1967). Coefficients of determination (r^2) of the regressions were always greater than 0.90 for all experimental and control broods in Experiments 2 and 3. (2) The mean of the maximum mass attained (at any age) by individual nestlings in a brood. (3) The rate of change in mean length of the ninth primary in a brood from 8 to 16 days of age, determined as the slope of the linear regression of mean primary length on mean brood age (to the nearest day). Primary feathers emerged at about 7 days of age. (4) The mean length of the ninth primary feather of young in a brood when its mean age was 16 days old (to the nearest day).

Statistical methods were chosen from Sokal and Rohlf (1981) and performed by SPSS (Nie et al. 1975, Cohen and Burns 1977, Nie and Hull 1981) using the "classic experimental design" (Nie et al. 1975) for
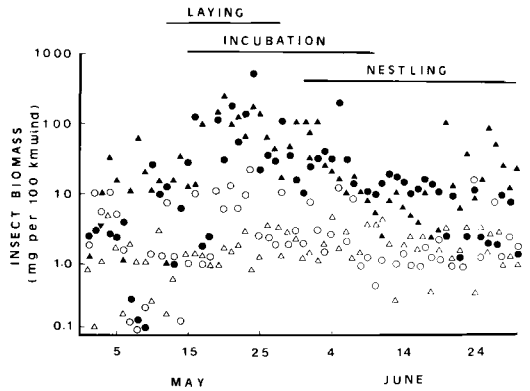
Fig. 2. Index of dry mass of flying insects. Mean values from two nets at each location. Horizontal lines below laying, incubation, and nestling represent the periods wherein at least the middle 90% of after-second-year females that laid 6 eggs at each location both started and finished the activity stated (1980 and 1981 pooled). Open symbols represent Backus Field, solid symbols represent Sewage Lagoon, circles represent 1980, triangles represent 1981.

two- and three-way analyses of variance. Other tests are mentioned in the text where they were employed. Mean values ± 1 SE are presented.

RESULTS

Weather and food supply.—Mean daily temperature (average of daily minimum and maximum) did not differ significantly between sites in May or June (Table 2). However, mean daily May and June wind speeds at the insect sampling nets were 52–73% higher at Sewage Lagoon (Table 2). This difference is probably a reflection of the generally more sheltered environment of Backus Field.

The boluses ($n = 91$) showed that the food supply consisted of a continuous range of small prey, with <0.7% of the insects in the boluses

TABLE 3. Influence of location and year on mass at hatching of nestlings used in Experiment 2.[a]

| | Mass (g) at hatching | |
	Lagoon	Backus
1980	1.74 ± 0.03 (13)	1.65 ± 0.03 (10)
1981	1.59 ± 0.05 (12)	1.63 ± 0.07 (9)

[a] Mean values ± 1 SE are given, with number of broods measured in parentheses. Main effects: location (not significant), year ($P < 0.05$, $r^2 = 0.08$). Interaction: location by year (not significant).
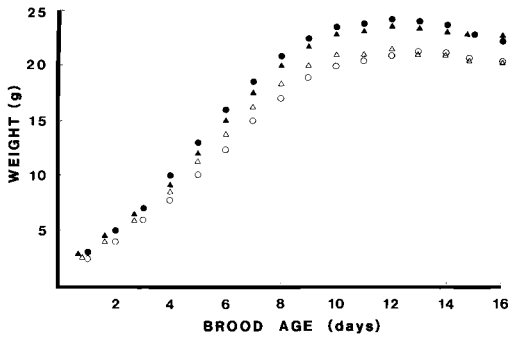
Fig. 3. Mean mass of nestlings in Experiment 2 (1980 and 1981 pooled). Solid circles represent nestlings hatched and raised at Lagoon ($n = 13$ broods), solid triangles represent nestlings hatched at Backus and raised at Lagoon ($n = 11$ broods), open triangles represent nestlings hatched at Lagoon and raised at Backus ($n = 13$ broods), open circles represent nestlings hatched and raised at Backus ($n = 9$ broods).

longer than 10 mm, regardless of location (Quinney and Ankney 1985). The taxa and the proportion of the taxa that were trapped by the suspended nets were very similar to those in the diet of the Tree Swallows (Quinney and Ankney 1985). The nets trapped about 32,000 insects in May and June of 1980 and 1981. Flying insects were over 5 times more abundant at Sewage Lagoon than at Backus Field (Fig. 1). Daily biomass of flying insects (Fig. 2)
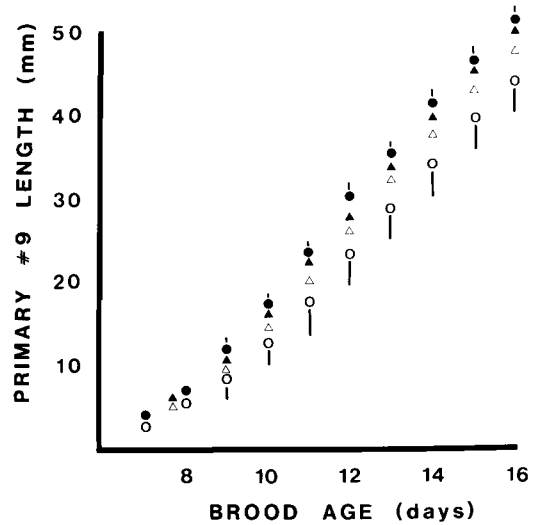
Fig. 4. Growth of ninth primary of nestlings in Experiment 2 with data for 1980 and 1981 pooled. Mean values $\pm$ 2 SE are shown as half error bars below the point for Backus Field and above the point for Sewage Lagoon. Solid circles represent nestlings hatched and raised at Lagoon ($n = 13$ broods), solid triangles represent nestlings hatched at Backus and raised at Lagoon ($n = 11$ broods), open triangles represent nestlings hatched at Lagoon and raised at Backus ($n = 13$ broods), open circles represent nestlings hatched and raised at Backus ($n = 9$ broods).

TABLE 4. Mass change and feather growth of experimental broods transferred between locations at hatching and control broods raised at the location where they hatched in Experiment 2.[a]

| | | Hatched at: | | | |
| | | Lagoon | | Backus | |
	Raised at:				
Slope of mass change	Lagoon	2.50 ± 0.05 (7)	1980	2.48 ± 0.07 (5)	
(1–9 days old inclusive)		2.60 ± 0.05 (6)	1981	2.56 ± 0.06 (6)	
	Backus	2.23 ± 0.09 (7)	1980	2.05 ± 0.15 (6)	
		2.29 ± 0.06 (6)	1981	2.22 ± 0.08 (3)	
Maximum mass (g)	Lagoon	25.1 ± 0.3 (7)	1980	24.2 ± 0.5 (5)	
		24.2 ± 0.6 (6)	1981	24.1 ± 0.3 (6)	
	Backus	22.7 ± 0.4 (7)	1980	22.6 ± 0.7 (6)	
		21.5 ± 0.5 (6)	1981	20.8 ± 0.1 (3)	
Slope of change in ninth primary	Lagoon	5.71 ± 0.11 (7)	1980	5.70 ± 0.10 (5)	
(8–16 days old inclusive)		5.62 ± 0.06 (6)	1981	5.50 ± 0.08 (6)	
	Backus	5.53 ± 0.16 (7)	1980	5.21 ± 0.32 (6)	
		5.20 ± 0.18 (6)	1981	5.00 ± 0.09 (3)	
Ninth primary length (mm)	Lagoon	51.8 ± 0.8 (6)	1980	49.8 ± 1.3 (5)	
(16 days old)		51.0 ± 0.2 (6)	1981	50.2 ± 0.7 (6)	
	Backus	47.0 ± 1.9 (7)	1980	42.5 ± 3.6 (6)	
		47.1 ± 1.9 (6)	1981	46.2 ± 0.7 (3)	

[a] Values presented are brood means ± 1 SE, with number of broods measured in parentheses.

TABLE 5. Percentage of variation attributed to several sources in Experiment 2 from three-way analysis of variance.

Source of variation	Growth variable			
	Mass (slope)[a]	Maximum mass	Feather (slope)[b]	Feather length[c]
Error	50%	36%	71%	65%
Area raised	41%***[d]	51%***	18%**	26%***
Area hatched	3%	1%	3%	5%
Year	4%	9%*	5%	1%
Interactions	2%	3%	3%	3%

[a] 1–9 days old inclusive.
[b] Ninth primary, 8–16 days old inclusive.
[c] Ninth primary, 16 days old.
[d] * = $P < 0.05$, ** = $P < 0.005$, *** = $P < 0.0005$.

is a more relevant indicator of food abundance because there were more insects and a greater proportion of larger insects at Sewage Lagoon. We defined the laying period as the interval wherein the middle 90% of ASY females at either location in 1980 and 1981 that laid 6 eggs started and ended egg laying (12–28 May). The median date of clutch initiation for these females in 1980 was 19 May at Sewage Lagoon and 20 May at Backus Field. In 1981 the median date was 16 May at Sewage Lagoon and 20 May at Backus Field. A minimum of 90% of the females began and ended incubation between 15 May and 11 June. At least 90% of all nestlings from 6-egg clutches hatched and fledged between 31 May and 30 June. The daily insect biomass index was significantly greater at Sewage Lagoon than Backus Field during laying, incubation, and the nestling period in both years (*t*-tests, $P < 0.001$). There were 7- and 10-fold differences between locations in the insect biomass index during the nestling period in 1980 and 1981, respectively. Coefficients of variation in the daily insect biomass index over

the nestling period were 201% and 108% at Sewage Lagoon and 110% and 59% at Backus Field in 1980 and 1981, respectively.

Growth.—In Experiment 1 broods raised by foster parents grew as well as those raised by their natural parents; body mass and ninth primary length when broods were 12 days old averaged 23.9 ± 0.5 g and 27.1 ± 0.7 mm ($n = 8$ broods) for nestlings raised by foster parents and 23.7 ± 0.5 g and 26.3 ± 1.8 mm ($n = 8$ broods) for nestlings raised by their natural parents ($P > 0.25$). Thus, in Experiment 2 we treated control broods raised by their natural parents and those raised by foster parents as identical. Nestlings used in Experiment 2 from Sewage Lagoon were heavier at hatching in 1980 than in 1981 ($P < 0.05$, Table 3). Eggs were slightly but not significantly lighter in 1981 (1.92 ± 0.3 g, $n = 27$ clutches for eggs from 6-egg clutches) than in 1980 (1.99 ± 0.03, $n = 24$ clutches).

Maximum masses were attained at Sewage Lagoon and Backus Field when nestlings in Experiment 2 were 12–13 days old (Fig. 3). Weight

TABLE 6. Mass change and feather growth of experimental broods transferred between locations at clutch completion and control broods incubated and raised at the location where they were laid in Experiment 3.[a]

	Incubated and raised at:	Laid at:	
		Lagoon	Backus
Slope of mass change	Lagoon	2.60 ± 0.05 (6)	2.58 ± 0.40 (5)
(1–9 days old inclusive)	Backus	2.36 ± 0.13 (5)	2.22 ± 0.08 (3)
Maximum mass (g)	Lagoon	24.2 ± 0.6 (6)	23.8 ± 0.6 (5)
	Backus	21.4 ± 0.7 (5)	20.8 ± 0.1 (3)
Slope of change in ninth primary	Lagoon	5.62 ± 0.06 (6)	5.58 ± 0.10 (5)
	Backus	5.19 ± 0.18 (5)	5.00 ± 0.09 (3)
Ninth primary length (mm)	Lagoon	51.0 ± 0.16 (6)	50.9 ± 0.58 (5)
(16 days old)	Backus	47.6 ± 1.48 (5)	46.2 ± 0.69 (3)

[a] Values presented are brood means $\pm$ 1 SE, with number of broods measured in parentheses.

TABLE 7. Percentage of variation attributed to several sources in Experiment 3 from two-way analysis of variance.

	Growth variable			
Source of variation	Mass (slope)[a]	Maximum mass	Feather (slope)[b]	Feather length[c]
Error	54%	38%	46%	43%
Area incubated and raised	44%**[d]	61%***	52%**	55%**
Area laid	2%	1%	2%	1%
Interaction	1%	1%	1%	1%

[a] 1–9 days old inclusive.
[b] Ninth primary, 8–16 days old inclusive.
[c] Ninth primary, 16 days old.
[d] ** = $P < 0.005$, *** = $P < 0.0005$.

recession before fledging is normal in swallows (Ricklefs 1968). Nestlings raised at Sewage Lagoon grew more quickly, reached heavier maximum masses, and had longer ninth primary feathers prior to fledging than did nestlings raised at Backus Field (Table 4). Growth of ninth primary feathers at Backus Field was also more variable than at Sewage Lagoon (Fig. 4). The greater variation was attributable largely to the highly retarded growth of one Backus brood in 1980. A three-way factorial analysis of variance (Table 5) showed that the area in which nestlings were raised significantly influenced all of the variables measured, the area in which nestlings hatched influenced none of the four growth variables tested, and year of breeding influenced only maximum mass of nestlings ($P < 0.05$), but explained only 9% of the variation in this variable (Table 5). This analysis was repeated excluding the slowest growing brood at Backus Field, but none of the significance levels given in Table 5 were changed.

Results of a two-way analysis of variance from Experiment 3 showed that location where eggs were laid did not affect nestling growth (Tables 6 and 7). Results were similar from a two-way analysis of variance that examined influence of location of incubation on nestling growth. Growth was not affected by the location where eggs were incubated. Thus, we did not detect prehatch influences on post-hatch growth in either Experiment 2 or 3. However, the area in which nestlings were raised accounted for 18–51% of the variation in nestling body mass and feather growth when both years were examined in Experiment 2. These experiments also revealed that there was considerable variation in growth attributed to residual error (Tables 5 and 7). That is, within a given location growth

varied, and possible sources of this variation are the local environment of individual nest boxes, influences of genotypes or phenotypes of young and parents on egg quality, growth rates, and parental care, and our measurement errors.

Maximum measured change in mean mass of broods for any one-day change in age in Experiment 2 for nestlings in broods that had hatched and were raised at Sewage Lagoon was 2.9 g in 1980 and 3.2 g in 1981. Maximum daily mass change of nestlings that hatched and were raised at Backus Field was 2.4 g in 1980 and 2.9 g in 1981. Maximum mass change occurred when broods averaged between 6 and 7 days old. Based on a logistic equation fitted to mean daily weights for each area, the growth rate constant, K (Ricklefs 1967), was 0.52 for nestlings that were hatched and raised at Sewage Lagoon and 0.48 for nestlings that were hatched and raised at Backus Field (brood age 1–9 days inclusive, 1980 and 1981 data pooled).

Hatch order did not influence the maximum mass attained by nestlings hatched and raised at Sewage Lagoon (Table 8). However, nestlings that hatched last in broods at Backus Field were significantly lighter (t-test, $P < 0.02$) than their siblings that hatched first. Lengths of the ninth primary at 16 days of age for first- and last-hatched siblings are more difficult to interpret because day 16 was calculated from the mean brood age. Thus, first-hatched young in a given brood were actually a little older than 16 days, while last-hatched nestlings were a little younger than 16 days; the age difference averaged 29 h at Sewage Lagoon. On average, the nestlings that hatched last in their broods at Backus Field had ninth primaries that were 9.5 mm shorter than their oldest siblings. Sim-

TABLE 8. Maximum mass and ninth primary length related to order of hatching within broods.[a]

Location		First hatched	Last hatched
Lagoon	Maximum mass (g)	24.2 ± 0.48 (12)	24.4 ± 0.44 (12)
	Ninth primary length (mm) at 16 days	52.9 ± 0.56 (12)	46.9 ± 0.75 (12)
Backus	Maximum mass (g)	23.1 ± 0.44 (9)	21.3 ± 0.44 (9)
	Ninth primary length (mm) at 16 days	50.4 ± 1.55 (9)	40.9 ± 1.77 (9)

[a] Nestlings that had hatched and were raised at either Sewage Lagoon or Backus Field (1980 and 1981 values are pooled). Means ± SE are given, with number of young measured in parentheses.

ilarly, last-hatched nestlings at Sewage Lagoon had ninth primaries 6 mm shorter than their first-hatched siblings. This suggests an effect of hatch order on feather growth in addition to that on weight gain at Backus Field.

Survival of nestlings.—Young remained in their nest boxes for 19–20 days. Nestling periods were slightly (0.8 day) but not significantly longer on average at Backus ($P > 0.05$).

Survival to fledging of nestlings chosen for Experiments 2 and 3 was greater than 90% regardless of where they were raised (Backus 154/ 168, 92%; Lagoon 174/174, 100%; $P > 0.20$). Thus, nestlings died only at Backus Field, where 6 nests lost a total of 14 young, including 1 nest with 6 young that failed completely. All dead nestlings presumably starved because all showed retarded growth before death compared with their siblings. Thirty-six percent of the nestlings that died were the youngest nestling in the brood. Overall, females that attempted to raise 6 nestlings in the experiments fledged an average of 5.5 young at Backus Field ($n = 28$) and 6.0 young at Sewage Lagoon ($n = 29$).

From 1976 to 1981, 705 eggs hatched at Backus Field and 1,081 eggs hatched at Sewage Lagoon. Only 28 and 51 birds returned to breed from Backus and Lagoon, respectively ($G = 1.101$, $P > 0.20$), but 4.7% of the nestlings at Sewage Lagoon and 4.0% of the nestlings at Backus Field have returned as breeders to either location.

DISCUSSION

The only major observed difference in the environments of the Tree Swallows was the superior food supply at Sewage Lagoon. The populations were similar in size, timing of breeding, age of female breeders, nest-box design and spacing, and exclusion of predators. Moreover, the two populations were in close proximity, and gene flow between them was unrestricted.

These conditions argue that food abundance was the only major cause of superior growth and survival of Sewage Lagoon nestlings compared with those raised at Backus Field. Although different parental genotypes might select different localities, this appears most unlikely for birds in the Tree Swallow populations we studied. Where food supply for parents has been measured or supplemented, growth rates correlate well with food availability (e.g. van Balen 1973, Bryant 1975, Crossner 1977, von Bromssen and Jansson 1980, Prince and Ricketts 1981). Cold and wet weather, presumably affecting food supply, influenced growth and survival of Common Swifts (*Apus apus*) and Tree Swallows (Koskimies 1950, Lack and Lack 1951, Paynter 1954, Chapman 1955, Lack 1956, Zach 1982, Zach and Mayoh 1982).

Tree Swallow nestlings show substantial phenotypic plasticity in growth. The location where nestlings were raised explained as much as 51% of the variation in growth in 1980 and 1981. Furthermore, nestlings died only in the population where food was less abundant, and nestling periods were also slightly longer there. De Steven (1980) showed that the duration of the nestling period was correlated inversely to ninth primary length at 16 days of age in Tree Swallows. Of lesser importance, the year of breeding explained about 10% of the variation in the maximum mass attained by nestlings.

Asynchronous hatching of nestlings can result in differential growth within a brood and in size hierarchies. This pattern of hatching may reduce the chance of all nestlings being lost when the food supply is restricted. The loss of one or two of the smallest siblings might be preferable to all siblings being affected by food shortage (Lack 1947, Ricklefs 1965, O'Connor 1978, Werschkul and Jackson 1979, Quinney 1982). Additionally, hatching asynchrony could lower nest losses to predators by reducing the time between clutch initiation and first fledg-

ing (Tyrvainen 1969, Hussell 1972, Clark and Wilson 1981). Hussell (1972) and Bryant (1978b) suggested that size hierarchies may spread the food needs of individual siblings and thus space the demands upon adults. Size hierarchies and brood reduction occurred commonly only at Backus Field (19% of Backus nests in Experiments 2 and 3 suffered partial brood loss but none did at Sewage Lagoon). Furthermore, the youngest nestlings in broods represented 36% of all nestling mortality. We attribute these differences between locations to the poorer food supply at Backus Field. Youngest nestlings at Backus grew more slowly than any others because Backus parents delivered less food, less often to their nests (Quinney 1983).

Experiments 2 and 3 showed that the locations where nestlings were raised significantly influenced their growth but that prehatch factors were not important. Thus, there were no differences *between locations* in genotypes of nestlings, egg quality, or incubation that significantly influenced the measurements of growth that we examined. (If mass at hatch or some age earlier than the maximum were examined, it might be possible to detect prehatch effects.) Substantial variation in growth was attributed to residual error as well as to effects of the area in which nestlings were raised. That is, *within a given location* growth varied, and this residual error variation is potentially attributable to prehatch factors (e.g. genotypes of individuals or egg quality), post-hatch factors (e.g. provisioning abilities of parents), or a combination of these factors. Both genetic variation of offspring and variation in provisioning abilities of parents could have been important components of within-area variation in growth of nestling Tree Swallows (Table 4). Ricklefs and Peters (1981) suggested that postnatal growth in a population of European Starlings was affected by aspects of parental care during the incubation and nestling periods but not by the genotype of the nestling or the composition of the egg. However, their experimental designs could not simultaneously separate the variation into components associated with the egg and the incubation and nestling periods. A new design allowed Ricklefs (1984) to distinguish egg, incubation, and chick-rearing factors as main effects. He concluded that neither genotype nor factors associated with egg composition, or expressed during the incubation period, influence measurements of nestlings.

Parental effects during the nestling period, probably associated with brooding or feeding the young, significantly influenced growth rates. Ricklefs (1984) then postulated that measurements of nestlings are influenced by the quality of parental care during the growth period, while final sizes of various appendages, achieved for the most part after fledging, are determined by genotypic factors. Our results indicate that food availability has an important effect on the quality of parental care during the nestling period, but other factors probably also influence parental care.

Finally, clutch sizes were significantly larger at Sewage Lagoon (Hussell and Quinney in press). Thus, in the absence of predation Tree Swallows respond to increased levels of food availability during the breeding season by increasing the number of eggs they lay and raising more young that show superior growth and survival.

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