DIRECT AND MATERNAL EFFECTS OF EGG-SIZE GENES ON HATCHABILITY¹

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Received September 15, 1969

ANIMAL breeders often select the extreme individuals in a population. This may conflict with natural selection for reproductive fitness. For example, chickens with intermediate body weights and egg weights usually have the highest hatchability. LATTER and ROBERTSON (1962) hypothesized that the decline in fitness with selection for a metric trait is a consequence of gene frequency changes of two kinds: one results from directional selection and the other from random fixation of genes due to the restricted size of the selected population, i.e., from inbreeding depression. The first objective of our study was to compare the relative effects of inbreeding depression and egg size on hatchability in small populations undergoing directional selection for egg weight. The second was to investigate the path by which egg size genes influence hatchability—whether as a direct effect on hatchability or as an indirect (maternal) effect.

MODELS AND ASSUMPTIONS

Two approaches were used. The first was to estimate empirically by multiple regression the effects of inbreeding and egg size on hatchability. The second was to use a single-locus model to estimate the average effects, dominance, and maternal effects of egg-size genes on hatchability.

I. Multiple regression model: The effects of inbreeding and egg size on hatchability were estimated from a multiple regression analysis using the model

$$H_{ij} = \mu + \gamma_i + b_1 Fx_{ij} + b_2 W_{ij} + b_3 W_{ij}^2 + e_{ij} \quad (1)$$

where H_{ij} = the hatchability of line j or cross j in year i

μ = a hatchability constant

γ_i = the effect of the i th year

Fx_{ij} = the inbreeding coefficient of line j or cross j in year i

b_1 = the linear regression of hatchability on inbreeding

b_2 = the linear regression of hatchability on egg weight, W

b_3 = the quadratic regression of hatchability on W^2

e_{ij} = the error of the H_{ij} observation with mean zero and variance σ^2

In particular, we wish to obtain least-squares estimates of inbreeding depression and the effects of egg size on hatchability using all the data i.e., including

¹ Journal Paper No. J 6360 of the Iowa Agriculture and Home Economics Experiment Station, Project 1711, in cooperation with the North Central Regional Poultry Breeding Project NC-89.

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the control line A. For a line, the value of Fx is the observed inbreeding coefficient from pedigree information; for any cross of two lines, the value of Fx was assumed to be zero.

Since line effects other than egg size were ignored in the model, they would be confounded with the egg-size effect and the error term. This seems reasonable under the assumption that the major difference between lines was in egg size which is accounted for as a separate variable. Also, from a preliminary analysis, sire line effects were small and statistically nonsignificant.

II. *Single-locus model*³: Hatchability is a component of reproductive fitness and is influenced by two kinds of genes: those affecting the embryo directly, e.g., lethal genes, and those affecting hatchability indirectly through the environment provided for the embryo (maternal effect). The size and quality of the egg in which the embryo resides is a clear-cut maternal characteristic of the hen laying the egg.

Direct effect of genes on hatchability: Since hatchability is a fitness component, it is reasonable to assume that direct hatchability genes have dominant effects. For example, lethals would be recessive. Accordingly, as with fitness traits in general, hatchability is depressed by inbreeding effects and increases with cross-line effects (heterosis).

Consider an allelic pair of genes, A_1 and A_2 , at locus A with gene frequencies p and q in a randombred population. If mating is at random, the genotypes, frequencies, and effects would be:

Genotype	A_1A_1	A_1A_2	A_2A_2
Frequency	p^2	$2pq$	q^2
Effect	a	d	$-a$

When $d = 0$ there is no dominance, and when $d = a$ dominance is complete.

If the population mean hatchability is H , the contribution of locus A to the mean would be $H(A) = (p - q)a + 2pqd$.

If selection changes the gene frequencies from p to $(p + \delta)$ and from q to $(q - \delta)$, the new mean in terms of the original population would be

$$H_1 = H + 2\delta\alpha - 2\delta^2d.$$

The quantity $\alpha = a + [d(q - p)]$ is the "average effect" of a gene substitution at locus A .

If the newly selected population with mean H_1 is crossed with the original with mean H , the increase in the progeny mean would be $H_x - H = \delta\alpha$.

If heterosis is measured as the difference between the cross and the parental average, then $H_x - (H_1 + H)/2 = \delta^2d$, which defines heterosis solely in terms of change in gene frequency and dominance effects of genes. If such effects are additive over n loci influencing hatchability, the expected heterosis, i.e., dominance, from a cross between two lines would be

$$\sum_{i=1}^n \delta^2_i d_i$$

³ The single-gene treatment of the theory is based largely on a paper by R. L. WILLHAM on the genetic consequences of crossbreeding (WILLHAM 1970).

Maternal effect of genes on hatchability: Since egg size affects hatchability, genes which determine egg size must influence hatchability. This is the indirect or maternal effect of egg-size genes. As a rule, eggs of intermediate size hatch the best. A simple but not wholly unreasonable assumption is that egg size is determined by genes with additive effects. This assumption is supported (but not proved) by the observation that parents whose egg-size genotypes are extremes produce progeny very close to the midparental mean (CASEY and NORDSKOG 1971). We assume that genes have either positive or negative effects and that hens laying large eggs have a predominance of genes with positive effects and hens laying small eggs have more with negative effects.

Let the individual gene contributions to the optimum over n loci be

$$(p_1 - q_1)a_1 + (p_2 - q_2)a_2 + (p_i - q_i)a_i + (p_n - q_n)a_n = E_o.$$

Even though there would be only one optimum egg size for hatchability, conceptually, there would be many different genotypes which are optimal for egg size.

Assume a particular population with mean egg size $\bar{E}$ and mean hatchability $\bar{H}$. Also assume that fitness declines with the square of the deviation from the optimum, E_o (WRIGHT 1935). The mean egg-size effect on hatchability would be $\bar{H} - H_o = K(\bar{E} - E_o)^2$ where K is a constant of proportion between egg size and hatchability.

For a specific pair of alleles, say B_i and B_j , with positive and negative effects on egg size and with gene frequencies p_o and q_o for a particular optimum genotype, locus B 's contribution to the egg size optimum would be, $E(B) = (p_o - q_o)a^*$, where a^* is the additive effect of, say, the B_i allele on egg size.

Now if by selection $p_o \rightarrow (p_o + \delta_1)$, then

$$E(B)' = [(p_o + \delta_1) - (q_o - \delta_1)]a^* = E(B) + 2\delta a^*.$$

The deviation from the optimum is

$$d(B)' = E(B)' - E(B) = 2\delta a^*, \text{ and the effect on hatchability would be } H[d(B)'] = -K(2\delta_1 a^*)^2 = -4K\delta_1^2 a^{*2}.$$

A clear distinction needs to be made between a direct effect, a , of a gene and an indirect effect, a^* , of a gene on hatchability. The following path diagram should make this clear:

Group A genes influence hatchability directly only and group B genes via egg size only.

Genes with both direct and maternal effects of hatchability: By analogy, we can show how hatchability is affected through egg size. For some optimum egg-size genotype, the gene frequencies of C_1 and C_2 are p_o and q_o , and the C locus contribution to egg size is

$$E(C) = (p_o - q_o)a^*.$$

The contribution to hatchability from locus C is

$$H(C) = H(d) + H(m)$$

where

$H(d) = (p_o - q_o)a + 2pqd$ is the direct contribution from locus C , and $H(m) = -K(p_o - q_o)^2a^{2*}$ is the maternal contribution.

For a positive change in gene frequency, δ , say eggs are made larger, then the change in hatchability is

$$\Delta H = 2\delta\alpha - 2\delta^2d - 4K\delta^2a^{2*}.$$

The first two right-hand terms represent the direct effect and the last term the maternal effect of the gene frequency change.

Likewise, for a negative change in gene frequency, $-\delta$, say eggs are made smaller, the total change in hatchability is

$$\Delta H = -2\delta\alpha - 2\delta^2d - 4K\delta^2a^{2*}.$$

Now suppose we have a population, L_o , which is at the optimum for egg size, and we form a line L_1 by selecting up for egg size, and a line L_2 by selecting down.

The gene frequencies at locus C in the lines are:

Line	C_1	C_2
L_o	p	q
L_1	$p + \delta_1$	$q - \delta_1$
L_2	$p - \delta_2$	$q + \delta_2$

The contribution of locus C to the means of the lines and crosses is shown in Table 1.

Estimation of effects: The above equations can be solved to estimate the effects α , d , and m of egg-size genes on hatchability assuming (1) that the effects are additive over all loci, (2) that the effects of random genetic drift on line differences are small relative to the directional effects of selection for egg size, and

TABLE 1

The expected C-locus contribution to the means of the selected lines and crosses

Line or cross I_o	Selected Control	Mean $X_o = \mu + (p - q)a$	Locus C direct effect $+ 2pqd$	Locus C maternal effect $-K_o(p - q)^2a^{2*}$
L_1	Up	$X_1 = X_o + 2\delta_1\alpha$	$-2\delta_1^2d$	$-m_1$
L_2	Down	$X_2 = X_o - 2\delta_2\alpha$	$-2\delta_2^2d$	$-m_2$
$L_1 \delta \times L_2 \varphi$		$X_{12} = X_o + (\delta_1 - \delta_2)\alpha$	$+2\delta_1\delta_2d$	$-m_2$
$L_2 \delta \times L_1 \varphi$		$X_{21} = X_o + (\delta_1 - \delta_2)\alpha$	$+2\delta_1\delta_2d$	$-m_1$

μ = effect of all loci other than locus C .

$m_1 = 4K_1\delta_1^2a^{2*}$

$m_2 = 4K_2\delta_2^2a^{2*}$.

(3) that the egg-size genes are additive in their effects on egg size but show dominance in their direct effects on hatchability.

It is convenient to show the expectations of the selected lines and their crosses in a diallel table where X_{ij} is the progeny mean of sire line i and dam line j :

	Dam line		
Sire line	L_1	L_2	Sire means
L_1	X_{11}	X_{12}	$X_{1.}$
L_2	X_{21}	X_{22}	$X_{2.}$
Dam means	$X_{.1}$	$X_{.2}$	$X_{..}$

The conventional dot notation is used to denote sire and dam line means in the margins of the table.

The estimators and expectations of effects are:

Estimators	Expectation
Sire effect $X_{1.} - X_{2.}$	$(\delta_1 + \delta_2)\alpha - (\delta_1^2 - \delta_2^2)d$
Dam effect $X_{.1} - X_{.2}$	$(\delta_1 + \delta_2)\alpha - (\delta_1^2 - \delta_2^2)d - (m_1 - m_2)$
Maternal: Sire-Dam	$m_1 - m_2$
Interaction	
$\frac{(X_{12} + X_{21})}{2} - \frac{(X_{11} + X_{22})}{2}$	$(\delta_1 + \delta_2)^2 d = \text{Heterosis}$

Note that the interaction (dominance) effects are cleanly estimated in terms of the gene frequency change and d . Both the sire and dam effects contain some dominance but the difference is a clean estimate of the maternal effect, $m_1 - m_2$.

If we assume that selection has been equally effective up as down, then $\delta_1 = \delta_2 = \delta$ and the expectations simplify to:

Sire effect	$2\delta\alpha$
Dam effect	$2\delta\alpha - (m_1 - m_2)$
Interaction	$4\delta^2 d$
Maternal	$m_1 - m_2 = -4(K_1 - K_2)\delta^2 a^{2*}$.

Separate estimates of the maternal effects m_1 and m_2 are possible if we substitute information from the control line with the assumption that *egg size in the control line is at the optimum for hatchability*. Letting X_0 be the mean hatchability of the control line,

$$m_1 = X_{.1} - 1/2 (X_{1.} - X_{2.}) - X_0 \text{ where } X_{.1} = X_0 + \delta\alpha + m_1 \\ = X_{.1} - 1/2 \text{ sire effect} - \text{control mean.}$$

Likewise,

$$m_2 = X_{.2} - (X_{1.} - X_{2.})/2 - X_0.$$

Comparing the two models, the inbreeding regression (b_1) and egg-size regressions (b_2 and b_3) of Model I correspond to d and m in Model II. If line effects had been included in Model I, they would have corresponded to α in Model II.

Finally, because the regression model includes direct information on inbreeding, no assumption is required that the effects of random drift within lines over generations are small compared to selection effects.

THE DATA

The data consisted of hatchability records on 5 lines of Leghorns and crosses between them (FESTING and NORDSKOG 1967; VERGHESE and NORDSKOG 1968). The lines were selected for single traits as indicated below with letters symbolizing the traits (body weight BW, egg weight EW) and the direction they were selected (high H, low L).

Line A—High egg production rate (Control)

Line B—High body weight (H BW)

Line C—Low body weight (L BW)

Line D—High egg weight (H EW)

Line E—Low egg weight (L EW)

For convenience these are called pure lines to contrast with cross lines. Line A, selected for high egg production, was included as a quasicontrol since selection seemed not to have influenced hatchability. The five years of results included in the study (1963–1967) were the 5th through 9th generation of selection.

The Leghorn lines selected for large and small egg size (D and E) were reciprocally crossed in each of the 5 test years. Likewise, the large and small body weight lines (B and C) were reciprocally crossed and the correlated effects of egg size on body weight were studied. The B and C lines and crosses are Set 1; the D and E lines and crosses are Set 2. Sets are assumed to be replicate samples of lines since they have a common origin, have essentially the same effective population number, and were handled together. On the other hand, the B and C lines were selected for body weight, so that in them the changes in egg weight were correlated responses to selection for body weight, whereas in the D and E lines the changes in egg weight were direct responses. The crosses were assumed to have zero inbreeding with respect to the foundation population while the egg-size effect on hatchability would be the same as the line used as female parent of the cross. This is, in fact, the maternal effect we are concerned with.

In each year, an average of 400–800 eggs of each line or cross was set in each of one or two fatches. For each hatch, eggs were collected over a 2-week interval from flocks of 75 to 200 hens. Hatchability was calculated as the fraction of fertile eggs hatching on or before the 22nd day of incubation.

Inbreeding coefficients of the pure lines were estimated from complete pedigree information.

RESULTS

Averages by lines, crosses, and generations: The inbreeding coefficients and egg weights by lines and years are given in Table 2. Inbreeding, which averaged about 2% per generation over the 5-year test period, is a consequence of the finite size of the selected populations and the peculiarities of the mating system, including avoidance of sib matings. The higher inbreeding in Line E implies that the families selected as breeders were fewer but larger than those in the other lines.

The average hatchability of each of the lines and crosses by years is given in Table 3. In order to show better the contrast between the performance of the lines and crosses, the hatchability of each line is paired with the cross of the same line used as the dam parent. Thus, Line B is paired with the C♂ × B♀ cross in the table. The difference in hatchability then reflects mainly the difference in inbreeding (or heterozygosity) between the developing embryos, since there would be no phenotypic differences in egg size. Sampling errors, of course, may be considerable; this probably accounts for the 4 cases out of 20 where the pure lines hatched better than the paired crosses. In one case (C × B in 1966) the

TABLE 2

Inbreeding coefficients and egg weights by lines and years

Line	Generation year					Average
	1963	1964	1965	1966	1967	
Average inbreeding coefficient (percentage)						
A	8.9	10.4	12.0	12.3	14.6	11.7
B	7.5	9.2	11.2	13.5	15.1	11.3
C	9.6	10.9	12.6	14.4	18.3	13.2
D	9.3	10.6	14.0	15.6	17.8	13.4
E	12.4	14.8	18.9	20.3	23.7	18.0
Average egg weight (grams)						
A	55.6	54.7	53.9	53.3	53.6	54.2
B	65.0	63.7	64.2	65.4	63.3	64.3
C	50.1	49.6	47.9	47.3	49.1	48.8
D	67.2	65.9	66.9	66.4	68.0	66.9
E	47.3	45.4	44.1	42.8	44.2	44.8

hatchability was clearly too low. We think the chicks were taken off too soon before the hatch was fully completed. In general, the large eggs required several hours more to complete hatching than the small or medium-sized eggs.

The average differences between the body weights of lines and crosses, B *vs.* C $\times$ B, and C *vs.* B $\times$ C, were both statistically significant while those between the egg-weight lines and their crosses were not. The comparison D *vs.* E $\times$ D was just below the 5% level of significance, while the average difference of E *vs.* D $\times$ E was negligible. On the other hand, the crosses of the egg-size lines hatched better than the pure lines in each of the years except 1963. Hatchability of the lines selected upwards was significantly lower than the lines selected downwards.

TABLE 3

Percent hatchability by lines, crosses, and year

Line or cross*	Selected for	Year					Average
		1963	1964	1965	1966	1967	
A	Control	81.2	89.0	88.0	81.1	85.0	84.9
B	H BW	66.0	72.7	70.9	71.5	70.9	70.4
C $\times$ B		82.1	80.1	86.5	(58.8)†	78.0	77.1
C	L BW	81.5	78.6	74.9	77.7	82.5	79.0
B $\times$ C		85.0	86.7	90.4	87.3	88.7	86.6
D	H EW	63.6	70.0	60.7	73.5	82.9	70.1
E $\times$ D		77.0	75.1	69.5	70.3	83.7	75.1
E	L EW	89.7	80.8	82.1	73.7	78.7	80.1
D $\times$ E		76.5	86.3	85.6	77.5	81.7	80.2

* For each cross the sire line is designated on the left and the dam line on the right.

† This value is probably too low because the hatch unfortunately was taken off a few hours too early.

TABLE 4
Least-squares analysis of hatchability variance

Source	df	Mean squares	F
Years	4	59.84	1.78
Inbreeding	1	149.27	4.45*
Egg weight:			
Linear regression	1	197.24	5.88*
Quadratic regression	1	237.01	7.06*
Remainder	37	33.56	...
	44		

* $P(F = 1) < 0.05$.

Model I: The data fitted to the multiple regression equation (1) gave the following values:

$\mu = -40.4$, an overall constant

$b_1 = -.26 \pm .125$, inbreeding effect

$b_2 = 4.95 \pm 2.26$, linear egg-size effect

$b_3 = .049 \pm .020$, quadratic egg-size effect

Σ year effects = 0

$Y_1 = -1.0$, $Y_2 = .4$, $Y_3 = .3$, $Y_4 = -3.2$, and $Y_5 = +3.5$.

To obtain a unique solution, the sum of the year effects was set equal to zero.

All regression coefficients were statistically significant at the 5% level while none of the year effects was significant (Table 4). The coefficient $b_1 = -.26$ means that for each 10% increase in inbreeding, hatchability is expected to decline by 2.6%. Since inbreeding increased about 2% per generation, averaged over lines, hatchability would be expected to have declined about 0.52% per generation.

FIGURE 1.—Influence of egg weight on hatchability. The dots are the line (or cross) by year means corrected for inbreeding and year effects.

TABLE 5

Analysis of variance of percent hatchability of two diallel sets of lines over five year-replications

Source	df	Mean squares
Years	4	53.31
Sets	1	25.44
Sire lines	1	4.16
Dam lines	1	829.01**
Sire $\times$ Dam	1	269.88**
Set $\times$ Sire	1	25.13
Set $\times$ Dam	1	2.26
Set $\times$ Sire $\times$ Dam	1	59.77
Year interactions	28	42.60
	39	

** $P(F = 1) < 0.01$.

The linear and quadratic effects of egg size on hatchability are best shown graphically. The observed hatchability means corrected for inbreeding and the fitted curve are shown in Figure 1. Optimum egg size is about 50 grams. The fit of the graph to the data is necessarily symmetrical because this is built into the model.

Model II: An analysis of variance of the diallel sets is given in Table 5. The actual data analyzed were the values given in Table 3 except that Line A was omitted. The nonsignificance of sire-line effects indicates that the direct average effect (α) of an egg-size gene on hatchability is small. In contrast, the dam-line effects were highly significant. This means that $(\alpha + m) > 0$. The statistically significant sire $\times$ dam interaction suggests that dominance is important ($d > 0$).

The results in Table 5 also strengthen the assumption that the two diallel sets for each set of lines are valid replicates. The main effects of Sets and the interactions of Sets $\times$ Sire, of Sets $\times$ Dam, and of Sets $\times$ Sire $\times$ Dam were not statistically significant. This is evidence that the two diallel sets are random samples from the same hypothetical population of lines with parameters α , d , and m .

The estimated effects for each of the sets of lines is given in Table 6. No special trends in the estimates over generations seem evident although sampling errors, being large, could mask such trends. Differences between sets of lines (BW - EW) were small and not significant, suggesting that the same parameters were common to each set. The average effect α , was not statistically significant in either line while the dominance effect, d , was significant in both. As an average over both sets, $\alpha = 1.0 \pm 2.0$ and $d = 3.0 \pm 0.8$. On the other hand, the indirect or maternal effect of genes for egg size was asymmetrical: with egg size above the optimum, the effect was large ($m_1 = -12.2 \pm 1.9$), but with egg size below the optimum, the effect was small ($m_2 = -2.9 \pm 1.6$). In terms of the notation used in the model (Table 1), the asymmetry means that $K_1 > K_2$. On the average, a 10 g increase in egg size above the optimum lowered hatchability by 10.7% while a 10 g decrease lowered hatchability by only 3.9%.

In general, these results indicate that egg-size genes have both a direct and an

TABLE 6

Estimated average effects (α), dominance (d), and maternal effects (m_1 large egg, m_2 small egg) of genes for egg size on percentage hatchability

Sets	Year	α	d	m_1	m_2
BW lines	1963	6.3	4.9	—10.4	5.2
	1964	—0.4	3.9	—12.4	—6.4
	1965	0.1	7.8	—9.3	—5.3
	1966	—11.1	—0.8	—10.3	—3.9
	1967	0.5	3.3	—10.7	0.9
	Average	0.5 ± 2.8	3.5 ± 1.4	-10.9 ± 1.0	-2.3 ± 1.9
EW lines	1963	13.3	0.0	—17.3	8.5
	1964	—0.2	2.6	—16.3	—5.5
	1965	2.6	3.0	—24.2	—2.8
	1966	—3.5	0.2	—7.3	—7.1
	1967	—1.1	1.0	—1.1	—5.3
	Average	2.5 ± 2.9	2.6 ± 0.6	-13.5 ± 3.6	-3.5 ± 2.5
Mean difference (BW — EW)		-3.0 ± 4.1	0.9 ± 1.9	-2.6 ± 3.8	1.2 ± 3.2
Overall mean (BW + EW)		1.0 ± 2.0	3.0 ± 0.8	-12.2 ± 1.9	-2.9 ± 1.6

indirect (maternal) effect on hatchability. Most of the direct effect seems to be due to dominance and not to the average effect of genes. However, the most important effect of egg-size genes on hatchability seems to be through their maternal influence. Also, large-egg genes lower hatchability more than small-egg genes.

DISCUSSION

Model I of this study shows that both inbreeding and extremes in egg size reduce hatchability. This is not new information except for the relative magnitudes of the effects: egg size was more important than inbreeding. Thus, the kinds and proportions of genes left in the population after selection (genes for big eggs or little eggs) seem to influence fitness more than their state (homozygous or heterozygous).

Inbreeding was measured strictly as a characteristic of the embryo and not of the dam. This assumes that the zygote's genetic influence on hatchability is direct only; clearly, the zygote has no control over the size of the egg in which it develops. On the other hand, the dam's genetic influence on hatchability might be both direct or via egg size (maternal). Although WILSON (1948) reported that inbreeding of the dam was important, this is at variance with several others who found that inbreeding of the embryo was most important in depressing hatchability (BLOW and GLAZENER 1953; SHOFFNER 1947; DUZGÜNES 1950).

Fairly good agreement between sets of lines was obtained, but the actual selection practiced in each set differed. The BW lines were selected for extremes in body weight and the EW lines for extremes in egg weight. Since these traits are highly correlated, the high and low lines of both sets differed widely in egg size (FESTING and NORDSKOG 1967). The BW lines generally had poorer hatchability which suggests that genes for body weight are also a factor in poor hatchability.

Yet we were unable to demonstrate a statistically significant difference between the two sets of lines.

The single-locus model (Model II) is obviously an oversimplification. Yet except for epistasis, the results would not be altered by including many loci in the model. Ignoring epistasis is equivalent to assuming that effects of genes, including dominance, are additive over all loci. Even though this may not be strictly realistic, the assumption that gene effects are additive over loci may give a fair approximation to the true genetic mechanism. The question of multiple alleles poses no special problem except that some additional complexity would be required in the model.

From Model II we concluded that egg-size genes have both direct and indirect (maternal) influence on hatchability. The genetic mechanism of the direct effect is largely dominance underlying both inbreeding depression and the cross-line heterotic effects on hatchability. Yet the most important action of the egg-size genes on hatchability seemed to be indirect: through the phenotypic size of the egg itself. Incorporation of the control population into the model to estimate the hatchability of optimum egg size made it possible to compare the effects of large-egg *vs.* small-egg genes. The results suggested that large-egg genes depress hatchability much more than small-egg genes.

The dominance effect is assumed to be due entirely to changes in gene frequency brought about by selection. This assumption ignores random drift which could be especially important in small populations. This would tend to make each line different by random changes in gene frequency. If so, we might expect that the analysis of variance in Table 5 would show statistically significant interaction of Sets $\times$ Sire and Set $\times$ Dam lines; neither was significant. On the other hand, most of the treatment variation in hatchability was associated with dam-line differences (large *vs.* small) to which each set contributed. Thus, the "egg-size" effect of the line and not other possible unique line effects was the major factor. Therefore, we believe that most of the dominance was due to changes in gene frequencies resulting from selection and not from random genetic differences between the lines.

The validity of assuming that genes with a direct effect on hatchability show dominance while those with a maternal effect are purely additive may be questioned. This assumption was made in the interests of a simple workable model. If a dominance term were included, a maternal effect, in terms of gene frequency change, would not be estimable.

Hatchability is clearly a fitness trait, and as such, we expect it to show inbreeding depression and heterosis in a cross. Our results and others reported in the literature bear this out. On the other hand, most studies on egg size show that when a large-egg line is crossed with a small-egg line, the progeny have intermediate egg size. This is not proof that genes for large eggs or small eggs are strictly additive in their effects. But clearly if genes for large eggs were all dominant and genes for small eggs were recessive at all loci (or *vice versa*), the progeny of a cross would not be intermediate. Thus the only way we could have dominance of egg-size genes with an intermediate phenotype from a cross of extremes would be if both large-egg and small-egg genes showed dominance.

The net effect would be essentially the same as a model of no dominance.

The alternative solution would be to include in the model only a phenotypic egg-size effect as deviations from an optimum. In essence, such a phenotypic deviation effect was used in Model I but with no explicit assumption regarding the genetic mechanism determining the phenotypic deviation. The gene action on a primary scale (effects on egg size) could have any level of dominance or no dominance. However, the effect of these genes on a secondary scale (effects on hatchability) would require an assumption of epistasis.

We appreciate the helpful statistical services and advice from Dr. DAVE COX and Dr. ED POLLAK of the ISU Statistical Laboratory. Also Dr. B. B. BOHREN, Department of Animal Science, Purdue University, offered useful suggestions in the analysis and interpretation of the single-gene model.

SUMMARY

From five years of data on four Leghorn lines selected up and down for body weight and for egg weight and from crosses between them, the decline in hatchability from selection for extremes was analyzed into a phenotypic egg-size component and an inbreeding depression component, using a multiple regression approach (Model I). In addition, a single-locus theoretical model was used to study the direct and indirect (maternal) effects of egg-size genes on hatchability. The estimated decline in hatchability was 2.6% for each 10% increase in inbreeding. Hatchability was maximal for an egg weight of about 50 grams. Results from the single-locus model showed that egg-size genes have an over-dominant direct effect on hatchability. However, the most important effect of egg-size genes on hatchability was indirect (maternal). Also the maternal effect was asymmetrical: genes for large egg size depressed hatchability more than genes for small size. A 10 gram increase in egg size above the optimum lowered hatchability 10.7%, while a 10 gram decrease lowered it only 3.9%.

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