COMPONENTS OF VARIANCE IN MEASUREMENTS OF NESTLING EUROPEAN STARLINGS (*STURNUS VULGARIS*) IN SOUTHEASTERN PENNSYLVANIA

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ABSTRACT.—I report the results of experiments designed to distinguish factors affecting within-population variability in measurements of nestling European Starlings (*Sturnus vulgaris*). Individuals were switched among pairs of nests at the beginning of the incubation period and at the beginning of the nestling period. Variables were analyzed in a replicated (nested), three-way factorial analysis of variance to distinguish the contributions of factors associated with (1) the genotype of the embryo or composition of the egg, (2) the incubation period, and (3) the nestling period. In addition, I analyzed the correlations among growth variables within the sample as a whole and among main effects in the experimental design to search for patterns of genotypic and phenotypic interrelationship. I also related growth variables of nestlings to the size and composition of sibling eggs and to the length of the incubation period.

The present experiment did not reveal any genetic or egg-quality component to within-population variation in rate of mass increase and mass asymptote achieved, length of the tarsus of fully grown nestlings, or rates of growth of the wing and outer primary feather. Similarly, the nest in which the individual was incubated had no effect on postnatal growth. The nest in which the individual was reared significantly contributed between 19 and 29% of the sums of squares in rate of mass increase, length of the tarsus, rate of increase in length of the wing, and the maximum length of the sheathed portion of the outer primary feather. Rearing nest did not have a significant effect on the mass plateau of the chick. These results, particularly the absence of some effects, are difficult to interpret, because a large proportion of the variation in several variables occurred between pairs of switched nests. These differences undoubtedly included some of the variation that might have been attributable to effects within experiments.

Growth variables were weakly correlated over the entire sample, revealing little pattern of variation in postnatal growth. Over certain of the effects in the experimental design, however, particular groups of variables were strongly correlated, indicating interrelated responses of some of the growth parameters to environmental and, perhaps, genetic factors.

The size of the egg had a small effect only on the mass plateau and the length of the tarsus of the chick. The composition of a sibling egg influenced only the maximum length of the sheath of the outer primary feather.

The present study was somewhat weakened by small sample size and an inexplicable between-experiment effect that reduced its power to distinguish among effects of interest. The experimental design has the potential, however, to disentangle many classes of factors associated with genotype and parental care that contribute to within-population variation in phenotypic measurements. *Received 16 May 1983, accepted 5 December 1983.*

WITHIN-POPULATION variation in growth parameters of passerines birds on the order of 5–15% of their mean values has been reported for the fitted constants of growth equations and for masses and measurements at particular ages (e.g. Ricklefs 1976, O'Connor 1977, Ricklefs and Peters 1979, Ross 1980, Zach 1982, Zach and Mayoh 1982). Such variation can arise from (1) general factors affecting the whole population, such as weather; (2) factors varying within the population related to variation among pairs of breeders; and (3) factors whose effects vary among offspring reared by particular parents. The second type of factor includes variables related to the quality of parental care, whether it is associated with genotypic differences among adults, related to age, or expressive of developmentally acquired characteristics. These components may reside in the genotype of the embryo, in the composition of the egg (hence

reflecting the female parent), and in influences exerted during the incubation, nestling, and postfledging periods of parental care. The third type of factor, whose variation is expressed within pairs of breeders, may be associated with intrinsic differences in the quality of the young arising from genotypic differences, the effects of competition and other interactions among siblings, and other largely unaccountable factors—the so-called "error" term in analysis of variance.

Although the role of extrinsic factors in producing within-population variation has received some attention recently (e.g. year, season, and habitat effects: Ricklefs and Peters 1979, Ross 1980), relatively little is known about how differences in quality of parental care contribute to intrapopulation variation in the characteristics of offspring. Within-population variation ultimately is related to variation in the action of external factors on individuals, either as the result of selection acting on genetic variation or through the developmental flexibility of individuals. Genotypic variation is transmitted from generation to generation by the rules of heredity. Nongenetic variation also may be transmitted through the response of offspring to nongenetic variation in the quality of adults as parents. The rules of such nongenetic inheritance are, for the most part, unexplored.

In altricial birds, much of the variation in measurements of nestlings is expressed among natural broods, reflecting the contributions of genotype and parental care. For example, among first broods of European Starlings (*Sturnus vulgaris*) in southeastern Pennsylvania, 73% of the variation in the mass asymptotes of nestlings and 51% of the variation in the rate of achievement of the asymptote occurred among broods in one study (Ricklefs and Peters 1979). The separate contributions of genotype and various aspects of parental care to this variation, however, can be determined only by experimental manipulation.

The genetic component of variation is most readily determined from the correlation of traits between parents and offspring and by the covariation among half-siblings (Falconer 1960). Both types of data are difficult to collect in the field, the first because offspring are difficult to recover as adults, at which time their measurements can be compared to those of their parents, and the second because the required mating schemes are either not present in natural populations or are difficult to control when they are present, as in polygynous species. Parent-offspring correlations have been measured in certain species in which offspring remain close to their natal sites and are easily recovered. Several of these studies have revealed high heritabilities for several size traits (e.g. mass, lengths of appendages) of fully grown birds (e.g. Boag and Grant 1978, Smith and Zach 1979, Van Noordwijk et al. 1980, Garnett 1981). Because nestlings were not assigned to parents at random within the population in these studies, it was not possible to separate the effects of nestling genotype from attributes of parents related to both their measurements and their qualities as parents. To circumvent this problem, Smith and Dhondt (1980) switched eggs and hatchlings among broods; their results confirmed that factors associated with the clutch (i.e. the natural genetic parents), and not the foster nest, were responsible for the observed correlations of traits within families.

Where it is impractical to calculate parent-offspring correlations and half-sib correlations, one may obtain an upper limit to genetic heritability by estimating the covariance among full sibs. This value is equal to the sum of ½ the additive genetic variance, ¼ the dominance variance, and the variance due to common environment, e.g. the nest in which the chicks are reared. When the common environment effect is eliminated by switching offspring at random among nests, the variance among genetic full sibs provides a reasonable upper limit to additive genetic variation, hence heritability.

Ricklefs and Peters (1981) performed a series of switching experiments with the European Starling in order to determine the contributions of genotype and parental care to variation in growth parameters of the nestlings. In one set of experiments, individuals were switched among nests at hatching; both natural and foster parents contributed significantly to variation in the rate constant of logistic equations fitted to body masses and to variation in the asymptote of the equation. In another experiment, in which individuals were switched among nests at the beginning of the incubation period, only the foster nest exerted a significant effect on growth parameters. The two experiments together suggested that postnatal growth was affected by aspects of parental care during both the incubation and nestling periods but not by the genotype of the nestling or the composi-

TABLE 1. Pattern of switching individuals among pairs of nests (X and 0) within each experiment.

	Individual							
	1	2	3	4	5	6	7	8
Nest in which egg laid	X	X	X	X	0	0	0	0
Nest in which egg incubated	X	X	0	0	X	X	0	0
Nest in which chick reared	X	0	X	0	X	0	X	0

tion of the egg. The second experiment was sufficiently sensitive to detect a heritability of about 12%.

The designs employed by Ricklefs and Peters (1981) were not fully adequate, in that variation could not be simultaneously separated into components associated with the egg and the incubation and nestling periods. For this reason, the experiments had relatively little power to detect effects with small contributions to variation.

The present study reports a new design that overcomes some of the weaknesses of previous experiments. It involves a double switching of individuals between pairs of nests, first at the beginning of the incubation period and second, with a partly overlapping set of individuals, at the beginning of the nestling period. Various measurements of nestling size and growth rate are analyzed in a three-way factorial analysis of variance replicated over (nested within) pairs of nests involved in each switching experiment. This design allows one to distinguish clutch, incubation, and chick-rearing factors as main effects. In addition, I have calculated correlations among growth variables, in the sample as a whole and over the main effects in the model, and between growth variables on the one hand and the size and composition of eggs and the length of the incubation period on the other.

METHODS

General.—The study was conducted during 1982 at a colony of free-living starlings attracted to nest boxes at the Waterloo Mills Field Station of the University of Pennsylvania, near Devon in southeastern Pennsylvania. The colony is similar to that described by Ricklefs and Peters (1979). Experiments were limited to nests initiated during a 1-week period at the end of April and beginning of May. Nests were checked each day during the laying period. Eggs were removed from nests within 1 day of laying and stored at room temperature until clutches were complete and switches between nests could be accomplished (see Ricklefs and Smeraski 1983). Each pair of nests selected for switching was chosen at random from nests in which clutches were initiated over a given 3-day period. Only the first 4 eggs in the laying sequence (of generally 5 or 6 eggs) were used in each experiment. Two of the 4 eggs in each nest of the pair were switched before replacing the eggs in the nests to be incubated (plaster eggs were substituted during the laying period). The switched clutches were replaced in the nests within a few minutes of each other. Hence, within each experimental pair, incubation of every egg was begun at the same time. Fifth and sixth eggs were removed from clutches for analysis of chemical composition (see below).

Switching.—Each pair of nests was referred to as an experiment designated by a capital letter (A, B, C, . . .). Switches between nests always involved the same numbered eggs in the sequence to avoid clerical confusion, but the pattern of switching was varied among experiments. The pattern of switching, illustrated for a single experiment in Table 1, was designed so that the effects of clutch, incubation nest, and rearing nest could be distinguished in a nested three-way factorial analysis of variance explained in detail below.

Measurements.—Lengths (L) and breadths (B) of eggs were measured to the nearest 0.01 cm with vernier calipers. The fresh mass (M) of each egg (g) was estimated from an empirically determined equation: $M = 0.035 + 0.530\ LB^2$ (Ricklefs 1984). Fifth and sixth eggs in a clutch were separated into shell, albumen, and yolk components. These were air-dried at 60°C; yolks were soaked in two baths of a 5:1 mixture of petroleum ether and chloroform to remove lipids (see Ricklefs and Smeraski 1983). The following calculated variables were used in this analysis: egg mass, yolk mass, yolk fraction (yolk mass/total mass), and the lipid fraction of the dry matter of the yolk. Based on a principal components analysis of egg composition, Ricklefs (1984) determined that egg mass, yolk fraction, and lipid fraction were the major orthogonal components of variation in the composition of starling eggs.

Incubation periods and the time of day at which eggs hatched were determined to within 2 h in most cases by periodically checking each nest during the 12th and, if necessary, 13th days of incubation (Ricklefs and Smeraski 1983). Incubation periods are re-

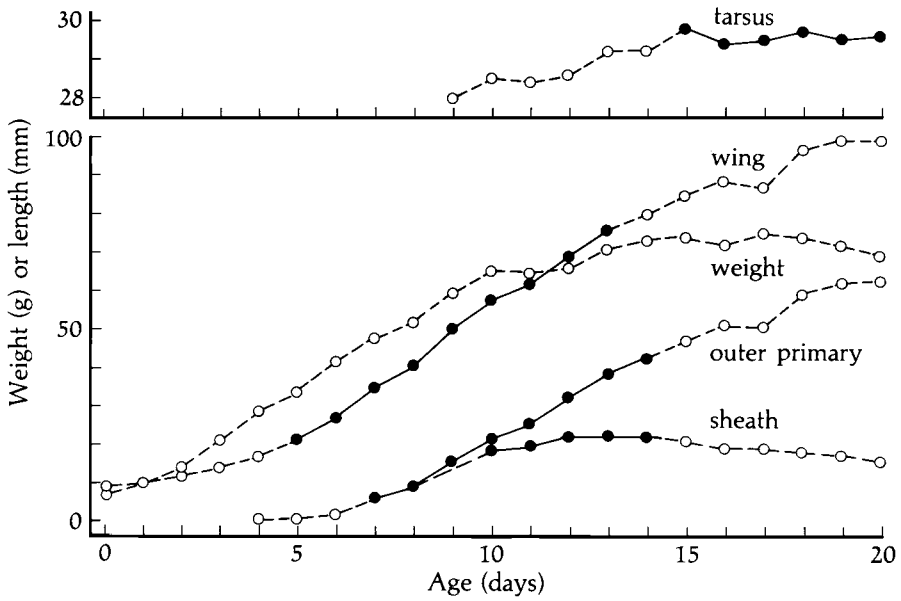

Fig. 1. Increase in mass and lengths of appendages of nestling European Starlings. Solid lines and symbols represent data used to calculate indices of growth and size used in this study.

ported as hours deviation from 12 days (288 h). In most of the experiments, incubation was begun during the mid- to late afternoon. Eggs that hatched during the night (between 20 h of one day and 6 h of the next) were considered as having hatched at 6 h on the second day. Only experiments in which all the hatchlings could be matched with certainty to eggs were included in this analysis.

At intervals of 1, most commonly 2, or 3 days, I weighed the nestlings to the nearest 0.5 g with Pesola spring scales (100-g capacity) and measured the lengths (mm) of the wing (bend of the wrist to the tip of the manus or the longest primary feather), outer primary, outer primary sheath, and the tarsus, using flexible plastic rulers. Masses of nestlings were fitted by logistic equations having the form

$$M(t) = A\{1 + \exp[-K(t - I)]\}^{-1},$$

where $M(t)$ is the mass (g) at age t days, A is the asymptote (g) of the growth curve, K is a constant (days^{-1}) describing the rate at which the asymptote is achieved, and I is the age (days) at the inflection point of the growth curve [$M(I) = 0.5A$] (Ricklefs 1967). Equations were fitted to data by a nonlinear least-squares method (SAS procedure NLIN, Helwig and Council 1979). Maximum mass of the nestling (*MAX*) was also included as a variable. Measurements of appendages were averaged over all nestlings in the experiments and plotted as a function of age (Fig. 1) to determine suitable derived variables for comparisons among treatments. The tarsus is too fully grown by hatching to estimate its rate of increase in length accurately, and so only its final length (*TAR*) was characterized by calculating the average of values obtained for each chick at age 15 days or later. The maximum length of the sheath of the outer primary feather (*SH*) was similarly estimated by calculating the average of values obtained between 10 and 14 days. Neither the wing nor the primary attains its full length by the end of the nestling period (about 21 days); hence, it is difficult to interpret asymptotic equations fit to the data, even though this technique has been used by Zach (1982) and Zach and Mayoh (1982). Instead, I fitted straight lines through approximately linear portions of the curves, 5–13 days for the wing (*WN*) and 7–14 days for the outer primary feather (*PR*) (see Fig. 1). These lines, having the general form $Y = a + bX$, were estimated by a least-squares procedure (SAS procedure REG). I selected the slope of the regression (b, acronyms *WNS*, *PRS*) and the intercept of the line on the X (age) axis ($-a/b$, acronyms *WNI*, *PRI*) as variables for comparison.

Data.—Several experiments had to be eliminated from consideration, because one or more eggs failed to hatch or nestlings could not be matched to eggs with certainty. Seven experiments (herein A–G: 14 nests, 56 chicks) were successful, with the exception of single eggs that did not hatch in each of experiments E, F, and G. These were replaced with nestlings from other nests, but the positions of these

TABLE 2. Outline of analysis of variance table for main effects.

Effect	Acronym	df[a]	Expected mean square
Expt	E	6	$V(error) + 4V[C(E)] + 4V[I(E)] + 4V[N(E)] + 8V(E)$
Clutch(Expt)	$C(E)$	7	$V(error) + 4V[C(E)]$
Incubation nest(Expt)	$I(E)$	7	$V(error) + 4V[I(E)]$
Rearing nest(Expt)	$N(E)$	7	$V(error) + 4V[N(E)]$
Error(Expt)		25	$V(error)$
Total		52	

[a] Degrees of freedom, discounting the error(expt) and total by 3 to take into account missing values.

chicks in the experimental design were treated as missing values. To balance the design fully, values for these individuals were replaced with the mean for both nests in the experiment. Sokal and Rohlf (1981: 364) recommend a more involved correction for missing values, but the additional calculations, when applied to a few cases, did not alter the statistical results of analyses in which the mean was substituted for missing values. Error and total degrees of freedom in the ANOVA were reduced by the number of missing values.

Analysis of variance.—The data were treated as a three-way factorial ANOVA nested within experiments. The experiments and each of the treatments within experiments are random effects; hence, this is a model II ANOVA. There are 7 degrees of freedom (df) within each experiment (E), three distributed among the main effects [clutch (C), incubation nest (I), and rearing nest (N)], three among three two-way interactions ($C*I$, $C*N$, and $I*N$), and one to the three-way interaction ($C*I*N$). Because there are no replications within cells, all two-way interactions were tested over the three-way interactions (Sokal and Rohlf 1981: 383). In those experiments with missing values, there were too few degrees of freedom to test the significance of the two-way interactions. Therefore, these were tested only in experiments A–D, with a total of 4 df for the numerator of F and 4 for the denominator. Because there were no a priori reasons to expect two-way interactions and because calculated interactions were very small (see Results), however, their sums of squares and degrees of freedom were added to those for the three-way interaction to yield an error term with 4 df (3 df with missing values) within each experiment (Sokal and Rohlf 1981: 285). The main effects in the model were then analyzed as outlined in Table 2. All two-way interactions were assumed to be zero in constructing this table. Sums of squares and degrees of freedom were added over experiments; therefore, each of the three main effects was tested by the ratio $F = MS(effect)/MS(error)$ with 7 and 25 df. The effect of experiments was determined by subtracting the sums of squares within experiments from the total, leaving 6 df. Because the mean square (MS) attributable to experiments contains terms with both error and main-effect variances, the statistical significance of differences between experiments cannot be tested by a simple F-ratio (Scheffe 1959). Instead, one may substitute

$$F'' = \frac{[MS(E) + 3MS(error)]}{\{MS[C(E)] + MS[I(E)] + MS[N(E)]\}}$$

(Winer 1971). Representing this equation as $F'' = (u + 3v)/(w + x + y)$, the numerator degrees of freedom may be estimated by

$$\mathrm{df(num)} = \frac{(u + 3v)^2}{\dfrac{u^2}{\mathrm{df}(u)} + \dfrac{3v^2}{\mathrm{df}(v)}}$$

and the demonimator degrees of freedom by

$$\mathrm{df(denom)} = \frac{(w + x + y)^2}{\dfrac{w^2}{\mathrm{df}(w)} + \dfrac{x^2}{\mathrm{df}(x)} + \dfrac{y^2}{\mathrm{df}(y)}}$$

(Satterthwaite 1946). The ANOVAs were calculated with the SAS procedure GLM; variance components for each of the main effects and among experiments were calculated by the SAS procedure VARCOMP.

Correlations among variables.—Correlation coefficients (r) among any two variables (X and Y) were calculated from the appropriate sums of squares and crossproducts (SS) by the expression $r = SS(XY)/[SS(X)SS(Y)]^{-2}$. Sums of squares of the main effects were calculated according to Snedecor and Cochran (1967: 425). In order to examine further the relationships among variables, I performed a principal components analysis (PCA) based on the correlation matrix calculated within the sample from all the experiments taken together, using the FACTOR procedure of SAS.

Postnatal growth variables were related to egg size (EGG), egg composition, length of the incubation period (INC), and time of hatching (T). Egg size, incubation period, and time of hatching were known for all the nestlings in experiments A–G. The effects of these variables (X's) on growth measurements (Y's) were tested by models of the form $Y = E + I(E) + N(E) + X + error$ for egg size, and $Y = E + C(E) + N(E) + X + error$ for INC and T. That is, variation due to differences in experiments, rearing nests, and either clutches or incubation nests within experiments was

TABLE 3. *F*-ratios (4,4 df) for two-way interaction terms in the analysis of variance model.[a]

Interactions	Variable					
	A	*K*	*TAR*	*WNS*	*PRS*	*SH*
Clutch *Incnest(Expt)	2.61	1.03	0.75	0.30	2.34	0.84
Clutch *Nest(Expt)	2.26	0.60	0.56	1.31	0.41	0.31
Incnest *Nest(Expt)	1.29	0.48	0.24	0.63	3.56	1.92

[a] None of the *F*-values was significant at the 0.05 level.

removed to reduce the error sum of squares. Effects of either clutch or incubation nest within experiments were not removed for each variable, because they included much of the variation in the predictor variables (see Results).

The composition of eggs was estimated from one egg per clutch. Most of the variation in egg composition within the population is related to differences between clutches (Ricklefs 1984), and so one egg provides a good estimate of the composition of others within the clutch. Because eggs were not analyzed from several of the nests in experiments A–G, analysis of the effects of egg composition on postnatal measurements was extended to other nests involved in incomplete switching experiments. Within each rearing nest (*N*), I averaged measurements for chicks from the same clutch; hence, all variation within nests could then be attributable to clutch and error. The effects of egg composition were analyzed according to the general model $Y = N + X_1 + X_2 + \cdots + error$ in a stepwise regression in which *X*'s were the egg-composition variables. The effects of rearing nest were factored out as a separate component to reduce the error term. The relationship of growth variables to incubation period and hatch time were analyzed in a similar fashion, except that values were averaged for individuals within nests sharing the same incubation nest. Further details of the analysis are presented in relevant parts of the Results section.

RESULTS

Analysis of variance.—Two-way interactions among the effects of clutch (*C*), incubation nest (*I*), and rearing nest (*N*) are presented in Table 3. Main effects [*E*, *C*(*E*), *I*(*E*), *N*(*E*)] were included in the model but are not presented in the table. None of the variables exhibited significant two-way interactions between the main effects *C*, *I*, and *N*. The largest *F*-ratios were for the rate of elongation of the outer primary, for which the *I***N*(*E*) term had a value of 3.56 ($P = 0.2$). The response profile for this variable (Fig. 2) shows that the interaction between *I* and *N* was due primarily to a single experiment (C). In the subsequent treatment of all variables, I assume that there are no significant two-way interactions and combine these interactions with the error term.

The nested three-way factorial analysis of

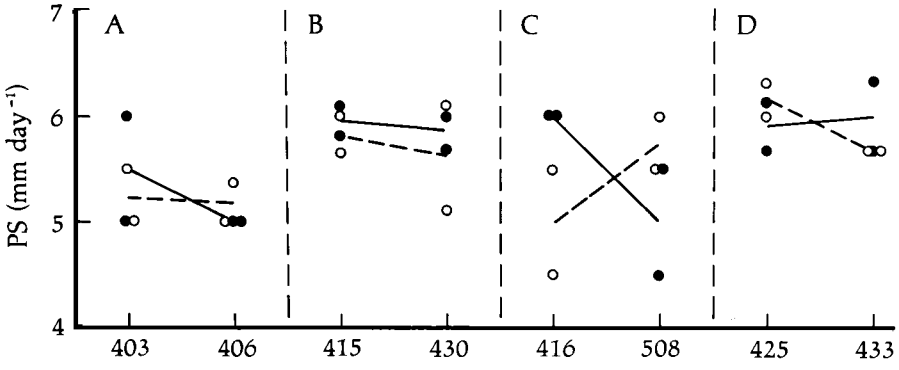

Fig. 2. Profile analysis of the effects on *PS* of nest(expt), distinguished among experiments along the horizontal axis, and incnest(expt), distinguished by differences in symbols and lines within experiments. Solid symbols refer to the nests at the left within each experiment.

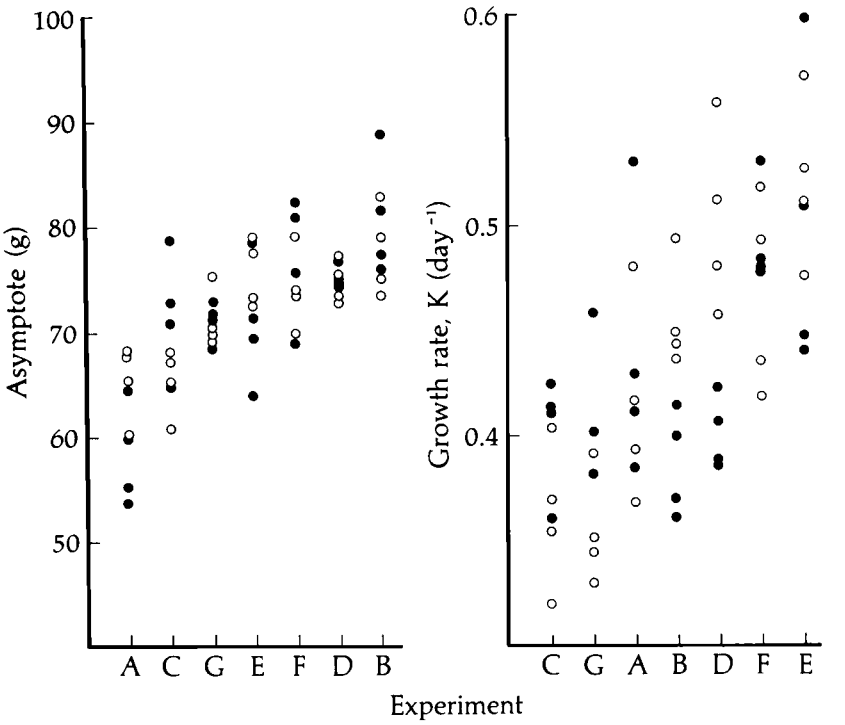

Fig. 3. Profile analysis of the effect of experiment on the asymptote (*A*) and growth rate (*K*). Solid and open symbols within experiments distinguish nests within which nestlings were reared.

variance is presented in Table 4. Coefficients of variation (CV) over the sample from all the experiments taken together varied from a low of 2.0% for (*TAR*) to 14.7% for the rate constant (*K*) of the logistic equation. Most of the other CV's were close to 10%. Clutch (*C*) was a significant main effect only for the size of the egg, which generally is uniform within natural clutches in most species of birds. This effect accounted for 68% of the total sum of squares (*SS*) within the sample. For other variables, *C* accounted for less than 10% of the total *SS* and was not a significant effect. The incubation nest (*I*) was a significant effect only for the length of the incubation period and time of hatching, confirming an earlier analysis focussing only on incubation variables (Ricklefs and Smeraski 1983).

Rearing nest was a significant effect for *K*, *TAR*, rate of elongation of the wing (*WNS*), and the length of the outer primary sheath (*SH*), each accounting for between 19 and 29% of the total *SS*. For the asymptote of the mass growth curve (*A*), nest was a marginally significant effect [$F(7,28) = 2.02$, $P = 0.08$] but accounted for only 11% of the total *SS*.

Differences between experiments accounted for a large and significant ($P < 0.05$) proportion of the variation (35–60% total *SS*) in *A*, *K*, *MAX*, and the intercept of the linearized wing growth curve (*WNI*) (Fig. 3). This result was surprising, because nests were assigned to experiments at random. One would, however, expect the experiment effect to account for a large portion of the total *SS* in the model, because it incorporates variances attributable to effects within experiments (Table 2).

Correlation structure and principal components.—Correlations among postnatal measurements are presented in Table 5. Most of the large correlation coefficients, on the order of 0.50 or greater, involve one or both of the intercepts of the wing and primary growth curves and the age at inflection of the logistic growth curve for body mass. Because of the manner in which intercepts were calculated, one would expect positive correlations between the slope of the regression and the intercept on the

TABLE 4. Descriptive statistics and analysis of variance for measurements of nestlings and characteristics of eggs and incubation.[a]

	Variables						
	A	*K*	*I*	*MAX*	*TAR*	*WNS*	*WNI*
Mean	72.07	0.436	5.23	74.03	29.61	6.85	1.84
Standard deviation	6.77	0.064	0.63	6.48	0.59	0.61	1.03
Coefficient of variation (%)	9.4	14.7	12.0	8.8	2.0	8.9	—
Sums of squares							
Total	2,523	0.225	21.7	2,313	19.46	20.2	57.9
Percentage of total							
Expt	60.4**	49.1*	33.1	58.5**	24.2	46.0	34.7
Clutch(Expt)	3.6	2.2	10.3	2.6	4.7	3.8	5.4
Incnest(Expt)	4.2	4.2	10.8	5.2	9.8	3.5	5.2
Nest(Expt)	10.7	19.2*	12.2	14.1	29.1*	27.7*	11.6
Error	21.1	25.2	34.0	19.5	32.1	19.0	43.1
Standard deviations (square roots of variances)							
Total	6.77	0.064	0.63	6.48	0.59	0.61	1.03
Among Expts	5.31	0.042	ns	4.81	ns	ns	0.64
Within Expts	4.52	0.048	—	4.43	—	—	0.88
Among Nests(Expt)	2.20	0.032	ns	ns	0.38	0.41	ns
Error	4.36	0.045	0.51	4.02	0.47	0.37	0.94

[a] *$0.01 < P < 0.05$; **$P < 0.01$; ns, effect not significant in ANOVA.

X(age)-axis, and therefore these correlations may have no biological significance. The same may be said of the strong negative correlation between the growth rate constant (*K*) and the age at inflection (*I*) (−0.71). Passing over the obvious correlation between *A* and *MAX*, there remains only one other value exceeding 0.50, a negative correlation between *K* and *WNS*.

The rather weak correlation structure among variables in this study is reconfirmed by a principal components analysis (PCA), presented in Table 6. Ten variables were entered in the PCA, based on the correlation matrix in Table 5; 5–6 components were required to account for 90% of the variance, and the first (I) accounted for only 34%. Correlations of the components with the original variables revealed that component I was associated primarily with *A* (0.80), *I* (−0.75), and *WNI* (−0.89). Although *I* and *WNI* are positively correlated, neither is related to *A* in Table 5. Component II was associated with *A* (0.79), *MAX* (0.73), and *PRS* (0.64); III distin-

TABLE 5. Matrix of product moment correlation coefficients (×100) among measurements of nestling starlings (df = 51).[a]

Variables	*A*	*K*	*I*	*MAX*	*TAR*	*WNS*	*WNI*	*PRS*	*PRI*	*SH*
A	100	10	03	95**	45**	09	−37**	30*	−23	−05
K		100	−71	26	21	−35**	−60**	−11	−39**	45**
I			100	−10	−06	40**	70**	04	35**	−41**
MAX				100	41**	09	−41**	30	−26	05
TAR					100	07	−20	31*	−00	15
WNS						100	61**	13	−10	−07
WNI							100	−06	45**	−28
PRS								100	55**	−14
PRI									100	−31*
SH										100

[a] * $0.01 < P < 0.05$; ** $P < 0.01$.

TABLE 4. Continued.

Variables					
PRS	*PRI*	*SH*	*EGG*	*INC*	*T*
5.72	6.33	21.2	7.07	7.05	10.9
0.73	0.87	1.7	0.66	13.59	3.6
12.7	—	8.1	9.4	—	—
29.0	41.9	163	24.1	10,152	705
20.5	22.5	32.8*	21.4	68.0	16.8
5.5	7.8	2.8	67.7**	1.8	11.8
21.4	16.3	5.3	3.3	26.0**	34.5**
10.0	10.9	26.4*	0.8	0.5	10.3
42.6	42.5	32.6	6.8	3.7	26.6
0.73	0.87	1.72	0.66	13.6	3.6
ns	ns	ns	ns	ns	ns
—	—	—	—	—	—
ns	ns	1.03	ns	ns	ns
0.66	0.80	1.38	0.24	3.65	2.6

guishes *WNS* (0.60) and *PRS* (−0.60), although the two are not strongly correlated among themselves (0.14), and *PRI* (−0.73); IV and VI are strongly associated with *SH* (0.63, 0.50); and V with *TAR* (0.56). ANOVAs for each principal component revealed that experiment was the only significant effect for I and II, and nest was the only significant effect for III, IV, and V; no effect was significant for VI. These results are consistent with the ANOVAs for each of the original variables, except that nest is not a significant effect for component I; this component is strongly associated with the variable *K*, for which nest was a significant effect (Table 4).

Correlations over effects.—For the variables *A*, *K*, *TAR*, *WNS*, *PRS*, and *SH*, I calculated intercorrelations both within and among effects. For the sample from all the experiments taken together, within experiments, and within effects (error), none of the correlation coefficients exceeded 0.50 and most were very low (Table 7). I take this result to mean that these variables are not intrinsically correlated by measurement, as are *A* and *MAX* for example, or by calculation, as are *WS* and *WI*.

The strong correlations revealed over experiments are difficult to interpret, because they incorporate all the correlations over effects within experiments. Furthermore, because the degrees of freedom over experiments were so small (4), none of the coefficients was statistically significant ($P < 0.05$). Variation in mea-

TABLE 6. Principal components analysis of measurements of nestling starlings.[a]

	Factor					
	I	II	III	IV	V	VI
Eigenvalue	3.41	2.37	1.44	1.04	0.63	0.52
Proportion of variance	0.34	0.24	0.14	0.10	0.06	0.05
Cumulative proportion	0.34	0.58	0.72	0.83	0.89	0.94
Factor pattern[b]						
A	48**	79**	18	−26	01	15
K	80**	−26	−07	20	−05	−25
I	−75**	38*	22	−12	27	24
MAX	57**	73**	17	−17	−11	13
TAR	37*	54**	−07	42**	56**	−25
WNS	−41**	40**	60**	40**	−32*	−22
WNI	−89**	07	23	26	03	−03
PRS	−03	64**	−60**	26	−35**	−02
PRI	−56**	21	−73**	15	03	13
MS	49**	−29	17	63**	−00	50**
Analysis of variance (F'')						
Expt	4.26**	3.20*	1.00	1.02	1.32	2.20
Clutch(Expt)	0.81	0.39	0.59	0.69	0.54	0.25
Incnest(Expt)	0.55	1.92	1.98	0.42	0.96	0.33
Nest(Expt)	1.21	1.60	3.39**	4.33**	4.18**	1.40

[a] * $0.01 < P < 0.05$; ** $P < 0.01$.

[b] Correlations (×100) of each original variable with each principal component (df = 41).

TABLE 7. Correlations (×100) among measurements over effects.[a]

Degrees of freedom	Effect						
	Total (51)	Expt (4)	Within expt (39)	*C*(*E*) (14)	*I*(*E*) (14)	*N*(*E*) (14)	Error (11)
A vs. *K*	10	32	−17	−30	−74**	−03	−13
TAR	45**	72	31	−14	66**	32	31
WNS	09	07	10	13	33	34	−14
PRS	30*	51	22	−28	12	40	25
SH	−05	−32	18	14	−15	35	14
K vs. *TAR*	21	03	32	13	−65**	60*	33
WNS	−35**	−53	−18	−77**	19	06	−42
PRS	−11	−05	−15	−49	−06	13	−27
SH	45**	74	27	33	35	59*	00
TAR vs. *WNS*	07	08	07	−27	−08	36	−17
PRS	31*	73	19	44	63**	−21	19
SH	15	−23	30	15	−56*	62**	24
WNS vs. *PRS*	14	43	01	62**	−14	−21	08
SH	−07	−60	27	−20	40	48	08
PRS vs. *SH*	−14	−16	−13	−23	−86**	32	−15

[a] * $0.01 < P < 0.05$; ** $P < 0.01$.

surements over experiments was nonetheless closely linked among *K*, *SH*, and *WNS*, and among *PRS*, *TAR*, and *A*. The correlation between *PRS* and *A* disappeared when correlations between *PRS* and *TAR* and between *TAR* and *A* were removed by partial correlation analysis (Sokal and Rohlf 1981: 656). The same was true of the correlation between *K* and *WNS*. Therefore, the only unique correlations involved the relationships of *PRS* and *A* to *TAR* and of *K* and *WNS* to *SH*.

Even though clutches and incubation nests accounted for very little of the total *SS* in the study, small differences distributed over these effects were highly correlated among several of the variables. Over clutches, variation in *WNS* and *PRS* were positively related ($r = 0.62$), even though the two variables were largely unrelated in other comparisons. I interpret this result to mean that clutch does exert a small but significant effect on some combination of variables, which cannot be detected by the analysis of each variable separately. The strong negative correlation of *K* and *WNS* over clutches (−0.77) is reflected less strongly over experiments (−0.53) and within the error (−0.42) and the study as a whole (−0.35). Incubation nests appear to exert similar effects on combinations of the variables, notably *PRS* and *SH* (−0.86) and *A* and *K* (−0.74). This is the only situation in which there is a strong relationship between *A* and *K*. Several variables (*TAR*, *K*, and *SH*), for all of which nest was a significant effect, were also intercorrelated over nests.

Relationship of growth to other variables.—For all the individuals within the seven experiments, I recorded the size of the egg (*EGG*), incubation period (*INC*), and time of hatch (*T*). None of these was significantly related to growth variables *A*, *K*, *MAX*, *TAR*, *WNS*, *PRS*, and *SH* in separate analyses of covariance (ANCOVA).

Egg composition was estimated for only one or two eggs per clutch, and data were not available for several of the clutches used in experiments A–G. Hence, the relationship of growth variation to egg composition, as well as to *EGG*, *INC*, and *T*, was examined over all of the nests in the study. In analyses involving *EGG*, *INC*, and *T*, only *PRS* [$F(1,74) = 3.05$, $P = 0.085$] and *SH* [$F(1,75) = 6.10$, $P = 0.016$] were related to *T* [*PRS* = −0.221 + 0.0215 (0.0123 SE) *T* and *SH* = 0.744 − 0.0722 (0.0292 SE) *T*].

An analysis of the relationships of growth variables to egg composition revealed that adjusted values of both *A* [$F(1,45) = 7.72$, $P = 0.008$, $R^2 = 0.15$] and *TAR* [$F(1,45) = 4.70$, $P = 0.036$, $R^2 = 0.10$] increased in direct relation to egg mass [*A* = −14.57 + 2.06 (0.74 SE) *EGGMASS* and *TAR* = −2.17 + 0.32 (0.15 SE) *EGGMASS*].

Hence, an increase of 1 SD in *EGGMASS* (0.66 g) corresponds to increases of 1.4 g (0.20 SD) in *A* and 0.21 mm (0.36 SD) in *TAR*. In addition, *SH* was related to egg composition by the following equation: $SH = 2.18 + 3.59$ (1.30 SE) *YOLK* [$F(1,44) = 7.58$, $P = 0.009$] − 38.09 (10.55 SE) *YOLK FRACTION* [$F(1,44) = 13.03$, $P = 0.001$, total $R^2 = 0.23$]. None of the other relationships was significant.

Discussion

Main effects.—The major results of this experiment may be summarized as follows. First, neither clutch nor incubation nest influenced any of the postnatal growth variables. Second, rearing nest was a significant effect, accounting for between 19 and 29% of the total sums of squares and 38–51% of the within-experiments sums of squares, for growth rate (*K*), rate of wing elongation (*WNS*), and the lengths of the tarsus (*TAR*) and sheath of the outer primary feather (*SH*). Third, significant proportions of the variation in asymptote (*A*), *K*, and, by correlation with *K*, intercept of the wing length regression (*WNI*) were distributed over the experiments.

The absence of a clutch effect indicates that genotype and maternal effects expressed through the composition of the egg did not affect the posthatching growth of the nestlings. In other studies, parent-offspring regressions have revealed high heritabilities in several characters, including measurements of the beak and tarsus as well as mass, in some populations (Boag and Grant 1978, Van Noordwijk et al. 1980, Garnett 1981). High heritabilities for measurements of both adults and growing chicks have also been reported in the poultry literature (Kinney 1969). Although some of the parent-offspring correlation revealed in natural populations may have been due to environment-genotype interactions (i.e. adults that nourish themselves well also feed their offspring well), Smith and Dhondt (1980) eliminated this problem by switching eggs and young of Song Sparrows (*Melospiza melodia*) to foster nests and obtained similar results. Measurements of offspring at 9 weeks of age were related only to their genetic parents and bore no resemblance to foster parents. Because regressions of offspring upon male and female parents did not differ, there were also no detectable maternal effects expressed through the composition of the egg. These results differ substantially from the findings of this study to the extent that midparent-offspring correlation and variance among full sibs estimate the same quantities (V_A/V_P in the first case and $V_A/2 + V_D/4 + V_{Ec}$ in the second). One way of reconciling the different results of these studies is to postulate that measurements of nestlings are influenced by the quality of parental care during the growth period, while the final sizes of the various appendages, achieved for the most part after fledging, are determined by genotypic factors.

The results of the present experiment also differ in several respects from the findings of Ricklefs and Peters (1981). These studies are compared in Table 8. In Experiment I of Ricklefs and Peters, nestlings were switched among nests at hatching, and effects were determined in a two-way factorial analysis of variance, much like the replicated three-way design of the present experiment. The total variance in *A* and *K* in the two sets of experiments was similar. In Experiment I, however, the clutch/incubation nest term was a significant effect for both *A* and *K*. In experiment II of Ricklefs and Peters, in which the total variance was considerably less than that in Experiment I and the present study, there was a strong incubation nest/rearing nest effect, but no clutch effect. In this respect, Experiment II was consistent with the present study. Experiments I and II led Ricklefs and Peters to conclude by subtraction that clutch was not a significant effect, whereas incubation nest was. The analysis of variance employed in the present study is able to distinguish these effects unambiguously but indicates that neither is significant. Three possibilities present themselves. First, the design of Experiment II, in which the offspring from each clutch were switched among a large number of foster nests, did not permit a two-way ANOVA and therefore had limited power to detect significant effects. In that experiment, the clutch effects accounted for 19% of the total *SS* in *K* and 39% of the total *SS* in *A*. Effects of this magnitude may have been significant if a factorial design had been used. Certainly, clutch explained a greater proportion of the *SS* of these variables than in the present study (2.2 and 3.6%, respectively), but the nonsignificance of the result for clutch is unaltered when *A* and *K* are adjusted with respect to the mean value for the incubation/rearing nest in order to re-

TABLE 8. Means, standard deviations of asymptotes (A), and growth rates (K) of starling nestlings among and within effects.

	Asymptote (A)[a]					Growth rate (K)[a]				
	A[b]	B	C	D	E	A	B	C	D	E
Means	78.7	79.9	75.9	76.1	72.1	364	358	442	446	436
Standard deviations										
Total	8.0	8.0	4.2	3.6	6.8	45	41	42	61	64
Within experiments		5.2	—	3.6	4.5		35	—	61	48
Clutches				ns	ns				ns	ns
		1.9					28			
Incubation nests			2.3		ns			28		ns
				1.8					54	
Rearing nests		2.8			2.2		18			32
Error	4.8	4.2	3.6	3.1	4.4	37	28	33	33	45

[a] Asymptote (A), g; growth rate (K), days^{-1} × 1,000.

[b] Columns are as follows: A = natural early broods 1970–1972 (n = 214), Ricklefs and Peters (1979); B = experimentally manipulated nests 1970–1972, experiment I (n = 86) of Ricklefs and Peters (1981); C = natural early broods of 1976 (n = 43) (Ricklefs and Peters 1981); D = manipulated nests 1976, experiment II (n = 37) of Ricklefs and Peters (1981); E = this study (n = 56).

duce the error mean square. A second possibility is that clutch effects in the present experiment may have been subsumed by the significant between-experiment effects (49 and 60% of the total *SS*) just by chance. Third, the experiments involved such small samples of nests that significant genetic variation may have been included in one year and not another, just by chance. Moreover, mean values of A and K (Table 8) suggest differences in environmental conditions that may have influenced the expression of genetic differences between sibships.

The significant experiment effect revealed in the present study suggests either that nests were distributed nonrandomly among experiments or that I was unlucky. Much of the *SS* in A of the experiments was associated with a single pair of nests (Expt A), and much of the *SS* in K was associated with two pairs of nests (Expts. C ang G) (see Fig. 3). In neither case was this variation related to laying or hatching dates, the length of the incubation period, or time of hatching, although the length of the incubation period itself had a large between experiments *SS* (68% of the total). Further resolution of these effects must await a larger data base. One may conclude from the present study, however, 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 rates of increase in body mass (K) and winglength (*WNS*) and the maximum lengths of the tarsus (*TAR*) and the sheath of the outer primary (*SH*).

Correlations among variables.—Within the sample of all experiments taken together, correlations among variables were generally weak, and large correlation coefficients were related primarily to age-scaling factors rather than to rates of increase and final sizes achieved. The size to which the nestling grows (A) bore little relation to any other variable. As growth rate (K) increased, the inflection point of the growth curve (I) occurred earlier and the wing and outer primary began to grow at an earlier age, but rates of elongation of the wing and outer primary were not related. Hence, except for its inception, growth of the feathers and wings is unrelated to rate of increase in body mass. Large values of K apparently are associated with faster early development, inasmuch as wing and feather growth commence at an earlier age.

A principal components analysis corroborated the general independence of growth measurements, singling out K on component I, A on II, a contrast between *WNS* and *PRS* on III, *SH* on IV and VI, and *TAR* on V. I and II exhibited significant variation over experiments, while III through V exhibited significant variation over nests within experiments. Hence, factors responsible for between-experiments variation appeared to act upon different

aspects of growth and development than those underlying the rearing-nest effect. In studies with larger data bases, principal components may provide less ambiguous and uncorrelated measurements of postnatal development than do the original variables.

Correlations over effects.—Even in the small study reported here, there were strong correlations among variables over certain of the effects, even when the effects did not contribute significantly to variation in the measurements individually. The correlations varied among the different effects, and it is not possible to attach particular biological significance to any of them without additional analyses. These correlations do, however, suggest certain functional relationships between measurements of growth that could form the basis of more detailed studied on patterns of intraspecific variation. They also indicate that the influence of certain effects in the model employed here may be most readily detectable when several variables are considered in combination. Correlations among variables over clutches are indicative of either genetic covariance between measurements or correlated effects of egg characteristics on postnatal growth. Correlations over incubation nests are indicative of effects on embryos that carry over developmentally into the nestling period.

The fact that correlations can be detected over effects where none are detected within the error term or in the sample as a whole suggests that the influence of effects is so complex that correlations cancel out as effects are added, or that the influence of effects is small compared to other sources of covariation, and that whatever factors contribute to the error term act independently on the several measurements of growth.

Relationships with other variables.—Among the nests in experiments A–G, none of the measurements of nestlings was correlated with the size of the egg from which the nestling hatched, contrary to the findings of several other studies. In the larger data set, adjusted values of both *A* and *TAR* were positively related to the mass of the egg (coefficient of determination $[R^2] = 0.15$ and 0.10, respectively). In several studies of passerines, the mass of the neonate was positively correlated with the size or mass of the egg (Schifferli 1973, Howe 1976, Nolan and Thompson 1978). Several authors also have claimed that the mass of the egg is correlated with the subsequent development of the nestling. For example, Howe (1976) found that, among nestlings of the same sex that hatched within 4 h of each other in the same nest, differences in egg mass of 0.3 g (ca. 5% of the mean) minimum were translated into differences in the masses of the nestlings of about 4 g (18%) at 4 days of age and 6 g (about 10%) at 12 days of age. Howe's data are somewhat difficult to interpret, however, because one cannot distinguish variation in *A* and *K* and because only 50% of the nestlings could be matched to eggs with certainty. Another 40% were matched on the "... basis of differences in egg masses and sibling masses of newly hatched young within the nest ...." This procedure may have artificially created some of the correlation observed. Within clutches of starlings, the masses of eggs have a standard deviation of about 0.38 g, or about 5% of the 7.2 g average (Ricklefs 1984). This is on the same order as the differences within clutches of Common Grackles (*Quiscalus quiscula*) studied by Howe (1976). Differences of 2 SD's in egg mass in this study were associated with an approximately 3-g (4%) difference in *A*.

Schifferli (1973) compared growth in body mass of nestlings of the Great Tit (*Parus major*) that hatched from large and small eggs. To my eye, the growth curves for the two sets of individuals are virtually superimposable, with nestlings from large eggs keeping slightly ahead of the others on the age scale. This suggests that nestlings hatch from large eggs a little farther along a growth curve common to chicks regardless of the size of the egg. Under these circumstances, one might expect larger eggs to lead to a somewhat longer incubation period, but Schifferli did not report on this. In the European Starling, incubation period is unrelated to the mass of the egg (Ricklefs and Smeraski 1983). O'Connor (1975) also reported differences in postnatal growth according to the size of the egg, but, because his measure of egg size was the mass of the hatchling at the time it was first discovered, hatching time confounded the results. I cannot find any compelling evidence that the size of the egg influences growth rates of nestling passerines, although there may be a positive correlation with final size achieved.

The composition of the egg did not exhibit any relationship to postnatal measurements, with the exception that 23% of the sums of squares of *SH* was related positively to the mass

of the yolk and negatively to the relative size of the yolk. The regression coefficients indicate that *SH* increases by 3.6 mm per g of yolk and decreases −0.38 mm per yolk percentage of egg size. The biological significance of these relationships will be made clear only with further experimentation on a larger scale.

Among nests in experiments A–G none of the posthatching variables was related to incubation period (*INC*) or to hatching time (*T*). Much of the variation in the length of the incubation period was distributed between experiments, perhaps by coincidence; hence, this analysis had reduced ability to detect relationships between incubation period and subsequent growth. In the larger analysis, in which all nests in the study were included, the rate of outer primary feather elongation (*PRS*) was positively but weakly related, and the length of the sheath (*SH*) more strongly and negatively related to hatching time. By extrapolation of the linear regression, the 12-h difference between 6 and 18 h corresponded to differences in *PRS* of 0.26 mm/day (0.35 SD units) and in *SH* of −0.87 mm (−0.51 SD units). These relationships suggest some developmental conditioning of the young nestling in response to factors associated with hatching time that carries over into the latter part of the nestling period.

General Conclusions

This experiment on factors contributing to variation in postnatal measurements of the European Starling suggests the following general conclusions. First, no genetic effect could be detected. The sums of squares attributable to the clutch effect were generally less than 10% of the total sums of squares, setting an upper limit to heritability in this study. Second, there was a fairly substantial effect of the nest in which the chick was reared, suggesting a direct influence of parental care on the postnatal development of the offspring. Third, correlations between growth variables were weak overall but were strong over some of the effects and in different combinations for each effect. This suggests that there may be complicated patterns of influence by the major effects on combinations of the growth variables. Fourth, I could detect little influence of egg size on postnatal development, nor could I find compelling evidence for such a relationship in the literature.

The experimental design used in this study appears capable of separating most parental effects upon postnatal development of nestling passerines and identifying most of the correlations between growth variables. Larger samples than the 14 nests presented in this study will be required for a full description of these relationships, and further experimentation will be required to determine fully the biological significance of the relationships revealed. It seems feasible, however, to determine the role of parental care and genetic inheritance in generating and maintaining variation within populations by this approach.

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