PARENTAL COMPONENTS OF VARIANCE IN GROWTH RATE AND BODY SIZE OF NESTLING EUROPEAN STARLINGS (*STURNUS VULGARIS*) IN EASTERN PENNSYLVANIA

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ABSTRACT.—We report a series of experiments designed to identify parental influences on the growth of young European Starlings (*Sturnus vulgaris*). Growth curves were fitted by logistic equations whose parameters are the asymptote, or final weight plateau (A), and growth rate (K). The latter is inversely related to the length of the growth period. We calculated variances in A and K among natural and fostered siblings in nests whose eggs or chicks were switched at the beginning of incubation (experiment II) or just after hatching (experiment I) and in unswitched nests. In unmanipulated nests, 30–60% of the variance in A and K was attributable to differences among nests. In experiment II, effects due to genotypic covariance among natural siblings and to variation in egg quality among females were too small to be detected, whereas foster parents exerted significant effects on growth (26% of the variance in A and 77% in K). Experiment I demonstrated that foster-parent effects were exerted during both the incubation period (14% of A and 18% of K) and the nestling period (28% of A and 27% of K). Furthermore, in experiment II, the foster nest had a significant effect on the length of the incubation period, whereas the natural nest did not, and the incubation period and asymptote were positively correlated. These experiments indicate that heritability for growth rate is low in Starlings, but that qualities associated with different nests exert strong effects on postnatal growth. These qualities may reflect aspects of parental care, physical attributes of the nest boxes, or the location of boxes with respect to suitable feeding areas. Additional experiments, which involve switching of eggs and nestlings and which control for various aspects of parental care, are needed. *Received 3 December 1979, accepted 19 August 1980.*

AMONG individuals in natural populations, variation is the rule. This variation results from a variety of environmental and genetic factors, and it bears upon a number of ecological and evolutionary phenomena. Genetic components of variation indicate the susceptibility of the population to selection. Nongenetic components of variation reveal the response of the genotype to environmental influences and therefore indicate both the condition of the environment and the response of individuals to its variation. In species with extensive parental care, variation in the quality of the egg, intensity of incubation and brooding, the rate of feeding additionally contribute to variation among the offspring of different parents.

The genetic component of variation within populations—broadly, the heritability of traits—can be measured by comparisons among relatives and has been the subject of extensive theoretical and experimental analyses, conducted primarily in conjunction with animal and plant breeding programs (Falconer 1960). But, although heritabilities are well known for such domesticated animals as the chicken (e.g. Kinney 1969), few studies have attempted to estimate the genetic component of variation in traits expressed within natural populations. Boag and Grant (1978) and Smith and Zach (1979) used parent-offspring regressions to estimate heritabilities of morphological traits in finches, and Perrins and Jones (1974) and Greenwood et al. (1979) used the same technique to estimate the heritability of size and dispersal distance in the Great Tit (*Parus major*). In this paper, we report on two experiments designed to estimate components of variation in the growth rate of nestlings and the body

size of fledglings of European Starlings (*Sturnus vulgaris*) in a population in southeastern Pennsylvania.

Although adult body size has been shown to exhibit significant correlations between parents and offspring in natural populations, heritable components of variation in growth parameters have not been studied. In the domestic chicken, heritabilities of body weights from 4 weeks of age to maturity are on the order of 50% (Kinney 1969). In these studies, heritability is determined under conditions made as uniform as possible so as to minimize the environmental variance. Under natural conditions, environmental variation would be expected to increase the phenotypic variance and therefore reduce heritability. In species like the Starling, in which the young are dependent upon their parents through most of the developmental period, differences between parents in the quality of parental care could further increase the phenotypic variance of traits expressed in the young.

Phenotypic variance (V_P) is the sum of genetic and environmental components and interactions between them: V_A = additive genetic variance in phenotypic values caused by the additive affects of alleles, V_D = variance caused by genetic dominance among alleles, V_I = variance caused by the interaction of the expression of each allele with other genes, and V_E = the environmental variance. The last component includes external factors (e.g. climate), effects attributable to variation in parental care, measurement error, and accidents of development (e.g. order of hatching within the brood).

Components of phenotypic variance may be sorted out by suitable comparisons of phenotypic values between relatives. These comparisons usually involve parents and offsping, full sibs, or half sibs. In field studies, these comparisons often are not feasible, either because offspring disperse widely or because matings cannot be controlled. When suitable comparisons can be made, the analysis of components of variance further assumes that the environmental variance is the same for all genotypes, that there is no genotype-environment interaction (i.e. that each genotype responds to variation in the environment in parallel fashion), and that genotypes and environments are uncorrelated. The first condition is impossible to test in the field and is usually assumed. The second factor, genotype-environment interaction, is normally included with environmental variance. The third factor, genotype-environment correlation, might easily arise through parental care if individuals that grow better also provide better for their offspring. This factor usually is included with additive genetic variance, although in experiments in which the environment is controlled or randomized it can be reduced or eliminated.

In our analysis of growth parameters in Starlings, we were able to make comparison only among full sibs. In such comparisons, the covariance in a phenotypic trait among full sibs is equal to one half of the additive genetic variance plus one-quarter of the dominance variance plus the variance resulting from the common environment in which the sibs are reared (Falconer 1960). Hence,

$$COV_{FS} = \frac{1}{2} V_A + \frac{1}{4} V_D + V_{Ec}.$$

The common environment includes the quality of the egg and attributes of parental care during the incubation and nestling periods, which may be considered as parental effects. By switching eggs or chicks at random among nests, we have separated noninherited parental effects, except for variation in the quality of the egg, from common inheritance. These experiments have allowed us to estimate the

magnitude of genetic variance in growth parameters and to subdivide the environmental variance into parental factors acting during the incubation and nestling periods and factors in the environment that affect growth independently of genotype or parent, such as year, season, and locality.

METHODS

General.—We conducted experiments in 1970, 1972, 1973, and 1976 at a breeding colony of Starlings occupying nest boxes placed in fields near London Grove (Avondale), Pennsylvania, approximately 48 km southeast of Philadelphia (Ricklefs and Peters 1979).

Nestlings were individually marked and weighed daily between 0800 and 1200, using an Ohaus triple-beam balance (scale to 0.1 g) in 1970 and Pesola spring balances with 1-g divisions subsequently. The growth rate and final weight achieved (asymptote) were calculated from data on the increase in body weight by fitting logistic equations to the growth curves. The logistic equation relates weight to three growth parameters according to the expression

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

where $W(t)$ is weight at age t, A is the asymptote (g), K is a growth rate constant (days^{-1}), and t_i is the inflection point of the growth curve (days), where $W(t_i) = A/2$. The equations were fitted to data collected in 1970–1973 by the graphical method described by Ricklefs (1967) and to data collected in 1976 by nonlinear least-squares regression. The two techniques applied to the same data gave similar results. The inflection point (t_i) merely translates individuals on a common time scale and is not considered in this analysis.

Experiment I.—In 1970, 1972, and 1973 we conducted six sets of trials in which nestlings were switched among nests within 24 h after hatching. Each trial involved three to five nests selected according to their proximity to one another and synchrony of laying dates. When the young hatched, they were switched among the nests so that each contained nestlings from every other in the trial. For example, in a trial with four nests, nest *a* would contain one nestling from each of nests *a, b, c,* and *d*. When one of the clutches contained more than the number of nests in the trial, the extra young was left in the nest of origin, and data for one of the nestlings picked at random were excluded from the analysis. This happened only in the two 1973 trials (5 and 6). In trial 1 (1970), broods of four were switched among five nests, and the empty cells in the experimental design were filled with the mean of values for all individuals in the trial; the total and residual degrees of freedom were reduced by the number of empty cells.

We treated the results for each trial as a two-way analysis of variance (ANOVA) without replication (Sokal and Rohlf 1969: 320), with rows representing the nest of origin and columns the nest in which the young were reared. The total sum of squares in each experiment was apportioned among rows with $n - 1$ degrees of freedom (df), among columns with $n - 1$ df, and the remainder to residual with $(n - 1)^2$ df, where n is the number of nests in the experiment and $n^2 - 1$ the total df. (In trial 1, however, the total df were 19 rather than 24, and the residual df 11 rather than 16).

Because both the natural and foster parents are random effects, the analysis is a model II ANOVA, and the appropriate F-ratios for testing the significance of variation among natural and foster parents are the row and column mean squares divided by the residual (error plus interaction) mean square. The sums of squares and degrees of freedom were summed over all experiments to provide an analysis of variance table for the study as a whole. F_{max} tests did not reveal any significant heterogeneity in the mean squares among the six trials. We applied an analysis of covariance (Snedecor and Cochran 1967: 425) to determine the relationship between asymptote and growth rate.

Experiment II.—In 1976, we switched 37 eggs from 12 nests among 10 of the same nests prior to the beginning of incubation. Eggs were removed from nests as they were laid and replaced with surrogate eggs from other nests. Lengths (L) and breadths (B) of eggs were measured with dial calipers to the nearest 0.01 cm, and the fresh weight (W) was estimated by the formula $W = 0.525 \ LB^2$ (unpubl.). When the clutches were complete and incubation of the surrogate eggs commenced, the original eggs, which had been stored at room temperature, were replaced in the foster nests. Hence, the beginning of incubation was known precisely. On the day of hatching, nests were checked every 2 h. For each neonate, we determined the egg that it had hatched from and the length of the incubation period ±1 h.

Because of the design of experiment II, we had to analyze the effects of natural parents and foster parents separately in one-way ANOVA's. For comparison, we did parallel analyses on the 1970–73 data. During each year, we also analyzed growth data in unmanipulated broods. For these, the covariance among full sibs included effects of common environments expressed during the entire nesting cycle.

TABLE 1. Summary of analyses of variance for asymptote and growth rate of Starlings switched among broods after hatching (Experiment I).[a]

Trial	Year	Season	n	Mean	Variance	Among clutches			Among broods			Residual		
						SS	df	MS	SS	df	MS	SS	df	MS
						Asymptote[b]								
1	1970	Early	20	76.2	35.5	231	4	58**	347	4	87**	96	11	9
2	1970	Early	9	77.3	35.5	62	2	31	139	2	69	83	4	21
3	1970	Late	9	66.0	10.0	51	2	25	13	2	6	17	4	4
4	1972	Early	16	85.3	21.3	18	3	6	71	3	24	232	9	26
5	1973	Early	16	84.6	28.8	33	3	11	118	3	39	290	9	31
6	1973	Early	16	85.1	27.3	161	3	54*	129	3	43	119	9	13
Total			86	79.9	63.3	555	17	33	816	17	48**	827	46	18
						Growth Rate[c]								
1	1970	Early	20	0.350	215	1,180	4	298**	1,990	4	498**	910	11	83
2	1970	Early	9	0.407	120	427	2	214	196	2	98	231	4	58
3	1970	Late	9	0.402	112	24	2	12	339	2	170	535	4	134
4	1972	Early	16	0.305	121	140	3	46	571	3	190	1,110	9	123
5	1973	Early	16	0.380	54	168	3	56	241	3	80	408	9	45
6	1973	Early	16	0.347	91	840	3	280**	198	3	66	333	9	37
Total			86	0.358	167	2,780	17	163*	3,530	17	207**	3,530	46	77

[a] SS = sum of squares, df = degrees of freedom, MS = mean square; statistical significance of among-groups mean squares: *$P < 0.5$, **$P < 0.01$.
[b] Means in grams; squares and variance in g^2.
[c] Means in days^{-1}; squares and variance in days$^{-2} \times 10^5$.

TABLE 2. Components of variation in asymptote and growth rate among Starlings (Experiment I).[a]

	Asymptote					Growth rate				
				s^2					s^2	
Component	SS	df	MS	b	c	SS	df	MS	b	c
All individuals in early broods 1970–1972 (from Ricklefs and Peters 1979)										
Total (n = 214)	14,554	213	68.33			0.447	213	0.00209		
Within years	12,718	211	60.27			0.430	211	0.00203		
Within broods	3,462	153	22.63			0.212	153	0.00138		
Experiment I (this study)										
Total (n = 86)	5,382	85	63.32	63.32		0.142	85	0.00167	0.00167	
Among trials	3,184	5	636.78	43.19		0.044	5	0.00879	0.00054	
Within trials	2,198	80	27.48	27.48		0.098	80	0.00123	0.00123	
Among clutches	555	17	32.65	1.66	3.71	0.028	17	0.00163	0.00013	0.00022
Within clutches	1,643	63	26.08	26.08		0.071	63	0.00113	0.00113	
Among broods	816	17	47.98	6.59	7.59	0.035	17	0.00207	0.00027	0.00033
Within broods	1,382	63	21.94	21.94		0.063	63	0.00100	0.00100	
Residual	827	46	17.98		17.98	0.035	46	0.00076		0.00076

[a] SS = sum of squares, df = degrees of freedom, MS = mean square, s^2 = estimated variance. Units are g^2 for asymptote and days^{-2} for growth rate.
[b] Variances in these columns are calculated for trial, clutch, and brood effects separately.
[c] Variances based upon clutch and brood effects in two-way ANOVA's.

RESULTS

Experiment I.—Analyses of variance for data from experiment I are presented in Table 1. Levels of variation and its apportionment among effects and the residual varied from trial to trial, but not significantly according to F_{max} tests. The statistical significance of effects was determined by calculating $F = MS_{effect}/MS_{residual}$ and testing the null hypothesis that the F-ratio did not differ significantly from 1. Natural parent effects were significant ($P \leq 0.05$) for both asymptote (A) and growth rate (K) in trial 1 and over the experiment as a whole ($F = 2.7$, $P < 0.01$, in both cases). Foster parent effects were significant for both A and K in trials 1 and 6. Over the experiment as a whole, foster parent effects had F-ratios of 1.8 ($0.05 < P < 0.10$) for A and 2.1 ($P < 0.05$) for K.

In Table 2, we compare the variance components within the experimental nests to the variance in A and K among 214 nestlings in unmanipulated first broods in 1970–1972 (Ricklefs and Peters 1979). Variances (s^2) attributed to each effect were calculated by the expression

$$s^2_{effect} = (MS_{effect} - MS_{residual})/n_o ,$$

where n_o is the adjusted number of nestlings in each clutch or brood, depending on the effect (Sokal and Rohlf 1969: 207). Variances among the unmanipulated nestlings were 68.33 g^2 for asymptote and 0.00209 days^{-2} for growth rate. Variances in experiment I (63.30 g^2 and 0.00167 days^{-2}) were not significantly different from the larger sample by F-ratio test. Hence, experiment I appeared to include a representative proportion of the total variation in the population. Within the experiment, variation among trials accounted for 59% (3,184/5,382) of the sum of squares of asymptotes and 31% (0.044/0.142) of the sum of squares of growth rate. Factors acting prior to hatching accounted for 10% (555/5,382) and 20% (0.028/0.142), respectively, of the sum of squares; factors acting after hatching accounted for 15% (816/5,382) and 25% (0.035/0.142). The residual attributable to neither type of factor

Table 3. Analysis of covariance between asymptote and growth rate (Experiment I).

| | Correlation statistics[a] | | |
	df	r	F[b]
Source			
Total	85	−0.039	0.12
Among experiments	5	−0.405	0.79
Within experiments	80	0.290	7.32*
Among clutches	17	0.312	1.72
Among broods	17	0.565	7.50*[c]
Error	46	0.000	0.00

[a] Analysis follows Sokal and Rohlf (1969: 419): df = degrees of freedom, r = correlation coefficient, F = ratio of explained mean square to unexplained mean square.
[b] * $P \leqslant 0.025$.
[c] Slope of the regression of growth rate upon asymptote = 0.0037 days^{-1}·g^{-1}.

nor to interactions between them accounted for 15 and 25% of the total sum of squares.

The analysis of covariance (ANCOVA) presented in Table 3 shows the relationship between values of A and K. Within the study as a whole, asymptote and growth rate were unrelated (correlation coefficient, $r = -0.04$, $P > 0.05$), as were their residuals ($r = 0.00$). Hence, there appears to be no inherent relationship between the two measurements nor any systematic correlation caused by the curve-fitting technique. The mean values of A and K for the six trials were inversely related, but not significantly so ($r = -0.41$). The trend suggests, however, that environmental factors responsible for the significant among-experiments component of variance may affect A and K in opposite directions. Within experiments, A and K were significantly and positively correlated ($r = 0.29$). This correlation appears to have been caused by a parallel response of the two variables to factors causing differences among foster parents ($r = 0.57$, $P < 0.05$) but not among natural parents ($r = 0.31$, $P > 0.05$). Among broods reared by foster parents, the slope of the regression line relating K to A was 0.0037 days^{-1} · g^{-1}.

Experiment II.—When eggs were switched at the beginning of incubation in 1976, foster parents were found to have a significant effect on variation in both A and K, but natural parents had none (Table 4). Furthermore, A and K were unrelated in the experiment as a whole and within both foster and natural parent groups.

Total variance in K within experiment II (0.00375 days^{-2}) considerably exceeded that in experiment I, while the total variance in A (12.63 g^2) was less than a quarter of the variance in experiment I. In nine unmanipulated broods in 1976, the variances were 17.81 g^2 and 0.00180 days^{-1}, 31 and 42% of which were attributable to differences among natural parents.

DISCUSSION

Among unmanipulated broods, considerable variation in both asymptote and growth rate can be attributed to differences among natural parents. In broods switched among nests at hatching (experiment I), both natural and foster parents contributed significantly to the total variance. When eggs were switched at laying, however, only foster parents exhibited significant effects on postnatal growth (experiment II). These results suggest that influences exerted during both the incubation and nestling periods influence postnatal growth but that genetic factors and maternal effects expressed through egg quality are small.

TABLE 4. Analysis of variance in asymptote and growth rate in Starlings (Experiment II).[a]

Sample and component of variation	Mean	SS	df	MS	s²	F	P
Unmanipulated clutches[b]							
Asymptote							
Total	75.88	748.22	42	17.81			
Nest		311.43	8	38.93	5.46	3.0	≤0.025
Error		436.79	34	12.85			
Growth rate							
Total	0.446	0.07544	42	0.00180			
Nest		0.03791	8	0.00474	0.00076	4.3	≤0.005
Error		0.03753	34	0.00110			
Experimental clutches							
Asymptote							
Total	76.13	454.62	36	12.63	12.63		
Natural parents		175.35	12	14.61	NS	1.3	≥0.30
Error		279.26	24	11.64			
Foster parents		196.87	9	21.87	3.34	2.3	≤.05
Error		257.75	27	9.55			
Growth rate							
Total	0.442	0.13496	36	0.00375	0.00375		
Natural parents		0.02622	12	0.00219	NS	0.5	≥0.90
Error		0.10873	24	0.00453			
Foster parents		0.10528	9	0.01170	0.00287	10.6	≤0.001
Error		0.02968	27	0.00110			

[a] SS = sum of squares, df = degrees of freedom, MS = mean square, s² = variance, F = ratio of effect mean square to error mean square, P = probability of F due to chance alone, NS = not significant (P > 0.05).
[b] Nine clutches of four or five eggs.

The within-brood variance in A ranged between 9.55 and 26.08 g² in the various ANOVA's reported here. These values represent standard deviations within broods of 3–5 g, which is on the order of 5% of the mean. According to an F_{max} test (Sokal and Rohlf 1969: 371), the various within-brood variances reported in this study did not differ significantly between unmanipulated and experimental broods, but they were significantly lower in 1976 than in 1970–1973. With respect to growth rate, within-brood variances ranged between 0.00076 and 0.00138 days⁻², representing standard deviations of 0.028 to 0.037 days⁻¹, or about 7% of the mean. The within-brood variances in K did not differ significantly among ANOVA's.

The within-brood component of variance (Table 5) expresses part of the genetic variance, interactions among siblings, and accidents of development, including the effects of disease, as well as stochastic elements resulting, for example, from parental distribution of food among progeny. Because experiment II revealed little evidence for genetic variance, we may assume that the within-brood variance is largely environmental. When hatching is asynchronous, weight hierarchies may be established among the young, and the last-hatched may grow less rapidly than its siblings. In experiment II, hatching was very synchronous (standard deviation within broods = 2.7 h). In unmanipulated broods, one chick usually hatched 1 day later than its siblings, yet the variances within unmanipulated and switched broods were similar. Moreover, the values of A and K for last-hatched chicks were not significantly lower than those of their siblings. We conclude that, in 1976, sibling interactions were not a major component of within-brood variance in A and K. Other studies have shown, in contrast, that sibling interactions strongly influence growth in passerines (Ricklefs 1965, Howe 1976, Bryant 1978, Strehl 1978), and further experimental study is desirable.

TABLE 5. Variance in asymptotes (A) and growth rates (K) of Starlings within broods.

	df	Variance	
		A (g²)	K (days⁻²)
Unmanipulated broods			
1970–1972, early	153	22.63	0.00138
1976	34	12.85	0.00110
Experiment I			
Natural parents	63	26.08	0.00113
Foster parents	63	21.94	0.00100
Residual	46	17.98	0.00076
Experiment II			
Foster parents	27	9.55	0.00110

The variance among sib groups, which is also the covariance among siblings within groups, is equal to ½ V_A + ¼ V_D + V_{Ec}. Experiments I and II were designed to remove components of the common environment (V_{Ec}) resulting from influences during the nestling and incubation periods, leaving only maternal (egg) effects with the genetic variance. The covariances between siblings in the various ANOVA's are listed in Table 6. It is not possible to compare values among ANOVA's, because the conditions during each period were different. Furthermore, the confidence limits around the variances are quite large. Yet we can draw the following conclusions: (1) genetic and egg effects on postnatal growth are small compared to total variation in A and K, and (2) factors in the common environment of siblings that affect postnatal growth exert their influences during both the incubation and nestling periods.

Comparisons among natural parents in experiment II should have revealed genetic and egg effects had they been present. In the experiment, the smallest significant F-ratio ($P = 0.05$) would have been 2.18, which represents an effect corresponding to 12% of the total variance (1.53 g² and 0.00045 days⁻¹). The experiment could not have detected a smaller "significant" effect. Because it was not possible to reduce the residual variance by the foster parent effect, the design of experiment II was less powerful than that of experiment I. The size of eggs varied significantly among natural parents in experiment II [$F(12,24) = 8.66$, $P < 0.0001$], but neither the length of the incubation period nor A and K was correlated with egg size. In Starlings, egg size is a poor predictor of yolk size (Ricklefs 1977, unpubl.) and therefore may not be a good indicator of attributes of egg quality that influence postnatal growth.

Experiment I, in which young were switched at hatching, indicated that postnatal growth is influenced by factors that act both before and after hatching. In experiment II, the incubation period varied significantly among foster parents [$F(8,25) = 6.28$, $P < 0.0002$] but not among natural parents [$F(21,33) = 1.13$, $P > 0.3$]. Therefore, incubation behavior of the parent appeared to be more important than egg quality or genetics in determining the length of the incubation period. Furthermore, the asymptote of the growth curve was positively related to the length of the incubation period [$F(1,32) = 5.5$, $P = 0.025$] with a slope of 0.34 (±0.14 SE) g·h⁻¹ within experiment II as a whole. We could not determine whether the effects of factors influencing incubation period carried over into postnatal development or were merely correlated with factors acting during the nestling period. The results of experiment

TABLE 6. Covariance in asymptote (A) and growth rate (K) between siblings.[a]

	df	$s_A{}^2$	$s_T{}^2$	$s_K{}^2$	$\% s_T{}^2$
Unmanipulated broods: $COV = \frac{1}{2} V_A + \frac{1}{4} V_D + V_{EC}$ (egg + incubation + nestling)[b]					
1970–1972 (early, within years)	58	37.64	62	0.00071	34
1976	8	5.46	31	0.00076	42
Experiment I					
Natural parents: $COV = \frac{1}{2} V_A + \frac{1}{4} V_D + V_E$ (egg + incubation)	17	3.71	14	0.00022	18
Foster parents: $COV = V_E$ (nestling)	17	7.59	28	0.00033	27
Experiment II					
Natural parents: $COV = \frac{1}{2} V_A + \frac{1}{4} V_D + V_{EC}$ (egg)	12	NS		NS	
Foster parents: $COV = V_E$ (incubation + nestling)	9	3.34	26	0.00287	77

[a] df = degrees of freedom, $s_A{}^2$ = variance in asymptote (g^2), $s_K{}^2$ = variance in growth rate (days^{-2}), $\% s_T{}^2$ = percentage of the total variance in either A or K.

[b] Model indicating the components of the between sibling covariance (COV): V_A = additive genetic variance, V_D = dominance genetic variance, V_{EC} = variance due to common environment, which may be partitioned into components deriving from the eggs and the incubation and nestling periods.

I suggest a carryover effect, but further experiments are warranted. Growth rate (K) was not significantly correlated with incubation period in experiment II.

Components of variance in growth rate and asymptote associated with differences among nests could derive from certain aspects of parental care, the physical environment of the nest box, or the location of the nest box relative to suitable feeding areas. We neither controlled these factors nor measured them as covariates in our experiments, although both these approaches would be feasible in field experiments.

Clearly, ornithologists should pay closer attention to the origin of variation in traits within populations. The experimental techniques are applicable to many species, and statistical analysis has been greatly facilitated by computer programs. The greatest difficulties in such studies are to design experiments to separate the effects of interest and to accumulate sufficiently large samples to detect small components of variance. As the results of such studies accumulate, we shall be able to make more general statements about the ecological and evolutionary (genetical) interactions of individual traits with the environment and about how these interactions are mediated through parental care.

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