# INTRASPECIFIC VARIATION IN THE GROWTH RATE OF NESTLING EUROPEAN STARLINGS

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## INTRODUCTION

Variation in growth rates of young within populations of birds has been related to season, brood size, hatching order, habitat, and geographical locality (for reviews, see Lack, 1966; Ricklefs, 1968; Klomp, 1970). In addition, growth has been interpreted as an index to ecological conditions, especially the availability of food (Gibb, 1950; Balen, 1973) and to interactions among siblings (cf., Parsons, 1975; Howe, 1976; Bryant, 1978; O'Connor, 1978a,b). By comparing variation within broods and between broods, one may investigate growth rate as an expression of the ability of parents to care for their broods and of genetic and maternal components of quality of the young. In this paper, we summarize a four-year study of intraspecific variation in growth rate and final weight achieved by nestling European Starlings (*Sturnus vulgaris*) in southeastern Pennsylvania. Our primary purpose here is to describe patterns of variation in growth, rather than to speculate on their causes.

## MATERIALS AND METHODS

Nest boxes were set out on property adjacent to the Stroud Water Research Laboratory near London Grove (Avondale), Pennsylvania, approximately 30 mi ESE of Philadelphia. Boxes were placed in old-fields bordered by hedgerows and, on some sides, by upland deciduous forest. A small stream runs through the study area. Local land use has created a mosaic of woodlots, pastures, and cultivated crops, primarily corn.

In 1970, 28 nest boxes were placed on steel poles, between 1.8 and 2.0 m off the ground, a minimum of 10 m apart in two adjacent fields. We recorded weights and measurements of all nestlings in all broods in 1970, 1971, and 1972, and in first broods in 1973. The inside dimensions of the nest boxes were 15 × 15 × 30 cm. Removable flat tops overhung the front of the boxes by 5 cm. A 4.4-cm entrance hole was centered 5 cm below the top of each box. The boxes were constructed of 2-cm thick pine and painted dark brown. They were cleaned out and repaired after the end of each breeding season.

Boxes were checked each day during the breeding season. Most visits to the nests were made after 1200 during the period of egg laying and between 0800 and 1200 thereafter. In 1970 and 1971, nestlings were identified individually by colored threads tied around one leg at 2 or 3 days of age. In 1972 and 1973, nestlings were given distinctive tattoos of India ink on their abdomens (Ricklefs, 1973). In all four years, young were given colored, plastic leg bands when 7 to 9 days old and aluminum Fish and Wildlife Service bands before fledging. Nestlings were weighed daily, using an Ohaus triple-beam balance (scale to 0.1 g) in 1970 and

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Pesola spring scales (10-g capacity with 0.1-g divisions, 30 g with 1-g divisions, and 100 g with 1-g divisions) in subsequent years. For each nestling that fledged, increase in body weight was described by fitting a logistic equation to the growth curve. The equation has the form

$$W(t) = A/\{1 + \exp[-K(t - t_i)]\}$$

where $W(t)$ is the weight (g) at age $t$ (days), $A$ is the asymptote or weight plateau (g), $K$ is the growth rate constant (days$^{-1}$), and $t_i$ is the age (days) at the inflection of the growth curve. Data were fitted by the graphical method described by Ricklefs (1967). The growth of each bird is characterized by two variables, one ($K$) related to the rate of development and the other ($A$) to the final size attained (Ricklefs, 1968).

Statistical tests follow procedures in Sokal and Rohlf (1969) and are described where they are applied in the Results section.

## RESULTS

### *Weather*

We referred to monthly summaries for Philadelphia (U.S. Climatological Summaries) to compare weather during the four years of the study (1970–1973). During the period of February through July, average monthly temperatures deviated less than 6°C from long-term norms. In addition, no unusually late frosts occurred. April and June 1971 had substantially less precipitation than normal (4.3 versus 8.6 cm and 2.5 versus 10.4 cm). Precipitation was 4.3 cm above average in both April 1970 (15.5 cm) and June 1972 (14.7 cm). The climatic data do not indicate any unusual conditions, particularly severe drought, that might have affected breeding by starlings. In June 1972, Hurricane Agnes brought a brief but severe storm that resulted in considerable mortality of nestlings in second broods. A storm in 1971 also caused the deaths of many young in second broods.

### *Laying Dates, Clutch Size, and Nesting Success*

Laying was well synchronized within a similar period each year. In 1970, among 26 first broods for which growth data were obtained, 10 of the clutches were initiated on 24 or 25 April; in 1971, 12 of 25 first clutches were initiated on 25 or 26 April; in 1972, 14 of 25 first clutches were initiated on 21 or 22 April. Excluding renesting attempts following nest failure or disturbance, the total spread of dates of nest initiation was no more than six days in any year.

Clutch size and survival of eggs and nestlings are summarized in Table 1. Most first clutches were four or five eggs, with an occasional set of six. Second clutches frequently were three eggs. In a one-way analysis of variance, clutch size did not vary significantly among years (first clutches, $F[3,159] = 1.96$; second clutches, $F[2,44] = 2.21$). Second clutches were significantly smaller than first clutches in 1970 ($F[1,37] = 10.7, P < 0.005$) and 1971 ($F[1,39] = 19.4, P < 0.001$), but not in 1972 ($F[1,56] = 0.57, P > 0.25$).

TABLE 1.

Clutch size and nesting success of European Starlings at the Stroud Water Research Center.[1]

| Year | Season | Number of nests | Average clutch size | Hatching success (%) | Fledging success (%) | Nesting success (%) |
|---|---|---|---|---|---|---|
| 1970 | early | 26 | 4.7 | 90 (121)[2] | 79 | 71 |
| | late | 13 | 4.0 | 67 (52) | 52 | 33 |
| 1971 | early | 25 | 4.9 | 84 (108) | 64 | 54 |
| | late | 16 | 3.8 | 65 (43) | 18 | 12 |
| 1972 | early | 40 | 4.5 | 84 (113) | 66 | 54 |
| | late | 18 | 4.3 | 85 (78) | 59 | 49 |
| 1973 | early | 72 | 4.5 | – | | |
| | late | 6 | 4.3 | – | | |

[1] Hatching success = percent of eggs that hatch; fledging success = percent of neonates that leave the nest; nesting success = percent of nests that fledge at least one young.
[2] Number of eggs in parenthesis, based only on those nests used in the study of growth.

More than 80% of eggs in first clutches hatched. Failure was due in small measure to infertility and addling of eggs, but more frequently to desertion of the entire clutch. Desertion sometimes followed accidental disturbance to the nest box or handling of the adults by the investigators. Contingency tables comparing successes and failures among early and late broods were tested for seasonal heterogeneity by chi-square. Late clutches had significantly lower hatching success in 1970 ($\chi_1^2 = 11.9$, $P < 0.005$) and 1971 ($\chi_1^2 = 5.7$, $P < 0.025$), but not in 1972 ($\chi_1^2 = 0.01$). Between 64 and 79% of hatchlings in first broods and between 18 and 59% in second broods fledged. Success of nestlings in late broods was significantly lower than that in early broods in 1970 ($\chi_1^2 = 8.3$, $P < 0.005$) and 1971 ($\chi_1^2 = 16.3$, $P < 0.005$), but not in 1972 ($\chi_1^2 = 0.02$).

Thus, seasonal declines in clutch size and breeding success were found in 1970 and 1971, but not in 1972. Evidently, suitable feeding conditions persisted later into the summer in 1972 than in the previous years. More pairs of starlings attempted second clutches and fewer nests were deserted. The fact that late clutches were significantly larger in 1972 than in 1970 and 1971 suggests that female starlings can perceive the general suitability of the habitat prior to or during the laying period.

*Year-to-year Variation in Growth*

Asymptotes ($A$) and growth rates ($K$) are summarized by year and by season within years in Table 2. We compared means for years among early and late season broods by $t$-test. Before performing the $t$-tests, we tested the homogeneity of variances of each pair of samples with an $F$ statistic. Variances differed significantly in the following comparisons: 1970 with 1972, early $A$ and late $K$; 1970 with 1973, early $A$; 1971 with

TABLE 2.

Growth parameters of European Starlings by year and season.

| Year | Season | n | Asymptote (g) Mean | Asymptote (g) SD | Growth rate (days$^{-1}$) Mean | Growth rate (days$^{-1}$) SD |
|---|---|---|---|---|---|---|
| 1970 | early | 84 | 73.4 | 7.9 | 0.374 | 0.043 |
| | late | 16 | 70.8 | 5.6 | 0.350 | 0.046 |
| 1971 | early | 58 | 82.0 | 7.2 | 0.354 | 0.052 |
| | late | 5 | 76.0 | 5.0 | 0.340 | 0.039 |
| 1972 | early | 72 | 82.2 | 6.1 | 0.359 | 0.041 |
| | late | 31 | 77.1 | 6.3 | 0.328 | 0.030 |
| 1973 | early | 37 | 84.8 | 5.1 | 0.363 | 0.036 |
| 1970–1973 | early | 251 | 79.6 | 8.2 | 0.364 | 0.028 |
| 1970–1972 | late | 52 | 75.0 | 6.5 | 0.336 | 0.037 |

1973, early $A$ and late $K$. When variances did not differ, we computed $t$ by equation 9.2 or 9.4 in Sokal and Rohlf (1960: 220–221); when variances differed we used the procedure on p. 374 of Sokal and Rohlf (1969). The average asymptote of nestlings in early 1970 broods was significantly smaller (73.4 g) than that in all subsequent years (82.0–84.8 g). The average growth rate of nestlings in broods in 1970 (0.374 days$^{-1}$) was correspondingly more rapid than that in 1971 (0.354) and 1972 (0.359), but not in 1973 (0.363). The average asymptote of nestlings in late broods in 1970 (70.8 g) was significantly less than that in 1971 (76.0 g) and 1972 (77.1 g); the average growth rate of nestlings in late broods in 1970 (0.350) was more rapid than that in 1972 (0.328). The average asymptote of nestlings in early broods in 1971 (82.0 g) and 1973 (84.8 g) also differed significantly. Overall, 1970 was distinguished by low asymptotes and rapid growth in both early and late broods. But the weather in 1970 was not unusual and both clutch size and nesting success were similar to those in other years.

*Seasonal Variation in Growth*

Averages of asymptotes and growth rates were compared among early and late broods in each year. Variances were homogeneous within all the comparisons. With the exception of growth rate in 1971, nestlings in early broods achieved significantly higher asymptotes and grew more rapidly than those in late broods. As we have noted above, these trends paralleled those for clutch size in 1970 and 1971, and trends in nesting success in 1970 and 1971. For all years combined, the asymptotes of nestlings in early broods were 4.6 g (6.0%) heavier and the growth rates were 0.028 days$^{-1}$ (8.0%) more rapid than those of nestlings in late broods.

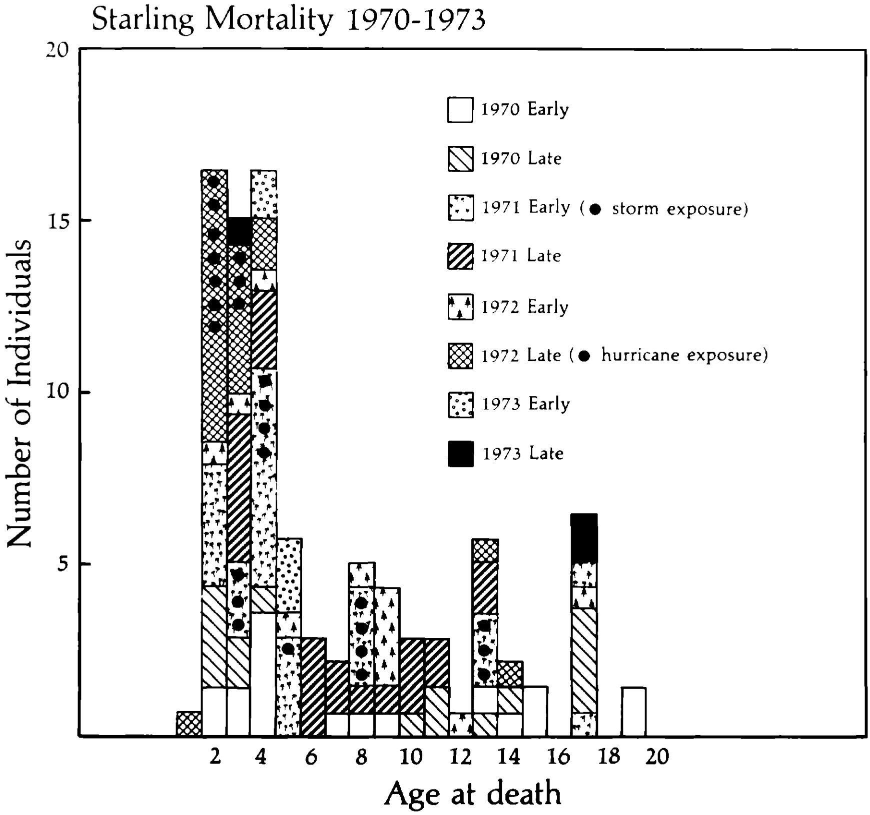


FIGURE 1. Age (day of hatching = 1) of nestling European Starlings at death.

*Growth of Young That Fail to Fledge*

In this study, we analyzed growth data only for young that left the nest fully fledged. Young that did not fledge died during storms, after long periods of weight loss, and, in a few instances, by predation. Most died during the first four days of the nestling period when the nestlings apparently are particularly vulnerable to storm-related mortality (Fig. 1). Growth curves of young that died after the first week of the nestling period in 1970 are shown in Figs. 2 and 3. In most cases, death followed varying periods of declining weight. Many of these young were the last to hatch in their broods and undoubtedly could not compete effectively for food. In most of these young, growth of the wing was retarded, slowed, or both. Two young in late broods in 1970 died after 11 and 12 days having gained very little weight since hatching; in both cases, feather growth and other indices to maturation were severely retarded.

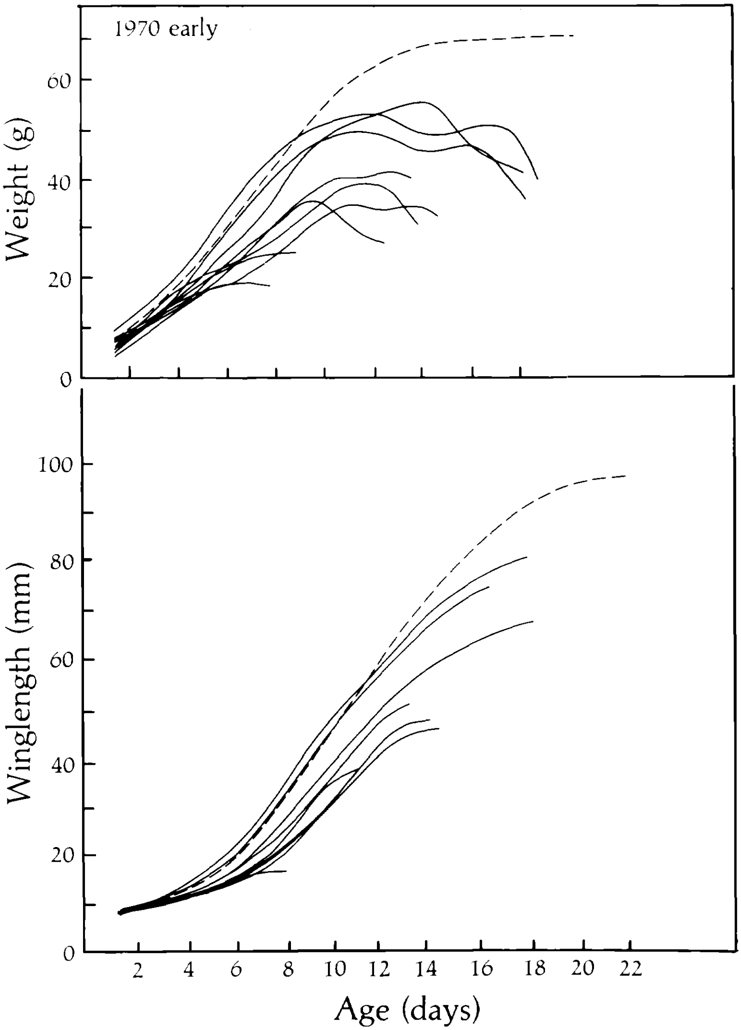


FIGURE 2. Increase in body weight and wing length of individual European Starling nestlings that failed to fledge. Individual curves are compared to mean curve for successful nestlings (dashed line). Early broods, 1970.

*Analysis of Variance*

An analysis of variation in growth rate and asymptote among nestlings in early broods during 1970–1972 is summarized in Table 3, revealing significant variation in asymptote among years (12.6%, $F[2,58] = 5.75$, $P < 0.001$) and among broods within years (63.6%, $F[5,153] = 7.05$, $P < 0.001$). The residual variation within broods was 23.8% of the

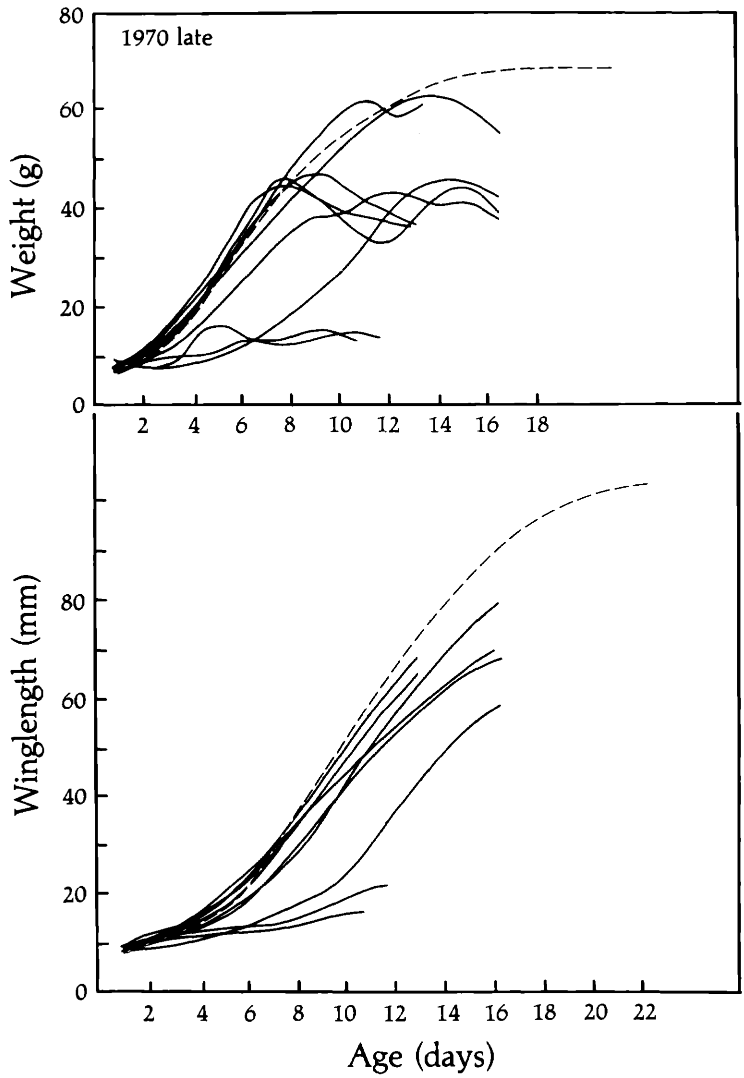


FIGURE 3. Increase in body weight and wing length of individual European Starling nestlings that failed to fledge. Individual curves are compared to mean curve for successful nestlings (dashed line). Late broods, 1970.

total. For growth rate, variation among years was not significant (3.8%, $F[2,58] = 2.27$, $P > 0.10$), but broods within years accounted for 48.8% of the total variance ($F[58,153] = 2.72$, $P < 0.001$). The residual variation within broods was 47.4% of the total. Hence, variation between years was a small percentage of the total. Variation in asymptote within

TABLE 3.
Analysis of within-broods, among-broods, and among-years components of variance in growth rate and asymptote for early broods in 1970–1972.

| Component | Sum of squares | Degrees of freedom | Mean square |
|---|---|---|---|
| Asymptote | | | |
| Total | 14,554 | 213 | 68.33 |
| Among years | 1,836 | 2 | 917.97[1] |
| Within years | 12,718 | 211 | 60.27 |
| Among broods | 9,256 | 58 | 159.58[1] |
| Within broods | 3,462 | 153 | 22.63 |
| Among broods | 11,092 | 60 | 184.86 |
| Growth rate | | | |
| Total | 0.447 | 213 | 0.00209 |
| Among years | 0.017 | 2 | 0.00850 |
| Within years | 0.430 | 211 | 0.00203 |
| Among broods | 0.218 | 58 | 0.00375[1] |
| Within broods | 0.212 | 153 | 0.00138 |
| Among broods | 0.235 | 60 | 0.00392 |

[1] Significant ($P < 0.05$) component of variance.

years occurred primarily among broods; variation in growth rate within years was about evenly divided among broods and within broods.

*Geographical Variation*

The growth of the European Starling has been studied in many localities in Europe and North America (Table 4). Statistical analysis of geographical variation is difficult for two reasons. First, the data are not strictly comparable in numbers of years, numbers of broods, and averaging techniques. Second, estimates of the variance of individual observations about the population mean are available only for our study in Pennsylvania, where they were 60 $g^2$ for asymptote and 0.016 $day^{-2}$ for growth rate. Assuming these variances and sample sizes of 20 (giving a conservative statistic), differences between samples would be accepted as significant ($P < 0.01$) if they exceeded 6.6 g for $A$ and 0.034 $day^{-2}$ for $K$. These values provide an approximate rule of thumb for the comparisons made below.

We found significant differences between the average asymptotes of nestlings in early and late broods in Czechoslovakia, New York, and possibly in Pennsylvania, but not in Scotland. Comparing asymptotes of nestlings in early broods among localities, we found that averages in Czechoslovakia, Pennsylvania, and British Columbia are similar and rather low, whereas those in Scotland and New York are significantly higher.

With respect to growth rate, significant seasonal variation appeared

TABLE 4.
Geographical comparisons of growth parameters of the European Starling.

| Locality[1] | Early broods | | | | Late broods | | | |
|---|---|---|---|---|---|---|---|---|
| | Years | n | *A* | *K* | Years | n | *A* | *K* |
| Scotland | 3 | – | 81 | 0.378 | 2 | – | 83 | 0.365 |
| Czechoslovakia | 2 | 81 | 75 | 0.366 | 2 | 23 | 62 | 0.369 |
| New York | 1 | 40 | 84 | 0.404 | 1 | 23 | 73 | 0.367 |
| Pennsylvania | 4 | 251 | 76 | 0.399 | 3 | 52 | 72 | 0.358 |
| British Columbia | 1 | – | 78.6 | 0.416 | 1 | – | – | – |

[1] Scotland: (Dunnet, 1955), mean growth curves of all broods containing five nestlings were presented for each year; we averaged the growth curves for the years and fitted logistic equations. Czechoslovakia: (Hudek and Folk, 1961), mean growth curves presented for early and late broods with both years combined; we fitted the equations. New York: (Kessel, 1957), mean growth curves presented; we fitted equations. Pennsylvania: (present study), growth data for all birds averaged and then fitted by equations. British Columbia: (Johnson, 1971), asymptote and growth rate calculated by author.

in Pennsylvania and New York, but not in the European localities. Comparing nestlings in early broods among localities, we found that growth rate is more rapid in the three North American localities than it is in Europe. Very little variation was found among late broods.

## DISCUSSION

Aside from a well-marked seasonal trend in growth rate and asymptote, almost two thirds of the variance in asymptotes and almost one half of the variance in growth rates of nestling starlings derive from differences among broods. The among-broods component of variance may result from differences in the quality of parents or their nest sites, or differences in the genotypes of the young. Age and experience influence nest success in many species and may be expressed in variation in nestlings' growth. To the extent that some individuals are better parents than others, growth may provide one index to quality of parental care.

In the European Starling, the among-broods component of variance in asymptote exceeds that in growth rate (76 versus 53%). The asymptote may more closely express the genetic potential of the individual, or the age, experience, or other measure of the quality of the parents; growth rate may be more sensitive to competition for food among siblings. Within-brood variation reflects inherent (genetic or maternal) variation in the quality of the offspring and interactions among siblings. These factors could be sorted out in the field by switching eggs or neonates among nests, by reducing brood size to reduce competition among siblings, or by altering hatching intervals to organize sibling competition differently.

The observations reported in this paper raise numerous questions about the origin and maintenance of variation in growth of birds. Most of these questions will be answered only by extensive experimentation.

## SUMMARY

Postnatal growth rates of 303 starlings measured near Philadelphia, Pennsylvania, over a four-year span, were analyzed to determine components of variation within a population. Growth curves were fitted with "logistic" equations, which have two parameters: asymptote ($A$) and growth rate ($K$). Clutch size and nesting success were greater in early broods than in late broods. Variation between years was less marked. $A$ and $K$ differed significantly between some years. In particular, for both early and late broods, asymptotes were lower and growth rates were more rapid in 1970 than in other years. In all but one year, nestlings in early broods grew faster and reached higher asymptotes than those in late broods. The total sum of squares of asymptotes were apportioned as 12.6% among years, 63.6% among broods within years, and 23.8% within broods. The total sum of squares of growth rate were apportioned as 3.8% among years (not a significant component), 48.8% among broods within years, and 47.4% within broods. Geographical variation in growth parameters is demonstrated but it follows no consistent pattern. To understand the significance of variation in growth parameters will require extensive experimentation, particularly switching eggs and young among nests to randomize the genetic and maternal components of within-brood variation.

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