RELAXED SELECTION IN A CLOSED FLOCK OF WHITE LEGHORNS¹

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Received September 18, 1963

THE practical importance of, and the possible explanations for, different consequences from relaxation of selection have been thoroughly discussed by LERNER (1950, 1958). A striking illustration of a decline in the mean of a trait following suspension of selection was presented by MATHER and HARRISON (1949) who had previously selected for high chaeta number in *Drosophila*. In this case, chaeta number was found to be negatively associated with reproductive fitness, as fertility declined under selection for chaeta number. On the other hand, CLAYTON, MORRIS and ROBERTSON (1957) found little decline in mean bristle number after suspension of selection. ROBERTSON (1955) found only slight declines in body weight as a result of relaxation of selection in three lines of *Drosophila* previously selected for large and small body weight.

Only a few studies of the effect on the mean performance due to relaxation of selection, have been conducted in poultry. Declines in shank length and viability after suspension of selection were reported by LERNER (1958), and declines in adult viability and hen-housed egg production were observed by MOULTRIE, COTTIER, and KING (1956). LERNER (1958) did not find a rapid decline in egg production and no decline in hen-housed egg production was observed by SHOFFNER and GRANT (1960) after relaxation.

It is clear, on theoretical grounds and from the results of empirical studies reported, that the consequences of relaxing selection may be quite different for different traits, and even for the same traits in different populations, depending upon the genetic situation existing at the time of suspension of selection. The purpose of this report is to present the results of relaxing selection in a closed flock of White Leghorns, previously selected primarily for egg production, and which had apparently reached or closely approached a plateau with respect to egg production.

MATERIALS AND METHODS

The selected White Leghorn line from which the relaxed selection experimental populations were derived has been described by YAMADA, BOHREN and CRITTENDEN (1958). Selection was primarily for percent production to January 1, at which time the pullets were approximately ten months of age. Some selection pressure was applied in favor of large egg size, and also to both juvenile and adult viability in order to keep reasonably large family sizes. On the basis of comparisons with control stocks at two locations, reported by YAMADA *et al.* (1958), it appears that

¹ Journal Paper No. 2208 of the Purdue University Agricultural Experiment Station.

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selection was ineffective in changing the mean performance of the population for egg production after about 1952. In the spring of 1953 the first random sample of the selected population was taken from the selected breeders. The sample consisted of 125 pullet chicks and 25 cockerels. These were grown out and housed at the Moses Fell Annex farm of Purdue University located at Bedford, Indiana. All healthy pullets were housed in a single pen along with ten cockerels. For the next year a sample of 125 pullet and 25 cockerel chicks was again obtained from the selected breeder pens, and the first relaxed selection generation sample of 125 pullet and 25 cockerel chicks was hatched from eggs obtained from the zero generation population at the Moses Fell Annex farm and incubated at Purdue University. Both lots of chicks were returned to the farm at Bedford for rearing, housing and the collection of the data. This process was repeated annually for a total of six years so that in each of the six years a sample from the selected breeding stock was compared with samples having one to five generations of relaxed selection. This design is quite similar to that used by SHOFFNER and GRANT (1960) except that more generations are involved.

Facilities and labor were not available for trapnesting the birds, nor were facilities available for replicating pens. Consequently, the data collected are the records of a single pen for each generation represented in the year. In retrospect, it would have been preferable to have replicated the pens in this experiment at the expense of other studies in progress at the facilities.

Recently, HINKLEMANN (1963) discussed the design used in this study and, in essence, concluded that a complete analysis of the factors (1) year of origin, (2) year of testing and (3) number of generation of relaxation was not possible because of the lack of linear independence of the three factors. Clearly, year of origin equals year of testing minus the generation of relaxation. It was pointed out that additional information obtained in parallel to the main experiment (such as information from controls) was necessary to effectively evaluate one of the factors before any useful conclusions can be drawn from such a design.

On the basis of controls carried concurrently with this experiment, it was concluded that the selected population had plateaued for the trait under primary selection (YAMADA, *et al.*, 1958). Hence, to facilitate analysis of the experiment of concern here, it was decided that the factor *year of origin* did not contribute to the variation of any of the measured variables. Since the factor *year of testing* is essentially qualitative and the factor *number of generations of relaxation* essentially quantitative, the model

$$Y_{ij} = \mu + T_i + \beta_1 X_j + \beta_2 X_j^2 + \epsilon_{ij}$$

was deemed suitable for analytical purposes, where μ = the experimental mean, T_i = the fixed effect due to year of testing ($i = 1, \dots, 6$), X_j = number of years of relaxation ($j = 0, \dots, 5$) and ϵ_{ij} = the random deviation of the observed mean, Y_{ij} , from its expected value, $\mu + T_i + \beta_1 X_j + \beta_2 X_j^2$. Since the number of observations making up the observed means did not vary greatly, it was felt that the assumption of homogeneous variance for the ϵ_{ij} was reasonably well satisfied.

The variables studied were:

- Y_1 , the percent of pullets started that were housed,
- Y_2 , the age at 50 percent production, in days,
- Y_3 , number of eggs per pullet housed,
- Y_4 , number of eggs per chick started,
- Y_5 , number of eggs per average hen (hen-day egg production)
- Y_6 , percent adult mortality, and
- Y_7 , the average monthly egg weight in ounces per dozen.

RESULTS

The mean values for each trait, and for each combination of test year and generation of relaxation in the characteristic triangular pattern, are shown in Table 1. The results of each standard least squares analysis are shown in Table 2. Specific hypotheses of interest were:

$$H_1: T_1 = T_2 = T_3 = T_4 = T_5 = T_6 = \beta_1 = \beta_2 = 0,$$

TABLE 1

Pen means for the seven variables, by years and generations of relaxation

Generation of relaxation	Year of testing					
	1953	1954	1955	1956	1957	1958
Percent of pullets housed (Y_1)						
0	91.2	94.4	84.0	83.2	85.1	84.0
1	...	95.2	82.4	80.2	85.9	87.2
2	...	...	91.7	82.8	86.4	94.4
3	...	...	...	84.0	91.5	87.2
4	...	...	...	...	84.1	90.4
5	...	...	...	...	...	89.6
Age in days at 50 percent production (Y_2)						
0	168	176	180	167	169	181
1	...	175	180	165	169	184
2	...	...	168	170	171	186
3	...	...	...	167	169	181
4	...	...	...	...	168	181
5	...	...	...	...	...	183
Number of eggs per pullet housed (Y_3)						
0	204.9	172.6	150.6	180.0	183.2	178.4
1	...	178.2	162.0	185.2	190.7	160.5
2	...	...	171.2	157.2	197.0	156.5
3	...	...	...	183.6	186.0	180.7
4	...	...	...	...	214.9	171.7
5	...	...	...	...	...	137.9
Number of eggs per chick started (Y_4)						
0	186.8	151.9	126.5	149.8	155.9	149.9
1	...	156.8	134.7	148.5	163.2	140.0
2	...	...	153.9	130.2	155.5	147.7
3	...	...	...	154.3	170.2	157.6
4	...	...	...	...	180.6	155.2
5	...	...	...	...	...	123.6
Hen-day egg production (Y_5)						
0	211.1	175.0	165.9	186.1	192.1	199.3
1	...	193.0	182.7	198.1	204.1	169.0
2	...	...	190.0	173.1	202.2	161.2
3	...	...	...	199.6	201.9	185.2
4	...	...	...	...	221.7	176.4
5	...	...	...	...	...	146.8
Percent adult mortality (Y_6)						
0	11.4	3.6	17.1	10.6	10.3	23.8
1	...	15.5	19.2	11.8	8.2	7.3
2	...	...	18.4	23.2	4.5	5.9
3	...	...	...	16.0	14.0	6.4
4	...	...	...	...	6.9	5.3
5	...	...	...	...	...	8.9
Average monthly egg weight in ounces per dozen (Y_7)						
0	24.1	24.7	25.3	24.1	24.3	21.9
1	...	24.5	25.9	23.9	24.3	23.4
2	...	...	25.9	23.8	24.0	22.8
3	...	...	...	23.7	24.0	23.8
4	...	...	...	...	24.3	22.7
5	...	...	...	...	...	23.0

TABLE 2
Least squares analyses

Source	Degrees of freedom	Mean squares					
		(Y_1)	(Y_2)	(Y_3)	(Y_4)	(Y_5)	(Y_6)
Years tested and relaxation (Fitting $T_1, \dots, T_6, \beta_1, \beta_2$)	7	39.886***	115.092***	599.32**	477.25**	538.22*	39.017***
Years tested ignoring relaxation (Fitting $T_1, \dots, T_6$)	5	47.720***	159.971***	798.99**	606.90**	695.16**	52.184***
Relaxation after years (Fitting β_1, β_2 after $T_1, \dots, T_6$)	2	20.299*	2.896	100.14	153.12	145.88	6.101
Years and linear effect of relaxation (Fitting $T_1, \dots, T_6, \beta_1$)	6	43.882***	†	†	†	†	†
Quadratic effect of relaxation (Fitting β_2 after $T_1, \dots, T_6, \beta_1$)	1	15.902	†	†	†	†	†
Years and quadratic effect of relaxation (Fitting $T_1, \dots, T_6, \beta_2$)	6	41.500***	†	†	†	†	†
Linear effect of relaxation (Fitting β_1 after $T_1, \dots, T_6, \beta_2$)	1	30.201*	†	†	†	†	†
Residual	13	8.696	9.969	190.05	127.79	214.42	35.357***
Estimated Theoretical Error	∞	8.822	†	†	†	†	9.540

† This part of the analysis omitted because the effect of relaxation is negligible.

‡ Theoretical error not available, since measurements are made on a pen basis rather than an individual basis. In these cases the error mean square used for tests is the residual mean square.

i.e., no effect of either factor. If this hypothesis is rejected, attention is focused on

$$H_2: \beta_1 = \beta_2 = 0,$$

since acceptance of this hypothesis implies no important effects of relaxation. If this hypothesis is rejected, a test is made of

$$H_3: \beta_2 = 0$$

to check for nonlinear effects, and if this is rejected, a final test is made of

$$H_4: \beta_1 = 0$$

to check for significance of linear effects.

In Table 2 may be seen the three distinct partitionings of the sum of squares due to fitting the full model, required to test each of the hypotheses H_2 , H_3 , and H_4 . These partitionings are indicated by brackets and referred to as (a), (b) and (c), respectively.

The observation in each cell consists of a single pen and no data on individual hens or pen replications were collected. Thus, measures of the reliability of the individual figures for each of the 21 cells are entirely lacking, so that, in general no test of adequacy of the model is available. However, in the case of the variables Y_1 (percent of pullets housed) and Y_6 (percent adult mortality) which are percentage data, an estimate of the theoretical error for any observation is obtainable from the usual binomial variance formula $p(1-p)/n$. In the case of Y_1 , the model appears to be entirely adequate, while in the case of Y_6 , the model is not adequate to explain all of the variation between pens. Pen effects are completely confounded with the observations, so that analysis of any trait which is sensitive to pen effects will detract from the analytical power of the model. In general, if pen effects are present, the use of the residual mean square will yield conservative tests, whereas the use of the theoretical error will result in somewhat inflated variance ratios.

Examination of the results in Table 2 show that only in the case of Y_1 (percent of pullets housed) is there any indication of an effect due to generation of relaxation ($P < .10$). In this case there is an increase in percent housed with advancing generations of relaxation. For every other trait, the effects of relaxation are negligible after taking into account the effects of the year of testing. The factors are nonorthogonal, but they are so far from being purely confounded that any real effect due to relaxation would appear in the residual sum of squares $R(\beta_1, \beta_2 | T_1, \dots, T_6)$. As a check, however, a regression on X and X^2 alone was run, and in no case was the regression mean square comparable in magnitude to the residual mean square. In the case of Y_6 , however, the regression mean square was significant at the 10 percent level when compared to the theoretical error. The means showed a decreasing mortality with years of relaxation. Logically, however, this may be discounted because of the probable effects of pens and years present in the regression mean square and when the pure effect of relaxation after years (Table 2) is shown to be negligible.

SUMMARY

Five generations of relaxed selection were studied in a population of White Leghorns previously selected for high percent egg production to January 1. The

population had apparently reached a plateau for this trait. Some weak selection had been applied for egg size and viability.

Analysis of the data by a least squares technique did not yield any evidence of either linear or quadratic effects of the generations of relaxation in any of the seven traits analyzed. The traits studied were percent of pullet chicks housed, age at 50 percent production, number of eggs per pullet housed, number of eggs per chick started, number of eggs per average hen (hen-day egg production), percent adult mortality, and average monthly egg weight.

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