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Random genetic drift in an egg-laying strain of poultry

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SUMMARY

A pedigreed control strain was divided into three lines which were maintained genetically distinct over nine generations. Mean coefficients of inbreeding of about 0·1 were attained. Results suggest that discernible genetic drift had occurred in several traits. Separate estimates of genetic variance were obtained from observed variation between and within lines. These estimates differed significantly in the case of only one of the eight traits observed. Observed variation between lines agreed reasonably well with that predicted.

1. INTRODUCTION

The usual function of a control strain is to provide a standard against which genetic progress in other strains may be measured. In his review of the topic, Hill (1972*b*) points out that this aim may be frustrated to a varying extent by errors arising from four sources: random genetic drift in the control, genetic changes in the control due to natural selection, different responses of the control and selected strains to environmental changes, and errors of estimation of the control mean.

He found little evidence of changes due to natural selection except perhaps in the first generation or two of relaxation after selection, while genotype–environment interactions are not expected to be important where there is a normal range of environments and when the control arises from a genetic base similar to that of the selected strains. Errors in estimation of the mean are always present but the variance of the mean can be relatively easily measured and an increase in the test population will proportionately reduce its size. Random genetic drift, however, can be a more serious problem in the long term because it accumulates over the generations. Also, due to the small number of individuals

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from which, by economic necessity, the control strain is reproduced, the drift will often be of significant size.

As control strains usually consist of a single line, direct evidence of the existence of genetic drift is not readily available. In the formation of an egg-laying control strain of poultry in 1967 as a standard for a selection programme it was therefore arranged that it should consist of three separate lines, the comparison of which would provide some empirical indication of the importance of genetic drift. This paper summarizes the results obtained over nine generations. The control strain has now been replaced.

2. MATERIALS AND METHODS

The origin of the flock, so far as it is known, is as follows. In 1959 hatching eggs of two White Leghorn strains called 'Babcock' and 'Mount Hope' were imported into Northern Ireland from U.S.A. They passed through one generation each year without conscious directional selection. In 1964 hatching eggs from each strain were sent to Hillsborough and in 1967 the two strains were reciprocally crossed. In the interval between importation and crossing it appears that the number of breeding individuals per sex per generation per strain always exceeded six. This account is concerned with ten successive generations after the crossing, the F_1 to F_{10} generations, which are numbered 0–9 respectively.

The control strain consisted of three lines of approximately equal size, which had been formed by matings arranged among the F_1 progeny. These matings were arranged at random except for a prohibition against half-sib matings. Matings were arranged henceforward only within lines. Each line was bred from eight sires, each sire being mated to a pen of four dams. The control strain passed through one generation each year.

The formation of a breeding population from the preceding generation was as follows. So far as was possible each female was the progeny of a different dam, each male the progeny of a different sire, and the four females in a breeding pen normally had a common sire and their dams were half-sisters. Thus the degree of relationship between the dams in a pen, excluding the effect of any changes in inbreeding, tended towards one third in later generations. If a dam had no suitable female progeny (non-laying females were excluded from consideration) a replacement was sought among the progeny of its half-sisters and, failing that, among the progeny of other dams in the line subject to the prohibition on half-sib matings. If a sire had no male progeny a replacement was sought among the progeny of other sires in the line. When choosing which of the four dams in the pen would contribute the male progeny or when seeking replacements, the aim, subject to the above restrictions, was to give equal emphasis in the line to each dam, pen and sire, and so help to maintain the stability of gene frequencies. Males were excluded from consideration only if they were in obvious bad health. The allocation of males to pens was by a 3-year cyclic mating scheme.

The birds were reared in groups with their hatch mates on litter. There were

two hatches of generations 1 and 2, three of generation 3, and a single hatch date in the remaining six generations. The third hatch in generation 3 was reared and recorded at Loughry Agricultural College. The remaining pullets remained at Hillsborough and at the age of 18–20 weeks they were weighed and moved to individual cages where their performance was recorded. These cages were in one of two houses; either in a battery breeding house where 96 hens chosen according to the above rules to produce the next generation were placed, or in a block of contiguous cages in a conventional battery house where the remaining pullets were placed in a random arrangement. Any differences between the two houses were ignored in the analyses on the assumption that either such differences were insignificant or that there was balanced representation of the lines in the houses. The number of pullets recorded for each trait in each line in each generation ranged from 20 to 252.

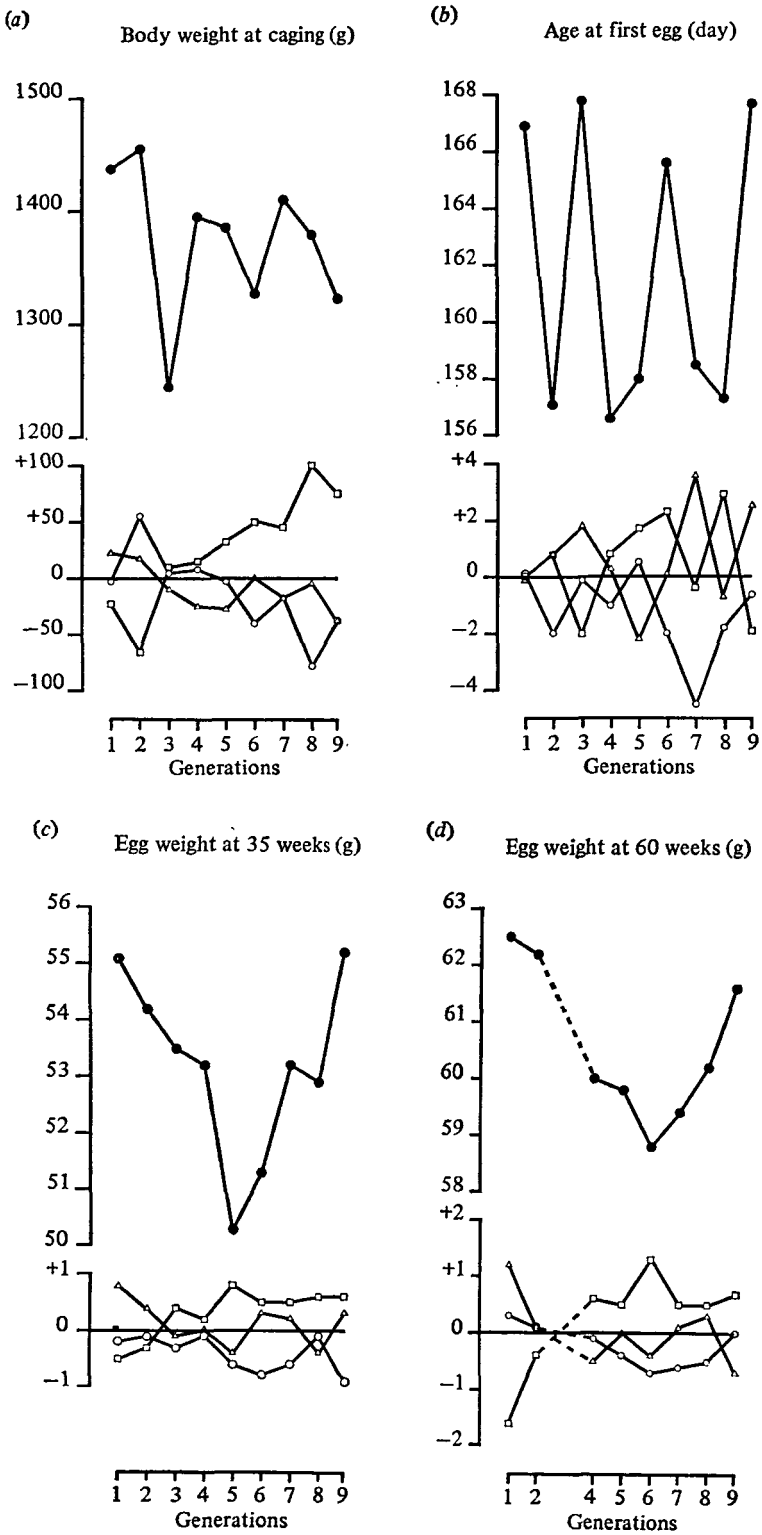
The battery breeding house also contained cages for the 24 selected cockerels. Artificial insemination was used to produce fertile hatching eggs during the breeding period which was arranged between the two assay periods.

Results were recorded on eight traits: body weight at caging, age at first egg, egg weight and shell deformation at 35 and 60 weeks of age (64 weeks of age in generation 1; shell deformation not recorded at 35 weeks in generation 1) and presumed ovulation frequency over two assay periods. The first assay period ran from 210 to 278 days (generations 2–4) or to 275 days (generations 5–9) while the second assay period was 69 (generations 2–4), 66 (generation 5) or 44 days (generations 6–9) about the age of 60 weeks. No assay of ovulation frequency was made in generation 1, and no second assays were made in generation 3 due to an outbreak that year of Marek's disease.

A description of the trait 'presumed ovulation frequency' was published by Foster (1972). Briefly it consists of an estimate made on the basis of records of times of oviposition and specifically attempts to include ovulations in which the yolk falls into the peritoneum to be absorbed rather than being collected by the infundibulum, the so-called 'internally laid eggs'. It can only be estimated in hens which maintain a reasonably regular ovipository clutch pattern. Unpublished results suggest that the trait is highly correlated with most measures of egg production but is less variable and more highly heritable.

3. RESULTS

The overall mean for each trait in each generation is shown in Fig. 1 as well as the deviations from this mean by each of the three lines which constitute the strain. Variation between generations in the overall mean performance can be attributed to genetic and/or environmental causes. Consistent deviations from the mean in the performance of an individual line indicate genetic differences between the lines. Genetic differences between the lines should also result in consistent deviations when traits in which pleiotropy is expected are compared



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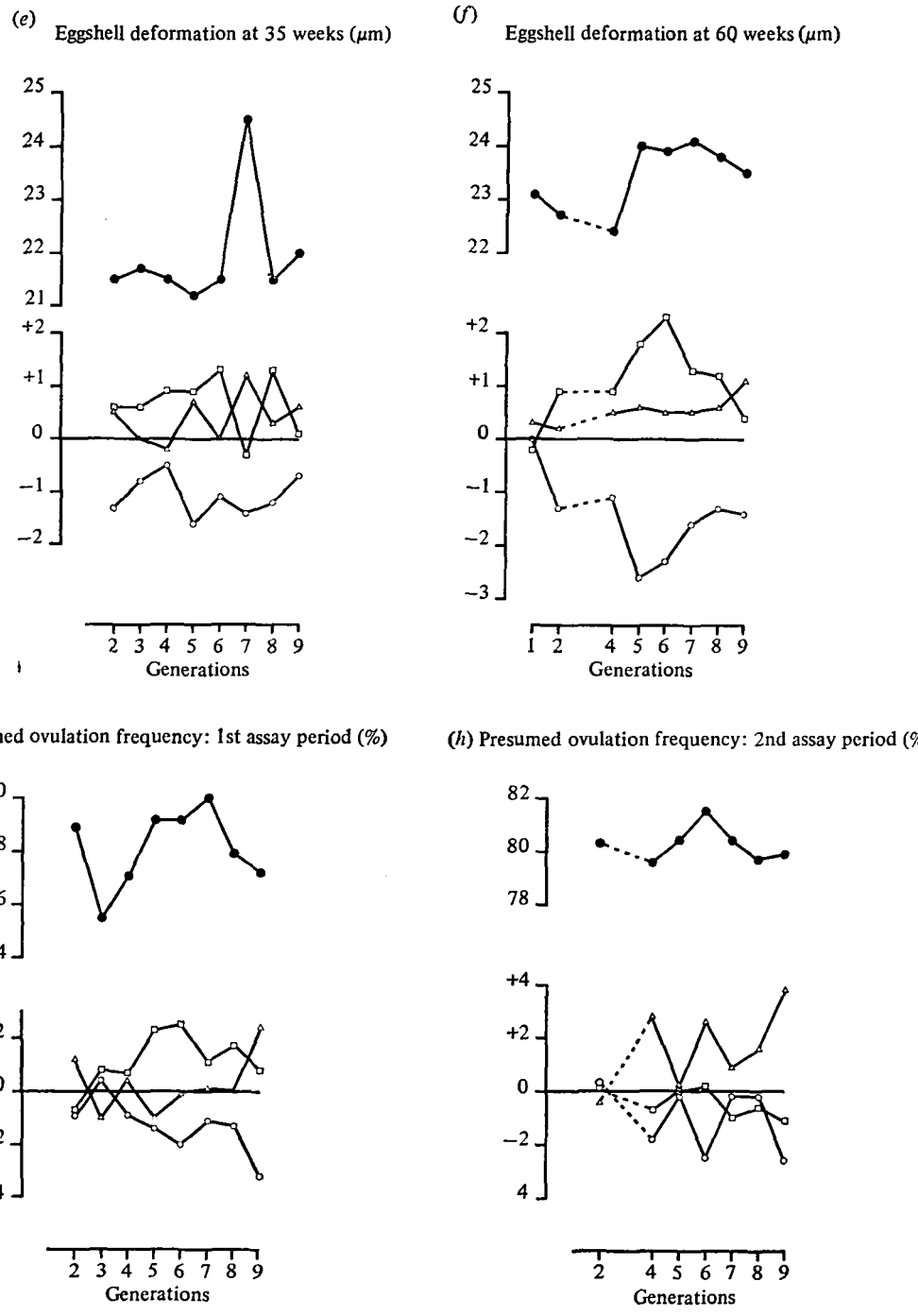

Fig. 1. Mean performance in eight traits of the control strain (●—●) over generations, and deviations from the mean of each of the three lines: line A (□—□), line B (○—○) and line C (△—△), which constitute the control.

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(i.e. early assays of egg weight, shell deformation and ovulation frequency with their respective later assays).

Effective population size (N_e) was calculated for each line in each generation by means of the argument presented by Latter (1959):

$$\frac{16}{N_e} = \frac{\Sigma^{M'} a_i(a_i-1)}{M^2} + \frac{2\Sigma^{M'} a_i b_i}{M.F} + \frac{\Sigma^{M'} b_i(b_i-1)}{F^2} + \frac{\Sigma^{F'} c_j(c_j-1)}{M^2}$$
$$+ \frac{2\Sigma^{F'} c_j d_j}{M.F} + \frac{\Sigma^{F'} d_j(d_j-1)}{F^2} + \frac{4}{M} + \frac{4}{F} - \frac{4}{M'} - \frac{4}{F'}, \quad (1)$$

where

a_i = number of breeding males from ith sire,
b_i = number of breeding females from ith sire,
c_j = number of breeding males from jth dam,
d_j = number of breeding females from jth dam,
M = total number of breeding males = $\Sigma^{M'} a_i$,
M' = number of sires,
F = total number of breeding females = $\Sigma^{F'} d_j$,
F' = number of dams.

Where each sire and dam contributes the expected number of progeny to the next breeding population, the effective population size for each line calculated in this fashion would be 39·4. The harmonic means of effective population sizes for each line for each generation are shown in Table 1, which also shows the mean inbreeding coefficient for each generation computed by tracing pedigrees back to 1966.

The variance effective size, which is relevant to this investigation, should be distinguished from the inbreeding effective size which predicts the increase in autozygosity (Kimura and Crow, 1963). Under random mating the two measures are the same and the accumulated inbreeding may be estimated by $\Sigma_{j=0}^{i-1} (1/2\, N_{e_j})$. A comparison of the first and last lines in Table 1 shows a discordance of 2–3 generations indicating that in this investigation there was an increase in genetic drift and/or a decrease in inbreeding compared to random mating. This presumably resulted from the cyclic mating scheme with its avoidance of the mating of closely related animals (Hill, 1972*a*).

After correction for any hatch effects, data from each generation were analysed to produce estimates of variance components (for the ith generation) between lines (L_i), between sire groups within lines (S_i), between dam groups within sires (D_i) and within full sib families (Q_i). These lead to estimates of the heritability coefficients. The ranges of these estimates and their means are shown in Table 2 together with pooled estimates of the variances between full sibs.

As a result of the breeding procedure, the variation between lines is expected to increase due to drift. If G represents the genetic variance in the base population then, on the assumption of additive gene action, drift in the ith generation is represented by $G\Sigma_{j=0}^{i-1} (1/N_{e_j})$. By equating this with L_i, an estimate of the genetic variance is obtained based on the between-line variation ($\hat{G}_B$).

Table 1. *Mean coefficient of inbreeding (F) and effective population size (N_e) in each generation*

	Generation (i)									
	0	1	2	3	4	5	6	7	8	9
F_i	0	0·010	0·020	0·017	0·032	0·043	0·065	0·066	0·078	0·086
N_{e_i}	27·4	40·2	35·5	29·3	38·5	35·3	38·1	39·4	39·3	—
$\Sigma_{j=0}^{i-1}(1/2\,N_{e_j})$	—	0·018	0·031	0·045	0·062	0·073	0·089	0·102	0·115	0·127

Table 2. *Heritability estimates, estimates of the variation within full sib families ($\hat{Q}$), genetic variation derived from within lines ($\hat{G}_W$), between lines ($\hat{G}_B$) and a pooled estimate ($\hat{G}_P$), and twice the difference in log-likelihood (LD) between two models for each trait*

	Heritability estimates*							
	Mean	Min.	Max.	$\hat{Q}$	$\hat{G}_W$	$\hat{G}_B$	LD	$\hat{G}_P$
Body weight at caging (g)	0·87	0·64	1·07	14855	18796	41090	1·84	19300
Age at first egg (days)	0·66	0·45	0·81	80·04	74·64	51·04	0·11	74·12
Egg weight at 35 weeks (g)	0·74	0·43	1·07	9·69	11·32	0·87	6·13	11·00
Egg weight at 60 weeks (g)	0·75	0·55	1·14	13·63	15·96	3·48	1·53	15·52
Shell deformation at 35 weeks (μm)	0·41	0·19	0·52	12·13	6·36	4·45	0·21	6·28
Shell deformation at 60 weeks (μm)	0·14	−0·26	0·49	22·63	5·08	9·03	3·64	6·60
Ovulation frequency: first assay (%)	0·50	0·07	0·68	42·30	27·80	7·70	1·97	26·92
Ovulation frequency: second assay (%)	0·66	0·24	1·78	54·43	36·52	7·71	2·22	35·08

* $h_i^2 = 2\,(S_i+D_i)/(S_i+D_i+Q_i)$. S_i, D_i and Q_i are estimates of variance components between sire groups, dam groups and within full sib families respectively in the ith generation.

Another estimate of the genetic variance, $2(S_i + D_i)$ can be derived from the variation within lines, on the assumption of no dominance or maternal effects. This estimate is denoted by $\hat{G}_W$. No account was taken of the reduction in genetic variation within lines due to drift, as this reduction is expected to be insignificant.

In order to test whether these estimates agree, two models were fitted. In the first model estimates of G_B and G_W were found by maximum likelihood. A second model was then fitted, assuming $G_B = G_W$, to give a pooled estimate of $G(\hat{G}_P)$. Twice the difference in log-likelihood between the two models is a measure of the difference between $\hat{G}_B$ and $\hat{G}_W$ and is distributed asymptotically as χ^2 with 1 degree of freedom if $G_B = G_W$.

The variance components from generations 1–8 and the cross-products of control lines between generations were used to estimate G_B and G_W. The cross-products were used because they should provide extra information on G and because Hill (1971) has shown there can be a large correlation between responses in different generations. The expectations of the cross-products were evaluated using formulae similar to Hill (1971).

A more complicated model which took account of the increasing relationship over generations between dams in a pen was fitted but as it was found to make only minor changes to the estimates, it is not reported.

Results are shown in Table 2. For only one trait, egg weight at 35 weeks, is LD greater than the 5% value of χ^2 (3·84). Further analysis shows that for this variate, assuming normality, there was significant variation between generations in the dam and residual components.

4. DISCUSSION

An inspection of Fig. 1 suggests the occurrence of obvious genetic drift in body weight at caging and in egg weight. The consistent deviations in shell deformation indicate genetic differences between the lines but, from Fig. 1*e* and 1*f*, it appears these may have arisen during the original sampling in the formation of the lines rather than by genetic drift over the generations of isolation. With the trait presumed ovulation frequency, there is less obvious evidence of genetic separation occurring since the establishment of the lines. The value of the control strain in its declared function is indicated, notably by Fig. 1*c* and 1*e*, where large variation between years, presumably due to environmental causes, has had little discernible effect upon the deviations of the individual lines.

It should be remembered that this control strain was devised primarily as a standard for a selection programme and not for the purpose of estimating genetic drift. The results therefore do not form a rigorous test of differences between $\hat{G}_B$ and $\hat{G}_W$. As can be seen in Table 2, the pooled estimates are much closer to $\hat{G}_W$ than $\hat{G}_B$, indicating the low accuracy of the latter estimate. With this limitation upon the precision of the results it is, however, noteworthy that in the case of only one of the eight traits was there evidence of a significant difference between estimates derived from theoretical expectations of drift, and to that extent

the existence of genetic drift and expectations concerning its magnitude are realized.

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