Theor Appl Genet (1984) 67:391–401

Age changes in genetic and environmental variation in laying hens *

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Received July 19, 1983
Communicated by H. Abplanalp

Summary. Effects of age on the genetic and environmental variation of egg production, egg weight and egg quality were investigated in two populations of laying hens. The first part of the study was based on data from a crossbred population in Sweden that allowed the estimation of sire and residual but not of dam variance components. Sire, dam and residual components of variance were estimated in the second part of the study that used data from eight generations of two unselected control and four high egg production-selected Canadian strains of chickens. – Although the data did not allow a clear-cut separation of the various genetic and environmental variance components, the results indicated that new genetic variation appeared parallel to an increase in the environmental variation with age of the birds. This was interpreted as a suggestion that the deteriorating process of aging impaired the organism's ability to cope with environmental conditions and this resulted in the observed increase in environmental variation. The simultaneous increase of the genetic variation was caused by the turning on of new genes in order to induce reactions counteracting the effects of aging. Alternatively, reduced accuracy of DNA transcription in older birds may cause impairment of the functional efficiency of metabolic systems thus increasing environmental variation parallell to an increase of genetic "error variation".

Key words: Age changes – Egg production and quality – Genetic and environmental factors

Introduction

As a rule, investigations of genetic and environmental variation in quantitative traits in various species have been carried out on animals during the early part of their life. Most of these studies used heritability (h^2) to express additive genetic variance as a proportion of total phenotypic variance.

Where different ages were considered, the heritabilities of traits like milk yield and egg production usually decreased with age. In chickens, Van Vleck and Doolittle (1964) found that the heritability of hen-housed egg production estimated from the sire variance component ($\hat{h^2_S}$) decreased from about 0.2 in the first month of production towards zero during the last of 11 months of production and that heritability as estimated from the dam variance component ($\hat{h^2_D}$) decreased from about 0.5 during the first month to values around 0.1 from the third through the sixth month, and again increased somewhat thereafter. A large part of the decrease in h^2 from the first to the second month of production was probably due to variation in age at first egg (AFE), which is highly heritable and increased the heritability in the first part of the production period. In a study of two random bred strains of Leghorn chickens in three consecutive years, Clayton and Robertson (1966) observed increased phenotypic variance and decreased h^2 of egg production compared for two 8-week periods starting at 26 weeks of age. They also reported declining h^2 of body weight from 12 to 44 weeks while h^2 of egg weight remained relatively stable.

In a genetic analysis of survivor egg number during six 8-week production periods, Flock (1977) found that the genetic and phenotypic standard deviations increased substantially from period 2 to 6. The genetic standard deviation was highest in period 1, probably reflecting the influence of the highly heritable age at first egg. Throughout the remaining periods, Flock found no consistent age trend in heritability. Similar to the results of Van Vleck and Doolittle (1964) and other reports, Flock found the heritabilities estimated from dam variance components to be considerably greater than those estimated from sire components.

The present study explores effects of age on the genetic and phenotypic variation of egg production and egg quality traits in laying hens. A general increase in genetic and non-genetic variance was observed in older birds. Although the data did not allow a complete

* Animal Research Centre Contribution No. 1151

analysis of the causes for this increase, it is suggested that it may be due to a continuation of ontogenesis, in a genetic sense, beyond sexual maturity that leads to a reduced ability of the organism to cope with environmental influences.

Materials and methods

Experimental animals, environment and traits measured

Part I

This part of the investigation used the second generation of chickens from the formation of a base population for the "Scandinavian Selection and Cross-breeding Experiment with Laying Hens" (Liljedahl et al. 1979). Briefly, the base population was formed by crossing seven internationally used commercial hybrids of White Leghorn laying stocks in all combinations with the exception that males from one of the hybrids were not available. The second generation was produced by mating 156 sires at random to 458 dams, all of the first generation. The dams were housed in multiple bird cages and therefore, the experimental birds could not be identified by dam families. It was assumed that each of the matings contributed approximately four or five daughters.

The birds were hatched in two groups one week apart in February, 1972. At hatch, the chicks were sexed and wing-banded with sire identified. All birds were brooded and reared in floor pens until 16 weeks of age, when they were transferred to a cage house and allocated at random one hen per cage to eight different commercial cage types. During the rearing period they received 24 h of light the first two days after hatching, with a gradual reduction to 8 h of light by 4 weeks of age which was maintained until 20 weeks of age. The daily light period was then increased by 20 min per week until a maximum light period of 17 h per day was reached and maintained to the end of the experiment. All-mash rations were fed ad libitum during the brooding, rearing and laying house periods.

The traits measured in this part of the study where the following:

1 Egg number. Individual egg production was recorded daily from the time the pullets were placed in the laying cages and was summarized for each hen into 28-day periods starting from the day the hen laid the first egg. Therefore, there was a confounding of environmental changes and periods for different hens. Since the environment was relatively stable, this was not considered a serious flaw.

2 Egg weight (g). Measurements of egg weight, and of the other egg quality traits described below, started at 171 and 164 days of age for pullets from hatches 1 and 2 respectively. After the initial egg was measured, additional eggs were collected for egg weight and egg quality measurements from each bird at four week intervals.

3 Egg shape index (%). Maximum egg width divided by egg length expressed as a percentage.

4 Shell thickness ($mm \times 10^{-2}$). Mean of three shell thickness measurements taken along the equator of the egg.

5 Albumen height ($mm \times 10^{-1}$). The height of thick albumen.

The data from this part of the study were analysed for each 28-day period separately. Because of the way the egg weight and quality measurements were taken, many birds had the initial egg measured in their second 28-day production period. Therefore, first period egg weight and egg quality traits were not statistically analysed, but all birds with production recorded were included in the analysis of egg number. In subsequent periods, all birds with valid records on all traits were included in the analyses.

The following model was used to describe the component effects of an individual observation:

$$y_{ijkl} = \mu + s_i + c_j + h_k + (sc)_{ij} + e_{ijkl}$$

where

y_{ijkl} = observation on the lth daughter from the kth hatch, jth cage type and ith sire,
μ = overall population mean
s_i = random effect of the ith sire,
c_j = fixed effect of the jth cage type,
h_k = fixed effect of the kth hatch,
$(sc)_{ij}$ = random effect of the interaction between the ith sire and jth cage type,
e_{ijkl} = random residual error.

The analyses of variance were performed using least squares-maximum likelihood methods for unequal sub-class numbers with program LSML 76 (Harvey 1972). The interactions between sire and hatch, and between hatch and cage type were found to be negligible and thus were not included in the final analyses. Variance components were estimated by equating the appropriate mean squares to their expectations and solving for the sire and residual variance components.

Part II

These data were collected on six strains of White Leghorn chickens from a selection experiment (Gowe and Fairfull 1980). Strains 1 and 9 were primarily selected for high egg production rate from the first egg to 273 days of age. Strains 3 and 8 were primarily selected for high number of eggs, produced per hen housed to 273 days of age. In addition, all four strains were selected for fertility, hatchability, viability, egg weight, egg specific gravity, Haugh units, blood spots, shell shape and, more recently, low body weight. The other two strains, 5 and 7, were unselected random bred controls. Strains 3 and 5 originated in 1950 from a narrow genetic base. Strain 1 was derived from strain 3 in 1971. Strain 7 was formed as a broad genetic base of commercial stocks in 1958, and strains 8 and 9 were derived from it in 1969. From 1950 on, one generation was produced per year in all strains with the exception of the first four generations of strain 3.

During the hatch years 1971 to 1979, chicks of all strains were hatched over a 2-day period and reared in a 3-deck cage system in a windowless house. Strains were reared separately with a stratified random assignment of the cages to strains. Sire and dam progeny groups were randomized to the 75-chick cage units assigned to each strain. During the rearing period, artificial light was provided for the first 24 h after hatching. Then the light period was reduced to 6 h of red light (1.6 lux) daily and kept at this length until the birds were housed in laying cages. All pullets were housed individually in 20 cm (8″) cages by 141 days of age to 1977 and by 134 days of age in 1978 and 1979 in two identical windowless cage houses. The light period was increased to 8 h (eight and a half hours in 1971) of normal white light (40 lux) at 141 days of age. At the end of each week, the daily light period was increased by 30 min until a 16 h period was reached and this period was maintained to the end of the test at 497 days. All pullets were dubbed and de-wattled at about 120 days of age

up to 1978, and in 1979, all birds were dubbed at hatch. All birds were vaccinated for Marek's disease, infectious bronchitis, epidemic tremors and Newcastle disease. All mash diets fed ad libitum were used throughout the brooding, rearing and laying house periods.

Egg production was recorded 5 days a week from housing to 497 days of age and converted to 7 day production. Egg weight and egg quality measurements were taken for individual birds at about 240 and 450 days of age. Eggs were collected over a 28-day period with the eggs of each hen being sampled on 5 days at 240 days of age and 5 days at 450 days of age, spread over the period. An average of 3.5 and 3.0 eggs per hen were sampled at 240 and 450 days respectively. The traits analysed in this investigation follow:

1 Egg production rate per hen housed (%). Number of eggs produced from housing to 273 days of age (Period P_1) or from 386 to 497 days of age (P_3) divided by the number of days in the respective periods for each hen housed in the laying house and multiplied by 100.

2 Hen-day rate of egg production from first egg of survivors (%). Number of eggs produced expressed as a percentage of the number of live hen days from age at first egg to 273 days (P_1); or from 386 to 497 days (P_3).

3 Egg weight (g) of survivors. Average egg weight of up to 5 eggs per hen. Egg weight as well as egg specific gravity and Haugh units were measured at approximately 240 (P_1) and 450 (P_3) days of age.

4 Egg specific gravity (−1× (1000)) of survivors. Specific gravity measured by determining which eggs float in brine solutions of predetermined specific gravity.

5 Haugh units of survivors. Albumen height corrected for egg weight (Wells 1968)

Data from all hens housed in the laying house were included in the analyses of hen-housed rate of egg production. The analyses of the remaining traits were performed on the data from birds that survived throughout the entire egg production period (to 497 days of age), laid at a rate of at least 20% in all three production periods (141–273 days, 274–385 days, and 386–497 days) and had at least one egg measured at about 240 days. In addition, birds included in the analyses of the late egg quality had to have at least one egg measured at about 450 days of age.

Data from each strain and year were analysed according to a nested ANOVA program with sires, dams within sires, and daughters within dams within sires included in the statistical model as follows:

$$y_{ijk} = \mu + s_i + d_{ij} + e_{ijk}$$

where

y_{ijk} = observation on the kth daughter of the jth dam of the ith sire
μ = overall population mean
s_i = random effect of the ith sire
d_{ij} = random effect of the jth dam within the ith sire
e_{ijk} = random residual error.

The means of the estimates for the period from 1971 to 1979 were averaged for selected strains and for the two control strains. To compare the size of the variance components between early (P_1) and late (P_3) parts of the egg production period, P_3/P_1 ratios of the estimates were calculated.

Biometric relationships

The biometric relationships between the observational and causal variance components (with the exclusion of the components due to gene interactions between three or more loci) are given in Table I according to Becker (1975). The expectations given in the table are based on the assumption of autosomal and sex linked inheritance within non-inbred populations with no assortative mating.

The genetic variance due to average effects of sex-linked genes in females (V_L) contributes to the sire component by $1/2\ V_L$, since in birds females are heterogametic. If the variance components due to maternal effects (V_M), sex-linked effects (V_L) and/or epistatic gene effects (V_{AA}, V_{AD}, V_{DD}) cannot be neglected, it is not possible to get estimates of any of the causal components completely free from the others.

Since σ^2_D could not be estimated in Part I, as explained earlier, it is included in σ^2_R. Thus, the "residual" variance component $\sigma^2_D - 3\sigma^2_S$ was calculated and will be presented in addition to σ^2_S in Part I of the investigation. It contains the environmental variance plus the major part of the non-additive genetic variance but no additive genetic variance. Similar expressions were formed in Part II of the study in an attempt to assess the role of the causal components of variance in the age effects observed.

Results

Part I

Total number of sires represented in the data for the individual 28-day egg production periods varied between 103 and 101, and total number of daughters declined from 1702 in the 1st 28-day period to 1183 in the 14th period. As mentioned earlier, the data were synchronized with regards to the physiological age (age at first egg) of the individual birds. The mean age at first egg, the beginning of the egg production period, was 170 days and thus the mean age at the end of the 14th 28-day period was 562 days. The overall means obtained by summing or averaging the period least square means over periods 1 to 14 for egg production and for periods 2 to 14 for the remaining traits were: total production 290 eggs, egg weight 59 g, egg shape index 72.4%, shell thickness 0.374 mm, and albumen height 5.25 mm.

The means ± one standard deviation over age periods for each trait are shown in Figs. 1–5. Egg number per 28-day periods starting from the day of first egg increased from the first to the second period and gradually decreased thereafter. Egg weight showed a curvilinear increase with age, while the monthly means of albumen height, shell thickness and also of egg shape index, generally decreased with the birds' age. The phenotypic standard deviations increased with physiological age of the birds, more in the egg production traits than in the egg quality traits.

The most conspicuous and consistent result was the substantial increase of the residual variance component σ^2_R with physiological age of the birds as shown in

Table 1. Biometric relationships between the observational and causal variance components for Part I and II of the study (based on Dickerson 1969; Becker 1975)

Observed variance component		Composition in terms of causal components[a]							
Description	Symbol or formula	V_A	V_{AA}	V_D	V_{AD}	V_{DD}	V_E	V_M	V_L
Part I									
Sire	σ^2_S	¼	1/16	0	0	0	0	0	½
Individuals within sire	σ^2_R	¾	15/16	1	1	1	1	1	½
	$\sigma^2_R - 3\sigma^2_S$	0	¾	1	1	1	1	1	−1
Part II									
Sire	σ^2_S	¼	1/16	0	0	0	0	0	½
Dam within sire	σ^2_D	¼	3/16	¼	1/8	1/16	0	1	0
Individuals within dam within sire	σ^2_W	½	¾	¾	7/8	15/16	1	0	½
	$\sigma^2_D - \sigma^2_S$	0	1/8	¼	1/8	1/16	0	1	−½
	$\sigma^2_W - 2\sigma^2_S$	0	5/8	¾	7/8	15/16	1	0	−½
	$\sigma^2_W + \sigma^2_S - 3\sigma^2_D$	0	¼	0	½	¾	1	−3	1

[a] V_A additive variance, V_D dominance variance, V_E environmental variance, V_M variance due to maternal effects, V_L variance due to sex-linked effects. Symbols with double subscripts designate interactions

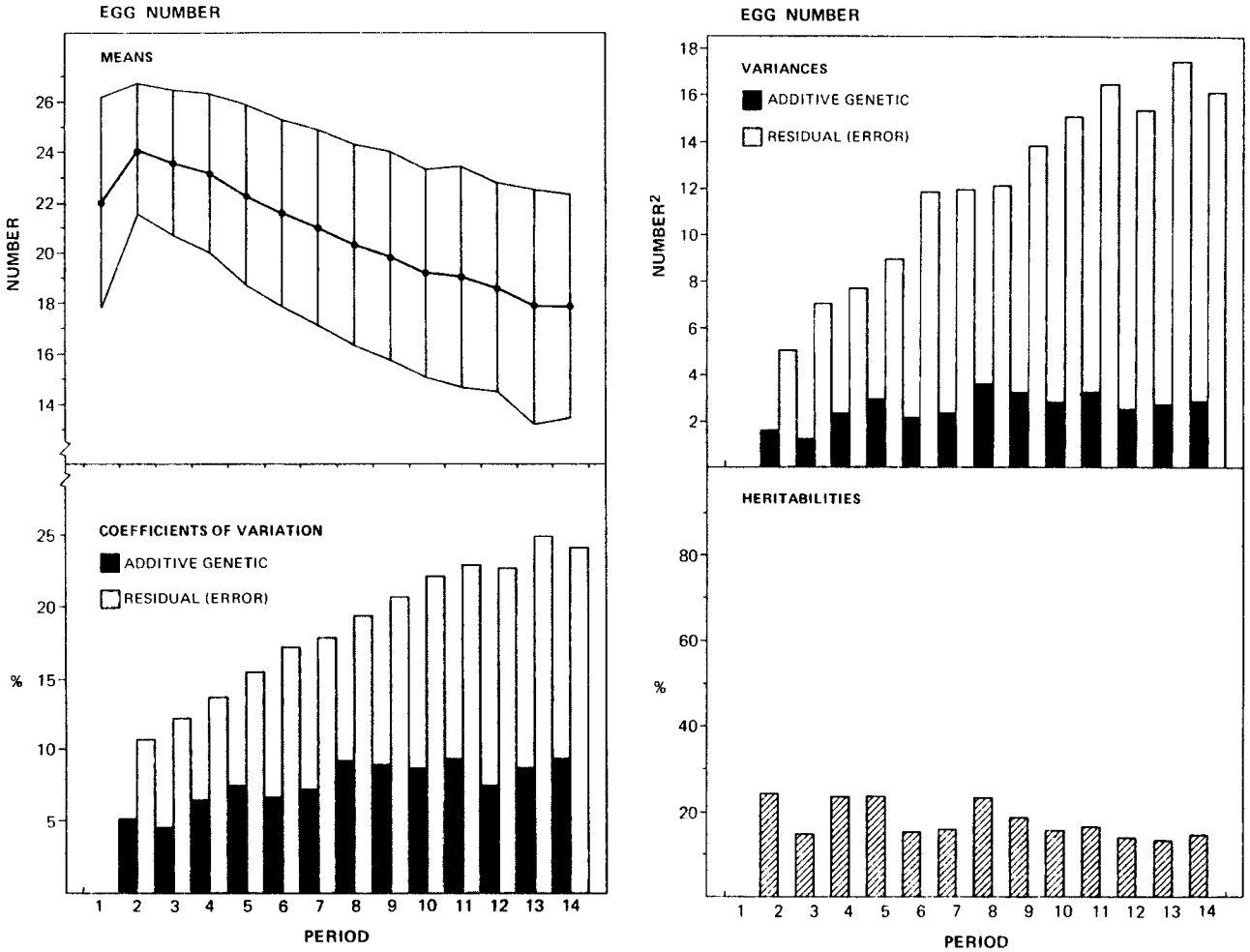

Fig. 1. Means, and estimates of the additive genetic and residual variance, their relative contributions to the total phenotypic variance, and coefficients of variation for egg number in each of 14 consecutive 28-day periods starting at the day of first egg (Part I of the study)

Table 2. Estimates of sire (σ^2_S) and residual (σ^2_R) variance components and sire heritability (h^2) and their regressions on monthly (28-day) period number for periods 2–14 in Part I of the study

Trait	Pooled estimates for periods 2–14			Regression of estimate on period 2–14		
	σ^2_S	σ^2_R	h^2 (%)	σ^2_S	σ^2_R	h^2 (%)
Egg no./period	0.67	12.24	18±0.94	0.026*	0.982**	−0.637*
Egg wt (g)	3.40	7.34	66±1.31	−0.018	0.820**	−2.764**
Shape index (%)	0.90	4.72	43±1.28	0.032**	0.186**	−0.017
Shell thickness ( )	96.2	521.0	42±1.41	−0.176	3.121**	−1.940**
Albumen height (0.1 mm)	11.08	36.65	54±2.50	−0.354*	1.514*	1.791*

* $P<0.05$; **$P<0.01$

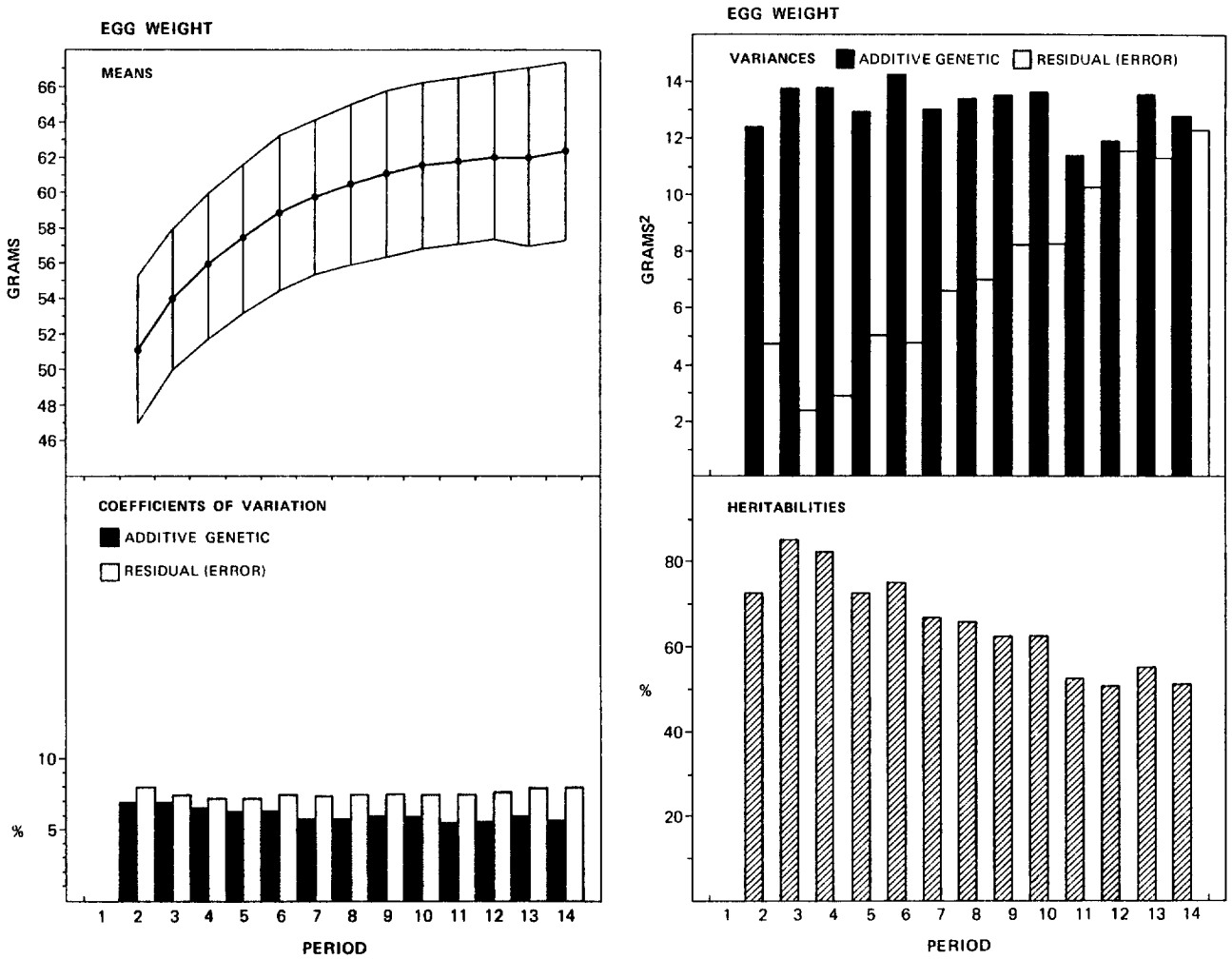

Fig. 2. Means, and estimates of the additive genetic and residual variance, their relative contributions to the total phenotypic variance, and coefficients of variation for egg weight in each of 13 consecutive 28-day periods starting 28 days after the day of first egg (Part I of the study)

Figs. 1–5. The regression of σ^2_R on period number was significant for all the traits (Table 2). The regression of the sire variance component σ^2_S on period number was also significantly positive for egg number, and egg shape index, though of smaller magnitude than for σ^2_R, while the regression was significantly negative for albumen height (Table 2).

When the variances were expressed as coefficients of variation the increases of both the additive genetic and residual coefficients of variation with physiological age of the birds were still marked for egg number but less pronounced or absent for the other traits.

As shown in Figs. 1–5 and Table 2, the heritabilities (%) decreased significantly with physiological age for

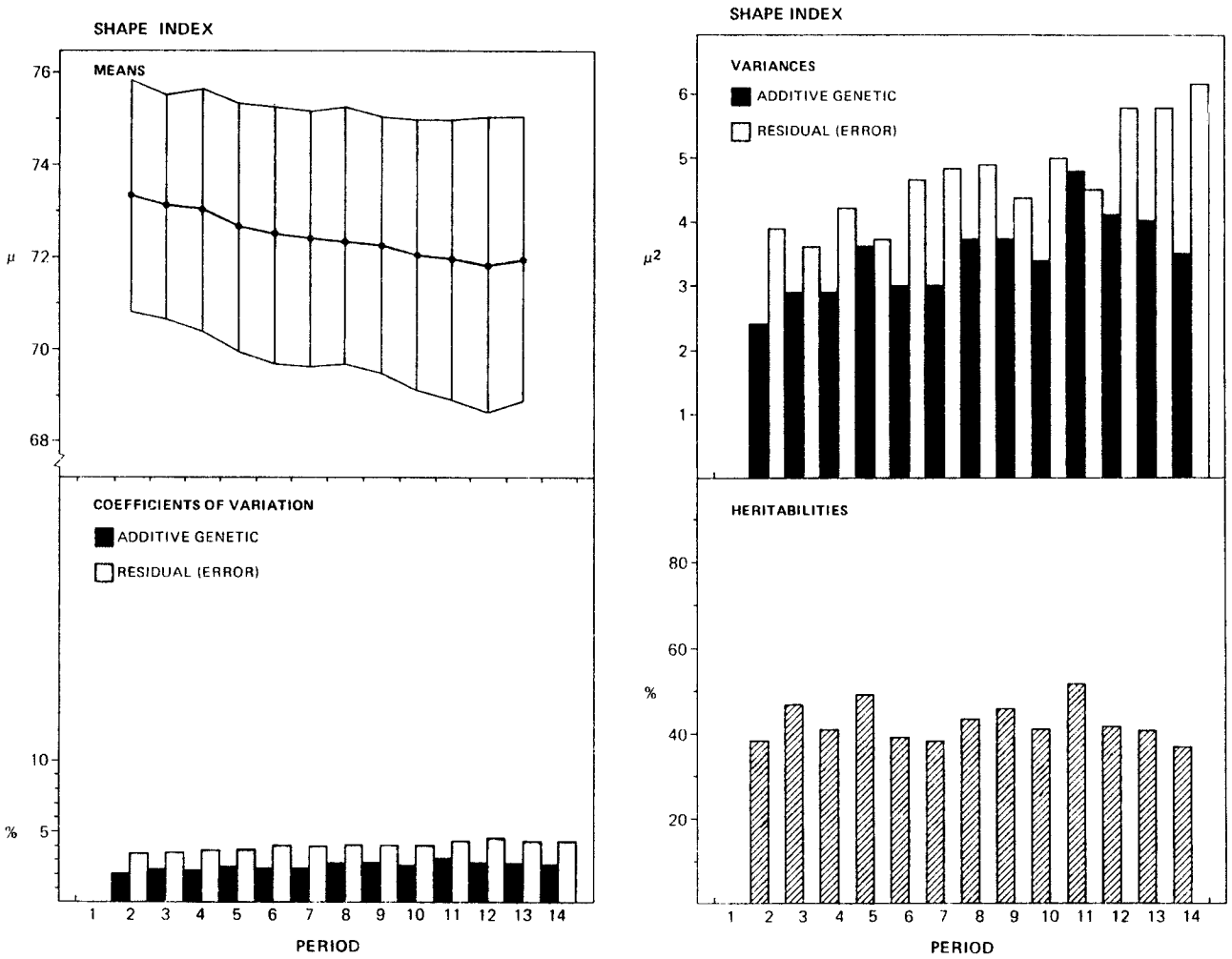

Fig. 3. Means, and estimates of the additive genetic and residual variance, their relative contributions to the total phenotypic variance, and coefficients of variation for egg shape index in each of 13 consecutive 28-day periods starting 28 days after the day of first egg (Part I of the study)

all the traits except egg shape index. The decrease as measured by the regression coefficient of h^2 on period number was greatest for egg weight and smallest for egg number. The significantly declining age trends of the heritabilities for these traits are obviously due to the fact that σ^2_R increased faster with physiological age of the birds than σ^2_S.

Part II

Mean egg production and egg quality of the Ottawa Leghorns strains are shown in the lower part of Table 3, and have been reported in some detail earlier (Gowe and Fairfull 1980). Direct comparisons with the performance of the birds in Part I are not possible because of different time frames, environments and breeding, but the birds in the two parts of the study could be considered to have comparable performance.

The sire, dam and individual variance components averaged over the years 1971 to 1979 for the selected and for the control strains are presented in Table 3, along with some linear combinations of the components. The pooling of the estimates across the two genetic bases from which the Ottawa strains originated was considered justified because similar trends were apparent in all strains. For the two egg production traits, the dam variance components were generally substantially larger than the sire components while for the three egg quality traits, the size of the sire and dam variance components was approximately equal as shown by the values of $\sigma^2_D - \sigma^2_S$ in Table 3. For all traits, the individual variance components were larger than either the sire or dam components.

The magnitude of all three variance components generally increased with advancing age of the birds. For the egg production traits, the absolute increase

Table 3. Sire (σ^2_S), dam (σ^2_D), and individual (σ^2_W) variance components and means of traits measured in an early (P_1) and late (P_3) part of the egg production period in Ottawa strains of Leghorns, averaged over years 1971/72 to 1978/79

Variance component or mean	Strain type[a]	Hen-housed rate of egg production (%)			Hen-day rate of egg production (%)			Egg wt (g)			Egg specific gravity (− 1 × 1000)			Haugh units		
		P_1[b]	P_3[b]	P_3/P_1	P_1[b]	P_3[b]	P_3/P_1	P_1[c]	P_3[c]	P_3/P_1	P_1[c]	P_1[c]	P_3/P_1	P_1[c]	P_3[c]	P_3/P_1
σ^2_S	S	8.8	16.8	1.9	2.4	10.7	4.5	1.7	2.7	1.6	2.2	3.2	1.5	4.1	5.6	1.4
	C	17.1	26.5	1.4	4.0	13.0	3.3	2.1	3.6	1.7	3.1	3.2	1.0	3.8	4.5	1.2
σ^2_D	S	19.1	54.1	2.5	3.7	16.4	4.4	1.4	2.5	1.8	1.9	3.2	1.7	3.9	5.9	1.5
	C	54.6	105.7	1.9	7.0	29.5	4.2	2.8	3.5	1.3	3.9	3.7	1.0	4.2	5.9	1.4
σ^2_W	S	241.1	642.5	2.4	44.8	222.9	5.0	9.1	15.2	1.7	12.6	25.4	2.0	18.1	34.8	1.9
	C	301.4	645.6	2.0	61.2	237.9	3.9	8.0	14.2	1.8	15.0	25.8	1.7	16.9	34.1	2.0
$\sigma^2_D - \sigma^2_S$	S	10.3	37.3	2.1	1.4	5.7	4.1	−0.3	−0.2	[d]	−0.3	0	[d]	−0.2	0.3	[d]
	C	37.5	79.2	1.5	3.1	16.6	5.4	0.7	−0.2	[d]	0.8	0.5	0.6	0.4	1.4	3.5
$\sigma^2_W - 2\sigma^2_S$	S	223.5	608.9	2.4	40.0	206.0	5.2	5.8	9.8	1.7	8.2	19.0	2.3	9.9	23.6	2.4
	C	267.2	592.6	2.0	53.3	212.0	4.0	3.7	7.0	1.9	8.8	19.4	2.2	9.3	25.1	2.7
$\sigma^2_W + \sigma^2_S - 3\sigma^2_D$	S	192.6	497.0	2.0	35.9	184.5	5.1	6.7	10.3	1.5	9.0	19.0	2.1	10.6	25.2	2.4
	C	154.8	355.2	1.9	44.1	162.4	3.7	1.9	7.5	4.0	6.4	17.8	2.8	8.1	20.9	2.6
Means	S	76.4	58.7	–	76.5	59.2	–	57.2	64.5	–	85.9	79.1	–	86.6	77.4	–
	C	61.6	46.6	–	61.7	47.0	–	53.0	60.9	–	85.0	78.6	–	84.1	74.6	–

[a] *S* = Average of four strains selected for high egg production and, in addition, for other economically important traits including the egg quality traits shown in the table
C = Average of two corresponding unselected control strains
[b] P_1 = 141 – 273 days of age; P_3 = 386 – 497 days of age
[c] P_1 = at about 240 days of age; P_3 = at about 450 days of age
[d] Ratios not calculated for variance components ≦ 0

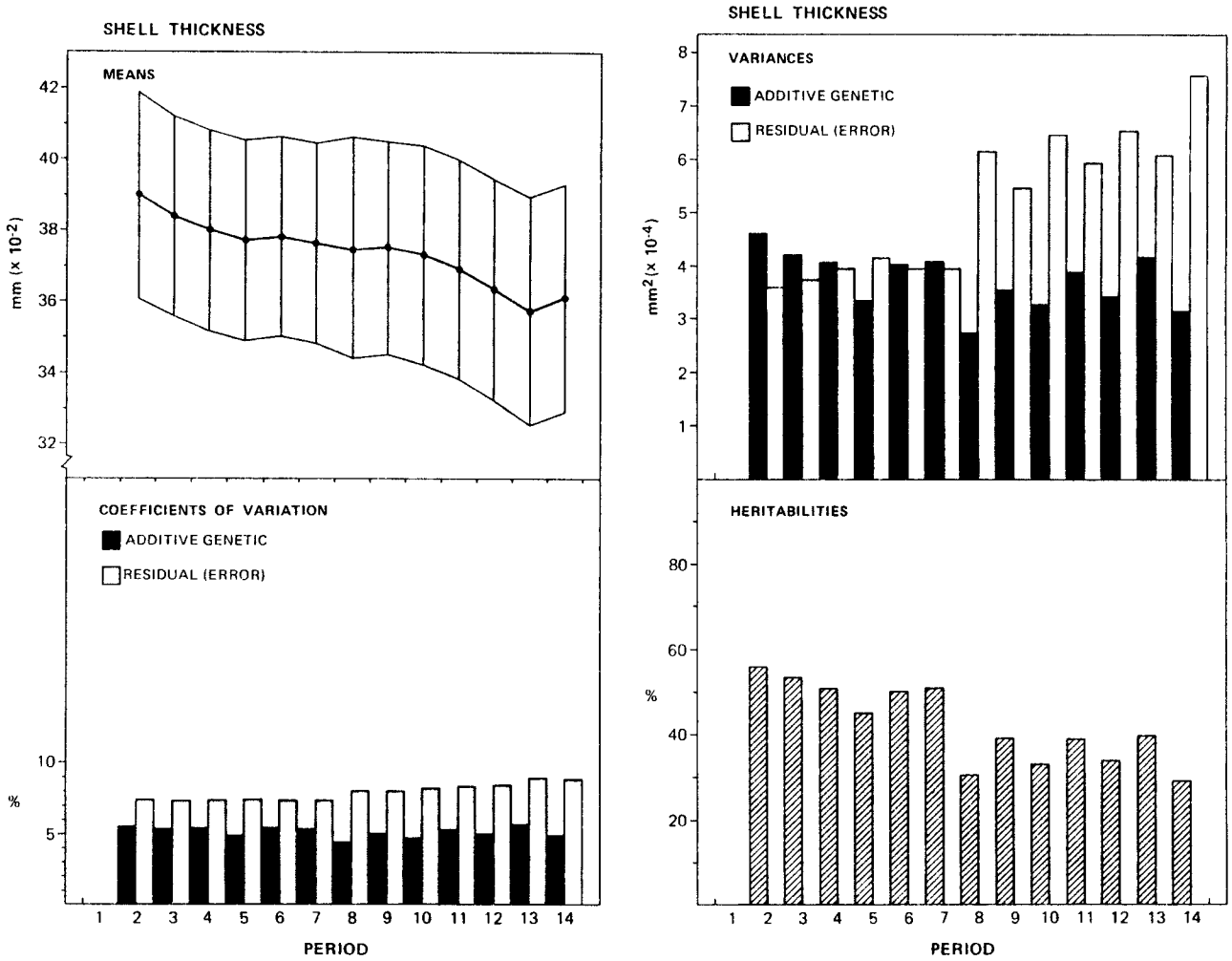

Fig. 4. Means, and estimates of the additive genetic and residual variance, their relative contributions to the total phenotypic variance, and coefficients of variation for egg shell quality (egg specific gravity) in each of 13 consecutive 28-day periods starting 28 days after the day of first egg (Part I of the study)

from period 1 to period 3 in the dam components was larger than in the sire components. Thus the difference between the size of dam and sire variance components increased with age of the birds. In the egg quality traits, the relative sizes of the sire and dam variance components remained approximately the same from period 1 to period 3. For all traits, the largest absolute increase between period 1 and 3 was in the size of the individual variance components. However, when the comparisons of the age change were made in terms of P_3/P_1 as shown in Table 3, the increases in the individual variance components with age were not, as a rule, larger than those for the dam or sire variance components.

Discussion

This study examined the changes in the variance components of the egg production and egg quality traits from sexual maturity to approximately one and a half years of age. During this production period, which would perhaps correspond to the first lifespan of the period, the birds were kept under intensive conditions. The conditions and the induced high egg production could be generally seen in changes in the appearance of the birds and their physical deterioration with age, observed as partial feather loss, discoloration of combs and wattles, etc.

Biological character of the traits studied

Rate of egg production per hen housed studied in Part II of the investigation combines age at sexual maturity, egg production rate from first egg and viability. Thus, it is a highly complex trait and its behaviour in aging birds would reflect the birds' ability to cope with environmental conditions, stress (including the "internal stress" of high production) and natural

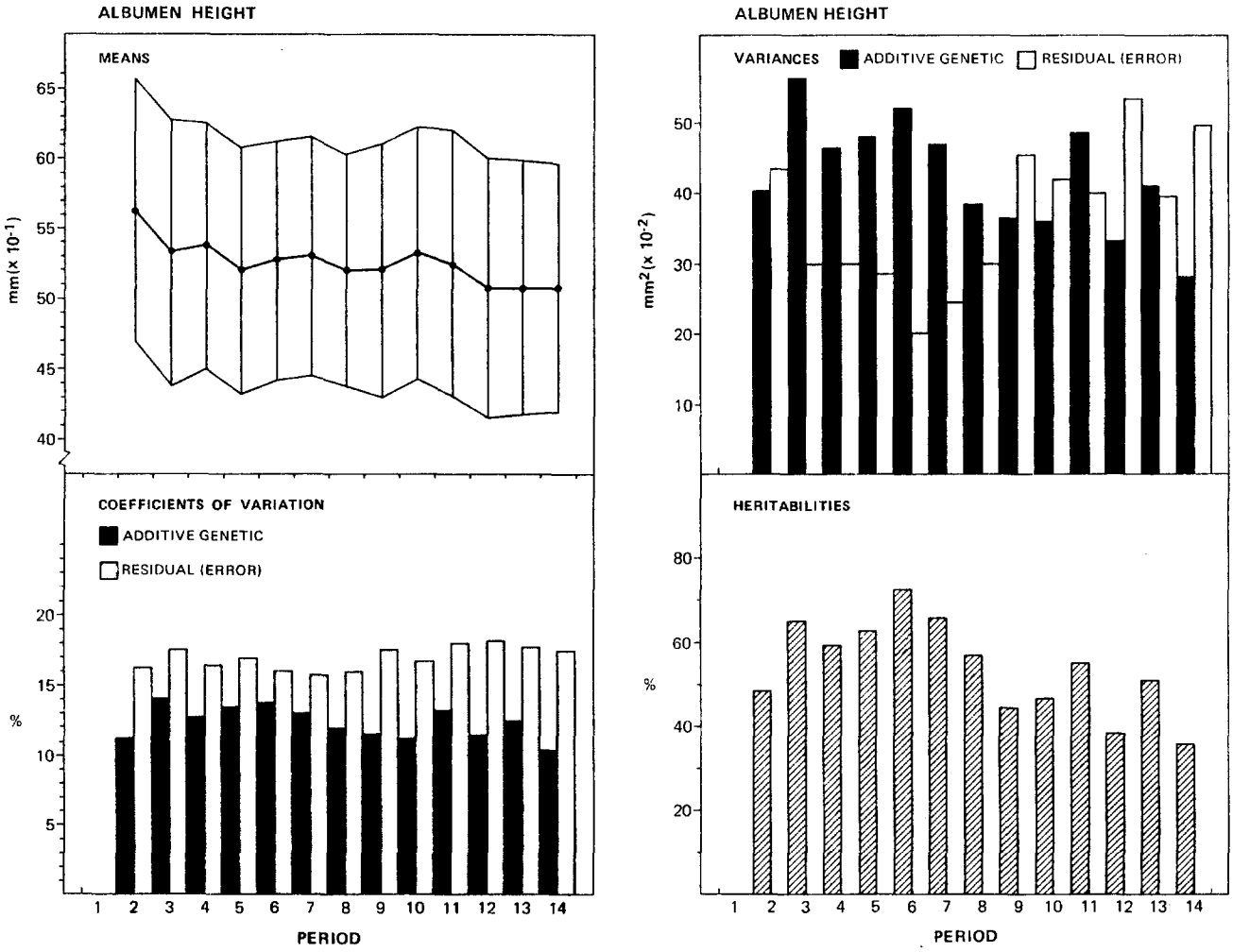

Fig. 5. Means, and estimates of the additive genetic and residual variance, their relative contributions to the total phenotypic variance, and coefficients of variation for albumen height (Haugh units) in each of 13 consecutive 28-day periods starting 28 days after the day of first egg (Part I of the study)

exposure to pathogens. Egg production rate, as measured by the number of eggs per 28-day period in Part I and hen-day egg production in Part II, are expressions of ovulation and egg formation rate. Particularly in Part II of the study, elimination of birds with egg production rates of less than 20% would be expected to minimize effects of disease resulting in morbidity and mortality. Many generations of selection for high egg production in chickens have resulted in a highly elevated ovulation rate. Since only the production of completely developed, hard-shelled eggs was recorded in this study, the trait includes also the birds' ability to produce quantities of the various egg components at the necessary rate. The quality of the eggs produced is described by the remaining traits. Egg weight is an expression of total egg size. Egg shell thickness (Part I) and egg specific gravity (Part II) both describe the quantity of shell deposited over the egg. Albumen height (Part I) and Haugh units (Part II) are descriptive of a physical property of the egg white proteins. Thus all traits examined in this study are related to egg production. Nevertheless, because of their complex nature and polygenic character, their genetic determination likely involves a substantial part of the bird's genome.

The synchronization of the data from Part I on age at first egg of the birds allowed an assessment of the patterns of the traits studied relative to physiological age (Figs. 1–5). All other studies to date dealt with the traits on a chronological basis. After a somewhat lower onset, egg production rate increases in the second month of lay and gradually decreases thereafter. This pattern agrees with that reported by Gavora et al. (1982) who used part of the same data to fit mathemati-

cal models of egg production. The age trends observed in the means of the remaining traits in Part I of this study are in agreement with generally accepted patterns indicating a decline of the traits with age with the exception of egg weight which increases in older birds.

Changes in additive genetic variance with age

Age trends in additive genetic variance (V_A) were assessed by examination of the sire variance components that are expected to contain additive variance, ($1/4\ V_A$), a small proportion of additive by additive interaction ($1/16\ V_{AA}$), as well as sex-linked effects ($1/2\ V_L$). In both sets of data the sire variance component increased significantly with age of the birds for most traits. Assuming that additive by additive interactions and sex-linked effects are negligible, this indicates an increase in the additive variance. Although Fairfull et al. (1983) reported sex-linked effects of a significant magnitude, these are unlikely to play a major role in the increase of the sire variance with age. The relative increase of σ_S^2 and consequently of V_A was larger for egg production rate than for the other traits.

It should be emphasized that the apparent decline in h^2 with age observed in this study and elsewhere (Van Vleck and Doolittle 1964; Clayton and Robertson 1966; Flock 1975) is not caused by a reduced additive genetic variance in older birds. On the contrary, this variance increased with age. If such an increase indicates the expression of an increasing number of loci, selection at older ages may be capable of affecting a broader spectrum of additive genes including those associated with effects of senescence.

Changes in non-additive genetic and environmental variances with age

The apparent absence of appreciable differences between the sire and dam variance components in the egg quality traits (Table 3), assuming small or negligible sex-linked effects, indicates that non-additive genetic and maternal variance components play a minor role in these traits (Table 1). The usually larger dam variance components for the egg quality traits in the late than in the early part of the production period tend to confirm the above suggestion that additive genetic variance increased with age of the birds. Thus the ratios between the dam variance components for P_3 and P_1 in egg quality traits ranged from 1.0 for egg specific gravity in the control strains, to 1.8 for egg weight in the selected strains (Table 3).

Under the assumption of negligible maternal and sex-linked effects the environmental component of variance in the egg quality traits can be assessed from the size of the linear function $\sigma_W^2 + \sigma_S^2 - 3\,\sigma_D^2$ (Table 1) which would then contain the environmental component and a small portion of interaction components. If non-additive genetic effects can be neglected as for egg quality traits and if sex-linked effects are also assumed to be small, the value of the linear function $\sigma_W^2 - 2\,\sigma_S^2$ could be used as another estimate of V_E. In fact the estimates of V_E from the two linear functions were similar and both increased generally with age of birds as shown by the variance rations P_3/P_1 from 1.5 to 4.0 (Table 3). This could be considered a fairly reliable indication that environmental variance also substantially increased in the aging birds.

The situation is much more complicated in the two egg production traits, where the magnitude of the differences between sire and dam variance components strongly suggests the presence of maternal and/or non-additive genetic effects. The magnitude of this difference increased markedly with the age of the birds. Thus the variance ratios P_3/P_1 were between 1.5 for hen housed egg production and 5.4 for rate of egg production for the control strains. Similar increases in what they called "maternal effects" with age were reported by King (1961) and Van Vleck and Doolitte (1964) without satisfactory explanation.

It is difficult to accept the observation of an increase of maternal effects with age since the influence of dam on the environment of her progeny should be decreasing as they grow older. However, there is one possible exception from this expected age trend in maternal variance component, viz. the presence of congenitally transmitted disease, such as lymphoid leukosis which was shown to reduce egg production, egg weight and egg specific gravity (Gavora et al. 1980).

The lymphoid leukosis virus is known to be present in the strains investigated in Part II of this study and was shown to influence egg production per hen housed in period 3 more than in Period 1 (Gavora et al. 1980). The virus is egg transmitted and sire does not play a role in its congenital transmission. Therefore, the effects of the virus on the rate of egg production may have contributed to the larger size of σ_D^2 compared to σ_S^2 and to the increase of the difference $\sigma_D^2 - \sigma_S^2$ with age of the birds (Table 3). However, this increase, as well as a similar increase due to larger effects of the virus on σ_W^2 in older birds, would appear to be a component of an overall trend towards more variation observed in older birds. However, calculations based on data from the investigations of Gavora et al. (1980) showed that these effects were relatively small.

Thus the increase in the difference between dam and sire variance components with age suggests that larger dominance and epistasis variance are present in populations of older than in populations of younger birds, again assuming the effects of sex linkage are negligible. However, since the sex-linked effects are also genetic, a fairly safe conclusion would be that the

genetic variation irrespective of its nature – additive, non-additive, or sex-linked – is expressed to a higher and higher degree as the birds grow older.

Since the environmental variance for the two egg production traits was obviously the greatest component of σ^2_W, as can be seen in Table 3, the marked increase in σ^2_W with age of the birds would reflect a corresponding increase of V_E.

The data available in the study did not allow a clear-cut separation of the various genetic and environmental variance components. Nevertheless the results indicated that genetic variation and environmental variation increased with age of the birds.

The observed increases of genetic and environmental variation with age could be explained by either of the two following hypotheses:

1. The deteriorating process of aging impaired the organism's ability to cope with environmental conditions and this resulted in the observed increase in environmental variation. The simultaneous increase of the genetic variation was caused by the turning on of new genes in order to induce reactions counteracting the effects of aging.
2. The increase of the genetic variation was due to an increased rate of DNA transcription errors with the age of the organism. Evidence of age-dependent post-transcriptional changes in the production of proteins by quail oviduet (Bernd et al. 1982) suggest possible involvement of such changes also in the phenomena described in this study. The simultaneous increase of the environmental variation was a consequence of the increased frequency of errors in the messages transferred to the ribosomes for synthesis of proteins or enzymes (Orgel 1963), which in turn would impair the metabolic function and its control.

Thus, the first hypothesis means that there are "reserve genes" that are switched on as needed during the course of aging, i.e. environmental signals would induce new genes with buffering effects to be expressed to make the deteriorating effects of aging less harmful. The second hypothesis means that a reduced accuracy of transcription in older DNA leads to an impairment of the functional efficiency of the metabolic system which in turn would increase the environmental variation parallell to an increase of genetic "error variation" in aging populations.

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