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BREEDING AND GENETICS

Effectiveness of Progeny Test Multiple-Trait Index Selection for Field Performance of Strain-Cross Layers. I. Estimated Responses[1]

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ABSTRACT Selection for egg production and egg quality traits in five Leghorn strains was based on pedigreed strain-cross (TX) progeny performance. About 24,000 TX pullets from 400 sires and 2400 dams were tested at 20 to 40 locations each year from 1956 through 1969. The TX pullet performance averages for 16 traits were combined in a linear index to evaluate sires in male lines and dams in female lines. Dams in male lines and sires in female lines were evaluated on the basis of full-sibs' progeny. Selection emphasis was primarily on rate of lay, viability, and egg size and secondarily on age at first egg, body size, egg shell and internal quality, temperament, and fertility. Each pair of pedigree crosses (TX1 or TX2) of one male line with two female lines was represented in a commercial cross (CX1 or CX2) of one male line with line-cross females. Generation lag from TX to CX equalled about 2 years of relaxed selection. Genetic changes for TX, CX, and control strain (C) were estimated as phenotypic deviations from environmental trends measured by repeating the same generation and age of C breeders in consecutive years.

Yearly genetic gains in economic index per bird from 1956 to 1969 in TX1, to 1968 in TX2, to 1967 in CX1 and CX2, and to 1966 in C were $.16, .18, .08, .11, and .10, respectively. Corresponding environmental trends averaged $-.13, -.11, -.14, -.14, and -.13 per year. Average yearly genetic gains for TX pullets exceeded those for CX pullets in adult mortality (-1.8 *vs.* -.5%), rate of lay (.50 *vs.* .17%), total eggs (2.9 *vs.* .8 eggs), and egg weight (.18 *vs.* .11 g) but were similar for other traits. Yearly genetic gain for total eggs and rate of lay accelerated significantly in TX pullets but not in CX pullets, possibly because TX response was measured for selection applied 3 or 4 years later than that for CX response. Contemporary superiority of TX over CX pullets was large for economic index ($.49), adult mortality (-5%), total eggs (12), and rate of lay (2.4%). When adjusted for the 2-year generation lag of CX, remaining superiority of TX over CX from temporary effects of pedigree selected parents and of pure line instead of line-cross dams was reduced to $.15 in economic index, -1.5% in adult mortality, 5.7 in total eggs, and 1.3% in rate of lay.
(*Key words:* poultry, selection response, egg production, strain crosses, field performance)

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INTRODUCTION

The system of selection evaluated in this report was designed to improve economic performance of widely distributed commercial stocks of egg-production chickens. For this purpose, direct selection for a multiple-trait index of strain-cross progeny performance under a random sample of commercial environments was expected to be more effective than index or culling level selection for pure strain individual and family performance in a single location environment.

Commercial egg producers consider many components of performance in evaluating a breeder's product. A linear index can use relative economic importance and the genetic and phenotypic variances and covariances for component traits of individuals and relatives to maximize accuracy of selection for net breeding value (Hazel, 1943; Lush, 1947; Osborne, 1957; Henderson, 1963). The expected advantage of index over culling level selection is greater when more traits (or relatives) must be considered and when there are important negative genetic associations among component traits (Hazel and Lush, 1942; Young, 1961).

In populations subjected to intensive individual and family selection for several traits over many generations, rate of response may

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diminish because of reduced independent additive genetic variation of traits and residual negative covariation of traits. If some degree of dominance exists for individual traits, there may even be higher degrees of dominance for multiplicative total performance and semi-plateau at equilibrium gene frequencies under continued selection (Hull, 1945, 1952; Crow, 1948, 1952; Dickerson, 1952, 1955).

Direct strain-cross progeny-test selection to maximize heterozygosity at overdominant loci between complementary populations was first proposed by Hull (1945) for recurrent selection with a homozygous line or F_1 cross as the constant tester stock. This approach was extended to cycles of reciprocal selection between two segregating populations by Comstock *et al.* (1949) to utilize both additive and non-additive genetic variance. Effectiveness expected from use of inbred and partly inbred lines and of F_1 crosses of partly inbred lines as constant tester parents was examined by Dickerson (1952) and verified by Crow (1953).

Experimental evaluation of direct selection for strain-cross performance (RRS) has been most extensive in *Drosophila* (Bell *et al.*, 1955; Rasmusson, 1956; Bowman, 1962), in *Tribolium* (Bell, 1972), and in mice (Bowman, 1962), but some evidence is available from experiments with swine (Dickerson *et al.*, 1974) and poultry (Saadeh *et al.*, 1968; Heisdorf, 1969). In general, experimental results indicate that: 1) RRS is less effective than within line selection (WLS) for improving nonheterotic traits of at least moderate heritability, but RRS gradually becomes more effective than WLS for heterotic traits of low heritability, especially in populations long selected on within-line performance; 2) RRS improves nonadditive superiority, but WLS improves additive superiority and thus, the additive performance of parental purebred lines is lower from RRS than from WLS selection; 3) unfavorable additive genetic correlations cause more adverse correlated responses from additive WLS selection than from nonadditive RRS selection and thus increase further the total performance advantage of RRS cross over WLS pure line response.

Interaction of genotypes with unpredictable variation in production environment is important for health-influenced traits such as mortality, rate of lay, and age at first egg (Dickerson, 1962). The RRS selection for average adaptability to, or tolerance of, environmental variation may increase selective advantage of heterozygosity at dominant loci above that for selection within a single environment (Lerner, 1954; Dickerson, 1955, 1963; Comstock, 1960).

The industrial trial reported here began in 1956, at a time when considerable evidence indicated meager response to continued conventional selection for increased egg production (e.g., Lerner and Hazel, 1947; Dickerson, 1955, 1964; Nordskog *et al.*, 1967). The procedures followed were designed to evaluate response in most important components of egg production under representative field environments from 1) multiple-trait index selection for average strain-cross progeny performance across random flock locations and from 2) index selection for individual and family pure strain performance at one location. Responses and levels of field performance also are compared for the pedigreed crosses and the corresponding commercial crosses used by producers. In a companion paper (Bennett *et al.*, 1981), realized responses in pedigreed crosses were compared with those predicted from selection actually applied.

EXPERIMENTAL PROCEDURE

Field Testing. Data for this study were collected at field locations from years 1956 to 1969, inclusive. Pullets produced were from Single Comb Leghorn stock. Five strains (1, 2, 4, 5 and 6) were involved in producing pedigreed pullets of four single crosses. Pullets were pedigree-hatched during 24 weeks each year in four periods of 5 weeks each. Hatching was restricted to December through May to coordinate with seasonal requirements for pedigree reproduction of grandparent lines for parent stock production.

Numbers used during each of four 5-week periods were 60 strain 4 males × 360 females in each of strains 2 and 5 (TX1) and 30 strain 6 males × 180 females in each of strains 1 and 4 (TX2). Each set of females was tested during two consecutive periods (1 and 2 or 3 and 4) in order to obtain a reasonable number of progeny per dam and to reduce confounding of dam effects on progeny with transmitted effects of the male to which she was mated. Females of each strain were distributed randomly among the single-sire pens of the appropriate male line.

In each of five weekly hatches, about 50 pullets from each of the two corresponding commercially distributed three-strain crosses

(CX1 = L4♂× L2·L5♀ and CX2 = L6♂× L1·L4♀) and of the two "repeat mating" control groups (CC and CR) were placed with pullets of the four single crosses at field locations equipped with either single- or multiple-bird cages.

The four single crosses were produced from single-sire pens, whereas the pure-strain control and commercial pullets were from flock matings. The commercial product samples were hatched from the latest generation of single-cross parent stock females available during the hatching season of pedigreed matings. Chicks of all mating groups were wing banded for identification.

Pullets from each group were randomly distributed among 5 to 14 field locations for each period by assigning chicks from each weekly hatch to a subsample of locations. In order to test pullets hatched from each sire, dam, or other breeding groups on a given date under the same sample of environments, pullets from each such group were randomly distributed among locations. No attempt was made to control the management practices (e.g., lighting, feeding, housing, or vaccination) at any location. It was not uncommon to have age groups from more than one hatching period in separate housing at the same location. Management practices varied from very good to fair among locations.

Repeat matings of a pureline control strain (Goodwin *et al.*, 1960; Dickerson, 1969) were used to estimate environmental changes between years. Control strain chicks were pedigree hatched from contemporary matings of unselected 1-year-old male and female breeders produced the previous year from 1-year-old (current, CC) and from 2-year-old (repeat, CR) selected parents. Pedigree hatching of CC chicks provided an opportunity to remove breeders whose parents were not available for repeat mating as 2 year olds because of mortality or poor fertility and hatchability. Change in mean performance from current generation controls of one year to repeat generation controls of the next year (CC_t to CR_{t+1}) provided an intrageneration estimate of yearly environmental changes and permitted estimation of genetic changes in the selected lines and crosses.

Beginning with the 1966 hatching season, control pullets were from one of the strain crosses rather than from the pure strain. Performance of the repeat mating strain-cross control was essentially equal to that of the pedigreed crosses and was expected to measure effects of environmental change on performance of the selected crosses more accurately than the pure strain repeat mating controls. The current and repeated generations of strain-cross pullets were produced by mating strain 4 males with strain 2 females. When these chicks were not needed as controls in field tests, they could be sold as commercial chickens, reducing the cost of the control procedure for measuring response from selection below that for maintaining a separate control population. Each year about 90 strain 4 males, one per trap family, were mated with about 400 females of strain 2. Then, survivors of these 90 strain 4 males were mated the next year as 2 year olds to 1-year-old pullets of the corresponding repeated generation of strain 2. Each year, about 120 strain 2 pullets, one per trap family, were mated with 16 strain 2 males, one per sire group of trap families, to produce 400 females of strain 2. Surviving parents were remated as 2 year olds to produce a second set of 1-year-old strain 2 pullets for the repeat-generation matings with the 2-year-old strain 4 males. The use of 2-year-old males to produce the repeated generation of strain-cross control chicks was a deviation from the earlier procedure in which only cockerel and pullet breeders were used to produce both current and repeated generations of the pure-strain control chicks.

Between 18 and 20 weeks of age, the surviving pullets at each single-cage location were badged in random order and distributed to individual (20 × 30 cm) cages. Wing bands were removed from all dead pullets and used for posting mortality. Any live pullets without wing bands at the time of housing could not be separated from missing birds and, therefore, were excluded in calculating mortality to 20 weeks of age and from other records.

At multiple-cage locations, sets of three or five half-sib pullets from each of the four single crosses were housed together. These sets were distributed to cages at random along with the samples of commercial crosses and control pullets. Only mortality and cannibalism data were obtained at the multiple-cage locations. From 10 to 20% of all birds were placed at multiple-cage locations.

Participating cooperators were encouraged to maintain accurate performance records by an

incentive program. Chicks were provided without charge, and cooperators were paid 25 cents for each pullet surviving to 72 weeks of age. Egg production records were recorded on specially designed cards mounted on each cage. Field supervisors gathered mortality and production records and samples of eggs for egg quality measurements during their monthly visits to the cooperator's farm. Any abnormal condition which might affect performance adversely was recorded: e.g., outbreaks of disease, changes in feed, or other factors affecting mortality or rate of production.

Selection Procedure. Location-hatch effects on performance were removed by subtracting the location mean deviation from the standard mean of each trait for all individual records at each location. The set of standard means used for this adjustment was the same as that for the expected average selection index. All data were adjusted for location-hatch effects before use in calculating progeny-test selection indexes for their sires and dams.

The list of traits with their accepted ranges, economic weightings, and heritability estimates used to derive the linear selection indexes are shown in Table 1 (see Emsley *et al.*, 1977). Selection indexes were revised three times since first used in 1955, each time to recognize changes in relative economic importance (a_i) and in estimates of the genetic paramenters (h^2 = heritability; $r_{G_{ij}}$ = genetic correlation; $\sigma^2_{p_i}$ = phenotypic variance; $r_{P_{ij}}$ = phenotypic correlation, for individuals and for sire and for

TABLE 1. *Economic weighting ($/unit) and heritability estimates (h^2) used to derive selection indexes, by year of index revision*[a]

Trait	Unit	Range	1955		1957		1962		1965	
			$/unit	h^2	$/unit	h^2	$/unit	h^2	$/unit	h^2
Fertility (FERT)	1%	0–100	.007	.07	.008	.14	.008	.09	.008	.20
Hatchability (HTCH)	1%	0–100	.007	.15	.008	.18	.008	.04	.008	.13
2 X cull ♀ (CULL)	1%	0–100	−.007	.15	−.008	.34	−.008	.12	−.008	.25
Mortality										
0–20 weeks (EMRT)	1%	0–100	−.02	.08	−.03	.06	−.012	.04	−.012	.01
21–72 weeks (AMRT)	1%	0–100	−.05	.08	−.05	.09	−.025	.09	−.025	.06
Broody (BROD)	1%	0–100	−.043	.09	−.043	.09	.....	....	.....	....
Age first egg (AGE1)	1 week	16–34	−.10	.36	−.10	.30	−.16	.58	−.140	.45
% Production (PR72)[b]	1%	10–100	.09	.30	.09	.16	.11	.20	.150	.21
Excitability[b] (EXCT)	1 Sc	1–3	....	...	−.75	.16	−.50	.15	−.300	.20
At 32 weeks										
Body weight (BDWT)	.045 kg	.9–3.2	−.038	.36	−.03	.30	−.035	.50	−.035	.53
Egg weight (EGWT)	1 g	35–70	.05	.49	.05	.50	.085	.53	.100	.57
Shell strength[c] (SPGR)	.1 Sc	0–9	.005	.36	.015	.43	.008	.32	.020	.34
Shell shape[d] (SHAP)	.1 Sc	2–8	−.009	.25	−.009	.30	−.005	.37	−.005	.27
Albumen score[e] (HU)	1 HU	50–120	.02	.36	.015	.40	.02	.29	.012	.32
Blood spots (BLOD)	1%	0–100	−.072	.09	−.08	.09	−.04	.13	−.036	.05
Shell color[f] (COLR)	.1 Sc	0–9	−.02	.10	−.045	.15	−.050	.43	−.050	.60
Early texture[g] (ETEX)	.1 Sc	0–9	−.02	.10	−.075	.28	−.050	.11	−.050	.06
Mature texture[a,g] (MTEX)	.1 Sc	0–12	....	...	.....	...	−.100	.14	−.100	.10

[a]Heritability of individual bird observations, except that fertility, hatchability, and culls were for all eggs set from each hen, and egg quality traits were for a 4-day sample (one to four eggs per bird) at about 32 weeks of age, or at about 60 weeks of age for mature texture.

[b]Percent production from first egg to 72 weeks of age or prior death. Excitability was average of four scores taken before 40 weeks of age; 1 < average, 2 = average; 3 > average response to striking top of individual cage.

[c]Specific gravity (shell strength) scored 0 to 9; 0 = 1.054; 9 class intervals of .004.

[d]Shell shape score was 10 X [(length/diameter) − 1].

[e]Albumen score was in Haugh units (HU) except in 1957 when albumen height (.1 mm units) was used.

[f]Color score: chalk white = 0 to dark brown = 9.

[g]Sum of scores (0 − 3) each for defects in 1) roughness; 2) wrinkles; 3) asymmetry; 4) cracks. Range: 0 = no defects to 12 = maximum defects.

dam progeny means). In general, economic importance for rate of lay, egg size, sexual maturity, shell strength (specific gravity), and texture was increased and that for mortality, excitability, and other egg quality traits was reduced over time.

Relative or "scorecard" weightings of traits included in the sire and dam progeny indexes are shown as percentages in Table 2. These weightings were calculated by summing the standardized partial regressions of aggregate breeding value (H = sum of $a_i \times G_i$ for individual performance over all traits included) on sire (or dam) progeny means ($\bar{P}$) for each of the component traits, ignoring signs. Order of emphasis in selection of tested sires and dams was: higher rate of lay, lower mortality, earlier maturity, larger eggs, smaller body size, whiter shells, and fewer blood spots. Relative emphasis changed considerably when index weightings were revised. Generally, emphasis increased over time for rate of lay, egg size, shell shape, color, and texture but declined for mortality, sexual maturity, excitability, blood spots, and shell strength.

The numbers of males and females selected for strain-cross progeny testing and for pure strain reproduction are shown in Table 3. The selection of tested males to reproduce parent strains 4 and 6 was entirely on their own strain-cross progeny performance. Families of strain 6 females were selected on their brother's strain-cross progeny performance, excluding only females whose individual performance was well below the mean of their full-sisters. Tested females of strains 1, 2, 4, and 5 were selected on the basis of their own and full sisters' strain-cross progeny performance. Males of strains 1, 2, and 5 were selected on the basis of mean strain-cross progeny performance of their full sisters.

Three summaries of strain-cross progeny performance were obtained during the laying year, grouping together consecutive pairs of 5-week hatching periods (1 + 2 and 3 + 4). Records were summarized when birds averaged

TABLE 2 *Relative scorecard weighting (%)[a] of traits included in sire and dam test cross progeny indexes, by year of index revisions*

	Sire index weightings (%)				Dam index weightings (%)			
Trait[b]	1955	1957	1962	1965	1955	1957	1962	1965
FERT	1.2	1.3	.7	2.7	1.4	.9	1.0	.1
HTCH	.3[c]	.8	− 1.1	− 1.0	2.0[c]	.9	− 1.5	− 1.6
CULL	.....	− 1.3	.5	− 2.0	.....	− 1.1	− 2.7	− 3.9
Mortality								
EMRT	− 8.7	−11.3	− 2.4	.5	− 7.8	−12.8	− .5	.5
AMRT	−23.7	−29.1	− 2.7	− 4.9	−20.9	−26.9	− 7.3	− 2.4
BROD	− 8.2	− 6.1	.....	.....	− 7.4	− 5.6	.....	.....
AGE1	− 8.0	− 4.1	−14.7	− .6	− 8.2	− 4.3	− 7.6	4.3
PR72	22.1	15.9	13.7	24.1	26.3	14.1	12.7	18.0
EXCT	.....	− 6.5	− 3.2	− 3.4	.....	− 7.5	− 1.9	− 1.5
At 32 weeks								
BDWT	− 6.2	− 2.6	− 6.9	− 3.0	− 6.5	− 1.4	−11.6	− 8.6
EGWT	5.6	3.0	11.0	7.3	3.1	1.6	7.9	9.4
SPGR	1.2	4.3	2.1	− .7	1.4	2.6	2.4	− 3.6
SHAP	− 3.8	− 1.3	− 5.2	−11.2	− 4.0	− 2.1	− 7.0	−11.8
HU	1.3	6.6	2.2	6.3	2.7	9.1	8.2	7.8
BLOD	− 8.8	− 2.1	− 5.0	1.1	− 7.4	− 3.4	− 2.5	.6
COLR	− .5	− 2.5	−11.0	−14.5	− .5	− 3.9	−16.2	−16.1
ETEX	− .4	− 1.2	− 3.5	− 3.8	− .4	− 1.8	− 1.0	− 4.0
MTEX	.....	.....	−14.1	−12.9	.....	.....	− 8.0	− 5.8
Total[a]	100	100	100	100	100	100	100	100

[a]Standard partial regressions of index on traits are coded so that the sum of absolute values, ignoring sign, equals 100.

[b]For complete descriptions of traits, see items under "Trait" in Table 1.

[c]HTCH - CULL.

TABLE 3 *Number of individuals and families of pure strain breeders per year, by strain, sex, category, and age of parents*

Category	Age of parents	4	2,5		6		1	1,4
		Males	Males	Females	Males	Females	Males	Females
Progeny tested	All	240	0	720	120	0	0	360
Parents of	1 year	30[a]	60[a]	720	0	0	30[a]	360
pure strain	2 years	12	18	180	8	60	8	90
progeny	3 years	12	12	120	7	40	8	60
Full-sib	1 year	...	...	60	...	0	...	30
families	2 years	...	...	90	...	60	...	45
trapped	3 years	...	...	120	...	35	...	60
Selected	1 year	0	...	60	0	0	...	30
full-sib	2 years	60	...	120	30	65	...	60
families	3 years							
Individuals	1 year	0	0	240	0	...	0	120
selected for	2 years	240	0	480	120	...	0	240
test crossing	3 years							

[a] 1- or 2-year-old males.

40 weeks and 60 weeks of age, and 72 weeks for each hatch. The 40-week strain-cross summary was used for initial selection of 2-year-old breeders to reproduce the pure strains and of their 1-year-old pure-strain pullet progeny for use in one-third of the strain-cross matings. The 60-week strain-cross summary for parents was used to choose the best one-half of the pure-line pullet families from 2-year-old parents to be trapnested. The 72-week strain-cross summary was used to choose 3-year-old tested parents to produce trapnested families of pure-strain progeny and also to select 1-year-old pure strain families from both 2- and 3-year-old parents for two-thirds of the next cycle of strain-cross matings.

All pullets of strains 1, 2, 4, and 5 used in strain crosses were immediately remated to reproduce pure strains. In addition, about one-fourth of the 2-year-old and one-sixth of the 3-year-old dams of lines 1, 2, 4, and 5 with strain-cross progeny were chosen for pure strain matings.

Pure strain families of 1-year-old pullets chosen for use in strain crosses represented about one-twelfth of those from 1-year-old dams (based on 40-week strain-cross summary) and four-tenths of those from 2- and 3-year-old dams (based on 72-week strain-cross summaries). Only about one-half of the pure-line pullets in families chosen for strain-cross matings were actually used; these were selected for individual superiority in egg quality traits and over 50% rate of early production.

The control strain used for unselected repeat-generation estimates of environmental change at field locations was itself reproduced from selected 1-year-old parents each year. Selection differed in that it was based on only pure strain performance in floor-pen housing at the central breeding farm. The index used to select 15 to 20 cockerel breeders on the part-year performance of their full sisters was similar to that described (Table 2) for selection of tested dams on field performance of their progeny, except that no records beyond 60 weeks of age were used in selection. Indexes for selecting 150 to 200 pullet breeders on early performance and 110 to 150 dams of trapnested families on 60-week performance included appropriate weightings for both individual and family performance. The generation interval for the control strain was 1 year, but that for strains selected on field strain-cross progeny performance was about 2.5 years.

Estimation of Genetic Change. Estimates of genetic and environmental trends were obtained by the repeat mating control procedure for all traits included in selection indexes (Table 1). Response to selection was estimated for all traits in the pedigreed strain-crosses (TX1 and TX2 in Tables 4 and 5), the corresponding commercial crosses (CX1 and CX2 in Tables 6 and 7), and the control strain (CC in Table 8). Average linear estimates of annual genetic (b_{GY}) and environmental (b_{EY}) change, partial

TABLE 4. *Phenotypic (P), environmental (E), and genetic (G) trends for pedigreed TX1 strain-cross birds and their mean superiority over commercial CX1 crosses* ($\bar{\Delta} = \bar{TX} - \bar{C}_{TX} - \bar{CX} + \bar{C}_{CX}$), *1956-1969*

	TX1 phenotypic		Control environmental				TX1 genetic				
	Mean	Linear	Mean	Linear	Partials		Mean	Linear	Partials		
Trait[a]	$\bar{P}$	b_{PY}	$\bar{E}$	b_{EY}	b'_{EY}	b'_{EY^2}	$\overline{\Sigma\Delta G}$[b]	b_{GY}	b'_{GY}	b'_{GY^2}	$\bar{\Delta}$
FERT	85.4	2.07	92.4	−.17	−3.24	.4377	−7.0	2.24	4.02	−.2554	−11.36
HTCH	92.3	−.05	88.8	.76	2.82	−.2943	3.5	−.81	−3.61	.3994	.77
CULL	2.5	−.01	4.9	−.27	−.07	−.0277	−2.4	.26	−.33	.0846	.57
Mortality											
EMRT	6.7	.20	13.9	.83*	.03	.0533	−7.2	−.63	−.96	.0219	−.17
AMRT	18.3	−.28	32.4	1.65*	−.70	.1569	−14.1	−1.93**	−.60	−.0884	−5.28
AGE1	23.7	.02	24.0	.05	.24	−.0127	−.3	−.03	.13	−.0111	−.24
PR72	68.5	.17	63.0	−.22	.38	−.0399	5.5	.39†	−.68	.0715†	2.53
EGGS[c]	218.6	1.21	192.0	−1.33	2.55	−.2587	26.6	2.54*	−2.25	.3197†	11.80
EXCT	1.9	0	2.0	.001	.04	−.0031	−.1	−.001	−.05	.0039*	.023
At 32 weeks											
BDWT	3.8	−.016	3.7	.004	.06	−.0046*	.1	−.019†	−.01	−.0004	−.023
EGWT	54.2	−.07	49.1	−.27**	−.02	−.0171	5.1	.20**	.09	.0068	.045
SPGR	5.4	.07	5.7	.06*	.26	−.0149*	−.3	.01	.08	−.0052	.152
SHAP	4.5	−.021	4.4	.004	−0	.0004	.1	−.025*	0	−.0020	−.053
HU	88.1	.23	84.3	−.25	−.21	−.0034	3.8	.48*	.65	−.0130	.415
BLOD	2.6	−.22	3.3	.03	.90	−.0665	−.7	−.25	−1.26	.0775*	−.29
COLR	.1	−.020	.4	.072**	.11	−.0027	−.3	−.052**	−.08	.0018	.022
ETEX	.11	−.001	.1	−.000	.06	−.0044	.01	−.001	0	−.0003	−.015
MTEX	.9	−.150	.8	−.084*	−.03	−.0028	.1	−.066	−.21	.0104**	−.033
ECON[d]	7.28	.027	5.52	−.135**	−.11	−.0017	1.76	.162**	.08	.0056	.504

[a] For complete descriptions of traits, see items under Trait in Table 1.

[b] $\overline{\Sigma\Delta G}$ is mean phenotypic deviation of selected population from environmental trend for the control strain, $\bar{P} - \bar{E}$.

[c] Total eggs per hen housed to 72 weeks of age or to prior death.

[d] Sum of component traits weighted by economic values for 1962 in Table 1, omitting FERT, HTCH, CULL, and MTEX.

† $P<.10$.

* $P<.05$.

** $P<.01$.

TABLE 5. *Phenotypic (P), environmental (E), and genetic (G) trends for pedigreed TX2 strain-cross birds and their mean superiority over commercial CX2 crosses* ($\bar{\Delta} = \bar{TX} - \bar{C}_{TX} - \bar{CX} + \bar{C}_{CX}$), *1958-1968*

	TX2 phenotypic		Control environmental				TX2 genetic				
	Mean	Linear	Mean	Linear	Partials		Mean	Linear	Partials		
Trait[a]	$\bar{P}$	b_{PY}	$\bar{E}$	b_{EY}	b'_{EY}	b'_{EY^2}	$\bar{\Sigma\Delta G}$[b]	b_{GY}	b'_{GY}	b'_{GY^2}	$\bar{\Delta}$
FERT	83.6	1.03	90.3	−.19	−3.27	.4398	−6.7	1.22	.34	.1265	−13.64
HTCH	87.45	−.53	88.8	.75	2.74	−.2839	−1.35	−1.28	−4.28	.4275	−3.84
CULL	4.02	.22	4.9	−.24	.04	−.0403	−.88	.46	−.49	.1352	1.43
Mortality											
EMRT	6.8	−.13	17.0	.67	−.44	.0694	−10.2	−.80**	−1.00	.0124	.31
AMRT	18.1	−.19	33.8	1.39	−4.70	.3805†	−15.7	−1.58†	2.43	−.2509	−4.75
AGE1	23.5	−.04	24.2	.06	.28	−.0139	−.7	−.10	−.07	−.0020	−.24
PR72	71.0	.41	61.8	−.19	.41	−.0377	9.2	.60*	−.80	.0875†	2.22
EGGS[c]	229.3	1.99	190.4	−1.35	5.90	−.4529†	38.9	3.34*	−5.03	.5230*	11.40
EXCT	1.8	−.003	1.9	−.006	.06	−.0044	−.1	.003	−.08	.0053*	−.007
At 32 weeks											
BDWT	4.0	−.03	3.8	−.01	.01	−.0015	.2	−.02	−.02	−.0001	−.002
EGWT	53.1	−.22	49.1	−.39**	1.05	−.0901**	4.0	.17†	.31	−.0091	.130
SPGR	5.1	.01	5.9	.05	.48	−.0286**	−.8	−.04	−.18	.0097	.097
SHAP	4.3	−.02	4.2	.01	.11	−.0064	.1	−.03†	−.10	.0051†	−.036
HU	87.5	.35	84.0	−.25	−1.45	.0802	3.5	.60**	1.82	−.0816	.223
BLOD	2.4	−.27	4.3	−.40	−1.64	.0826	−1.9	.13	.05	.0055	−.62
COLR	.2	.016	.5	.069**	.15	−.0053	−.3	−.053**	−.17	.0077**	−.043
ETEX	.2	−.009	.1	−.005	.06	−.0044	.1	−.004	.01	−.0011	−.017
MTEX	1.0	−.094	.9	−.073*	−.14	.0040	.1	−.021	−.17	.0087†	−.063
ECON[d]	7.44	.064	5.28	−.113**	.14	−.0161	2.16	.177**	.04	.0083	.482

[a,b,c,d] As in Table 4.

† $P \leq .10$.

* $P \leq .05$.

** $P \leq .01$.

TABLE 6. *Phenotypic (P), environmental (E), and genetic (G) trends for commercial CX1 strain-cross birds, 1956-1967*

	CX1 phenotypic		Control environmental				CX1 genetic			
	Mean	Linear	Mean	Linear	Partials		Mean	Linear	Partials	
Trait[a]	$\bar{P}$	b_{PY}	$\bar{E}$	b_{EY}	b'_{EY}	b'_{EY^2}	$\overline{\Sigma\Delta G}$[b]	b_{GY}	b'_{GY}	b'_{GY^2}
FERT	96.5	.64	92.1	−.30	−3.93	.5183	4.4	.94	7.00	−.8659
HTCH	89.6	−.09	86.8	0	4.20	−.6003	2.8	−.09	−3.13	.4351
CULL	5.4	.17	5.7	.37	−1.84	.3157	−3.0	−.20	2.54	−.3911
Mortality										
EMRT	9.3	.88	15.8	1.08†	−.91	.1528	−6.5	.20	−6.00	.4770*
AMRT	22.6	−.35	29.4	.31	−.55	.0660	−6.8	−.66	−3.21	.1964
AGE1	24.03	.08	24.04	.04	.10	−.0040	−.01	.04	.07	−.0019
PR72	64.9	−.38	62.6	−.46†	.22	−.0530	2.3	.08	.38	−.0228
EGGS[c]	200.6	−1.48	189.3	−2.02	3.11	−.3945	11.3	.54	3.58	−.2341
EXCT	1.9	.09	2.0	.032*	.02	.0006	−.1	−.023**	−.06	.0026
At 32 weeks										
BDWT	3.8	−.02	3.7	−.01	.05	−.0047†	.1	−.01	−.02	.0009
EGWT	54.5	−.07	49.7	−.18*	−.01	−.0129	4.8	.11	.14	−.0026
SPGR	5.3	.10	5.7	.09*	.24	−.0117	−.4	.01	.01	.0000
SHAP	4.5	−.02	4.4	−0	−.02	.0014	.1	−.02†	0	−.0017
HU	87.6	.33	84.3	−.27†	−.64	.0286	3.3	.60**	.07	.0404
BLOD	3.3	−.06	3.7	−.04	.35	−.0300	−.4	−.02	−.37	.0273
COLR	.2	.03	.4	.077**	.09	−.0009	−.2	−.053**	−.05	−.0004
ETEX	.12	.001	.10	.000	.05	−.0040	.02	.001	.02	−.0016
MTEX	.9	−.12	.8	−.099*	−.21	.0067	.1	−.018	−.01	−.0005
ECON[d]	6.7	−.065	5.6	−.145**	−.07	−.0052	1.1	.077*	.26	−.0138

[a,b,c,d] As in Table 4.

† $P \leq .10$.

* $P \leq .05$.

** $P \leq .01$.

TABLE 7. *Phenotypic (P), environmental (E), and genetic (G) trends for commercial CX2 strain-cross birds, 1956-1967*

	CX2 phenotypic		Control environmental				CX2 genetic			
	Mean	Linear	Mean	Linear	Partials		Mean	Linear	Partials	
Trait[a]	$\bar{P}$	b_{PY}	$\bar{E}$	b_{EY}	b'_{EY}	b'_{EY^2}	$\overline{\Sigma\Delta G}$[b]	b_{GY}	b'_{GY}	b'_{GY^2}
FERT	99.0	.99	92.1	−.28	−3.84	.5075	6.9	1.27	4.59	−.4742
HTCH	89.4	.48	86.9	.05	4.19	−.5914	2.5	.43	.57	−.0202
CULL	3.5	.47	5.7	.36	−1.82	.3114	−2.2	.11	1.66	−.2210
Mortality										
EMRT	6.59	−.17	15.7	.81	−2.13	.2258	−9.11	−.98†	−.81	−.0129
AMRT	21.4	−.12	31.4	.19	−.54	.0564	−10.0	−.31	−.40	.0065
AGE1	23.5	.08	24.0	.06	.14	−.0068	−.5	.02	.23	−.0159
PR72	67.2	−.33	61.1	−.60*	−.35	−.0193	6.1	.27	.57	−.0226
EGGS[c]	210.4	−.77	185.7	−1.75	4.48	−.4793†	24.7	.98	−.18	.0892
EXCT	1.9	.008	2.0	.026*	0	.0018	−.1	−.018*	−.03	.0011
At 32 weeks										
BDWT	4.0	−.02	3.8	−.01	.08	−.0064**	.2	−.01	−.04	.0020
EGWT	53.4	0	49.7	−.12†	.21	−.0257	3.7	.12†	−.10	.0169
SPGR	4.8	.11	5.7	.12*	.35	−.0175	−.9	−.01	.01	−.0014
SHAP	4.4	−.03	4.3	−.02	−.10	.0065	.1	−.01	.02	−.0023
HU	86.4	.35	83.7	−.28†	−.65	.0283	2.7	.63**	.62	.0007
BLOD	2.8	−.11	4.0	−.05	.41	−.0360	−1.2	−.06	−.53	.0363
COLR	.2	.023	.4	.076**	.08	−.0005	−.2	−.053**	−.06	.0007
ETEX	.2	.001	.1	−.003	.04	−.0031	.1	.004	.04	−.0030*
MTEX	.9	−.115	.8	−.099**	−.20	.0062	.1	−.016	0	−.0011
ECON[d]	6.9	−.032	5.4	−.140**	−.09	−.0039	1.5	.108**	.11	−.0001

[a,b,c,d] As in Table 4.

† $P \leq .10$.

* $P \leq .05$.

** $P \leq .01$.

TABLE 8. *Phenotypic (P), environmental (E), and genetic (G) trends for current CC generation control strain birds, 1956-1966 (weighted for deviations from TX1 ped crosses)*

	CC phenotypic		Control environmental				CC genetic			
	Mean	Linear	Mean	Linear	Partials		Mean	Linear	Partials	
Trait[a]	$\bar{P}$	b_{PY}	$\bar{E}$	b_{EY}	b'_{EY}	b'_{EY^2}	$\overline{\Sigma\Delta G}^{b}$	b_{GY}	b'_{GY}	b'_{GY^2}
FERT	93.2	−.18	92.4	−.17	−3.24	.4377	.8	−.01	.16	−.0245
HTCH	85.6	.02	88.0	.76	2.82	−.2943	−2.4	−.74	−.73	−.0025
CULL	5.9	.05	4.9	−.27	−.07	−.0277	1.0	.32	.24	.0125
Mortality										
EMRT	10.2	.13	12.8	.66	.01	.0541	−2.6	−.53	.56	−.0909
AMRT	24.8	.11	29.8	1.26	−2.27	.2941†	−5.0	−1.15	1.41	−.2136
AGE1	24.4	.12	23.9	.07	.21	−.0115	.5	.05	.38	−.0278*
PR72	65.0	.12	63.6	−.09	.65	−.0611	1.4	.21	−.11	.0262
EGGS[c]	200.4	.67	194.6	−.50	4.21	−.3922	5.8	1.17	−2.26	.2859
EXCT	1.87	0	1.9	.002	.05	−.0043	−.03	−.002	−.02	.0018
At 32 weeks										
BDWT	3.6	−.004	3.8	.006	.08	−.0058*	−.2	−.01	−.07	.0050†
EGWT	49.4	−.16	49.7	−.23*	.21	−.0362*	−.3	.07	−.48	.0459**
SPGR	5.0	−.04	5.7	.07*	.27	−.0167†	−.7	−.11**	−.35	.0196*
SHAP	4.3	−.02	4.4	−.01	.06	−.0060	−.1	−.01	−.03	.0010
HU	87.6	.09	84.6	−.38*	.51	−.0739	3.0	.47*	1.05	−.0479†
BLOD	2.0	−.16	4.3	.10	.89	−.0661	−2.3	−.26	−1.07	.0670†
COLR	.2	.033	.4	.077**	.09	−.0013	−.2	−.044**	−.09	.0038
ETEX	.15	0	.14	.002	.07	−.0057	.01	−.002	.01	−.0012
MTEX	.85	−.111	1.0	−.073	−.02	−.0047	−.15	−.038	−.05	.0010
ECON[d]	6.2	−.030	5.7	−.130**	−.03	−.0081	.5	.100**	−.04	.0116†

[a,b,c,d] As in Table 4.

† $P \leq .10$.

* $P \leq .05$.

** $P \leq .01$.

regression coefficients (b') on year and square of year for the fitted quadratic changes, and statistical significance are shown in Tables 4 through 8. Standard errors of regression coefficients on years were adjusted to include expected cumulative error contributions from genetic drift and estimated environmental change (see Bennett, 1980). The actual phenotypic trends (ΔP), estimated environmental trends (ΔE), and the genetic trends estimated as $\Delta G = \Delta P - \Delta E$ are shown for adult mortality, rate of lay, egg weight, and economic index in Figures 1 to 4 for TX1 and CX1, in Figures 5 through 8 for TX2 and CX2 and in Figures 9 through 12 for CC including the fitted quadratic genetic trend.

Numbers of pedigreed and commercial crosses were not exactly proportional at different locations, and the pedigreed TX2 crosses were not tested during the first 2 years. Hence, comparison between a pedigreed cross (TX) and its corresponding commercial cross (CX) was based on the mean ($\bar{\Delta}$) over all years in which

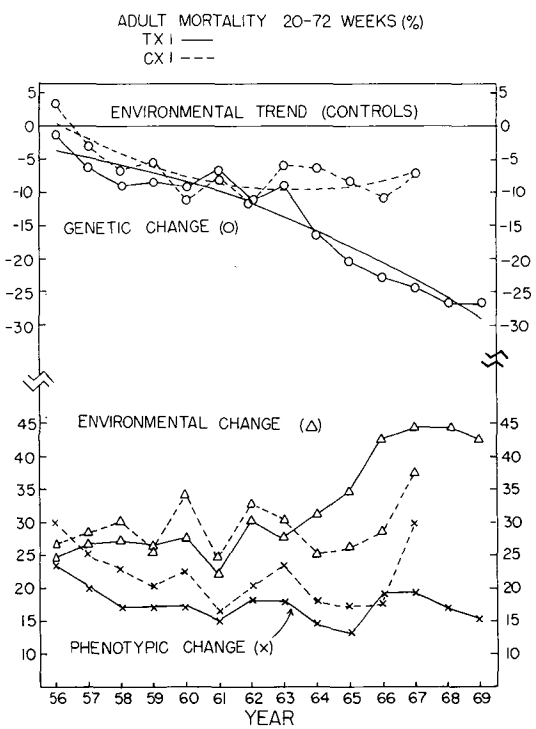

FIG. 1. Phenotypic (X), environmental (Δ), and genetic (o) changes in pedigreed TX1 (———) and commercial CX1 (-----) strain crosses for adult mortality. Smooth curves for genetic change are quadratic fit (AMRT in Tables 4 and 6).

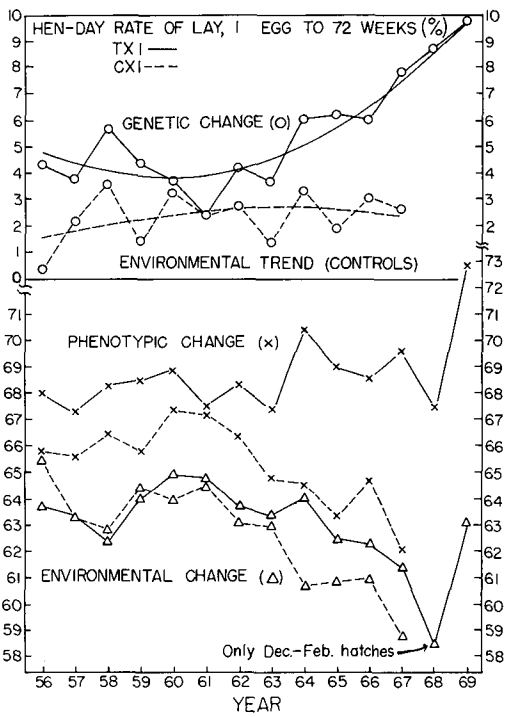

FIG. 2. Phenotypic (X), environmental (Δ), and genetic (o) changes in pedigreed TX1 (———) and commercial CX1 (-----) strain crosses for rate of lay. Smooth curves for genetic change are quadratic fit (PR72 in Tables 4 and 6).

complete information was available of individual year deviations (Δ_i) of TX and CX from the same controls, ΔTX for pedigreed and C_{CW} for commercial (i.e., $\Delta_i = TX - C_{TX} - CX + C_{CX}$ for 1 year). The C_{TX} and C_{CX} differed only in weighting of hatch locations within years. In order that the mean difference over years in accumulated genetic deviations from environmental trend ($\Sigma\Delta G_{TX} - \Sigma\Delta G_{CX}$) also should equal $\bar{\Delta}$, the appropriate adjustment would be $\alpha = \bar{\Delta} - (\Sigma\bar{\Delta}\bar{G}_{TX} - \Sigma\bar{\Delta}\bar{G}_{CX})$. Because cumulative changes in actual values of TX_i equal $\Sigma\Delta E_i + \Sigma\Delta G_i$, any adjustment added to $\Sigma\Delta G_i$ must be subtracted from $\Sigma\Delta E_i$. The adjustment can be added to $\Sigma\Delta G_i$ for TX or subtracted from $\Sigma\Delta G_i$ for CX or divided between them. This adjustment was appreciable only for TX2 because its field testing began in 1958, 2 years behind all other stocks. The same calculated average adjustment (α) was added to all $\Sigma\Delta G_i$ and subtracted from all $\Sigma\Delta E_i$ values in the TX1 or in the TX2 pedigreed crosses (TX) in Figures 1 to 8.

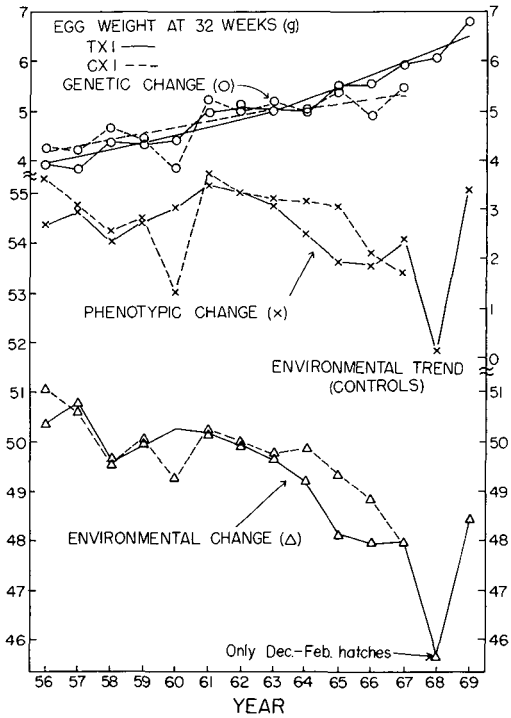

FIG. 3. Phenotypic (X), environmental (Δ), and genetic (o) changes in pedigreed TX1 (———) and commercial CX1 (-----) strain crosses for egg weight. Smooth curves for genetic change are quadratic fit (EGWT in Tables 4 and 6).

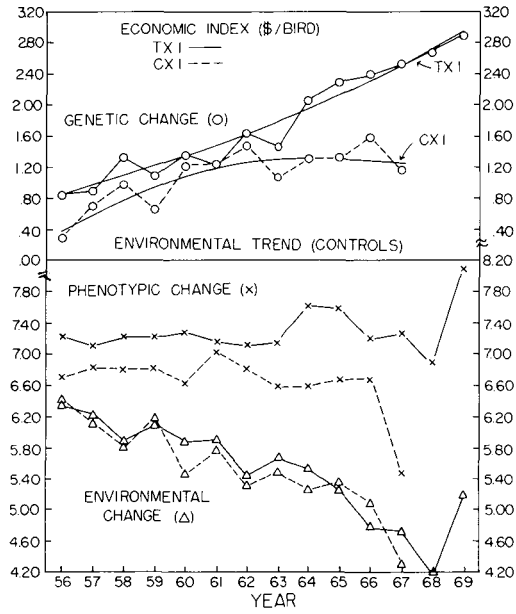

FIG. 4. Phenotypic (X), environmental (Δ), and genetic (o) changes in pedigreed TX1 (———) and commercial CX1 (-----) strain crosses for economic index. Smooth curves for genetic change are quadratic fit (ECON in Tables 4 and 6).

RESULTS AND DISCUSSION

Environmental Trends. Average environmental trends (b_{EY} in Tables 4 to 8 and Δ in Figures 1 to 12) were estimated separately for the TX1 and TX2 pedigreed, for the CX1 and CX2 commercial crosses, and for the CC selected control strain itself by weighting the current (CC) and repeated (CR) generation of the control at each location for a year, according to the inverse of the error variance, separately for its deviations from each of the selected populations ($w_i = \frac{n_1 \cdot n_2}{n_1+n_2}$). Thus, estimated average environmental change per year (b_{EY}) was expected to be similar for the five selected populations, except as their records included different years (e.g., beginning TX2 in 1958, ending CC in 1966, CX1 and CX2 in 1967, and TX2 in 1968) or different proportions distributed to locations within years (e.g., CX *vs.* TX crosses, especially in 1964 or later years).

Environmental trend (per year) was definitely ($P<.01$) unfavorable for economic index of TX1, TX2, CX1, CX2, and CC ($-.14, -.11, -.14, -.14, and -.13, respectively), because of increasing adult mortality (1.65, 1.39, .31, .19, and 1.26%), declining rate of lay (-.22, -.19, -.46, -.60, and -.09%), 32-week egg weight (-.27, -.39, -.18, -.12, and -.23 g), albumen scores (-.25, -.25, -.27, -.28, and -.38 H.U.) and increasing shell color scores (.07 to .08). Early mortality also increased (.7 to 1.1%), but hatchability improved .75% per year only in TX and CC. Environment improved also in shell strength (.05 to .12 SPGR scores) and shell defects (-.07 to -.10 MTEX scores). The 16% increase in adult mortality (Figures 1, 5, and 9) occurred mainly from 1964 to 1966 in TX1 and TX2 but not until 1967 for the CX1 and CX2. Environmental decline in rate of lay was slight for TX but occurred in 1964 and 1967 for CX. Environmental decline in egg size accompanied the increase in mortality and thus occurred earlier in TX than in CX. The large environmental drop in egg size in 1968 (Figures 3 and 7) was associated with restriction of hatches to December through February and the consequent increasing day length during development. Field outbreaks of Newcastle disease forced elimination of test locations

where March to May pullets had been placed. Egg size consistently averaged 3 to 4 g lighter for birds from winter than from late spring hatches.

During the period from 1956 to the early 1960's, the birds were placed at test locations where producers were changing from floor pens to single-bird cages, usually with "all-in all-out" systems of growing and housing birds to limit exposure to diseases. However, as poultrymen expanded operations and introduced multiple-bird cage housing in attempts to reduce housing and labor costs, the isolation rearing and housing control of diseases gradually relaxed. It may be that the control pure strain birds (CC and CR) used to estimate environmental changes were more sensitive than the selected crosses to the increasing exposure to disease and thus caused overestimation of the environmental decline actually occurring in the strain-cross birds. If real, such genetic × environmental interaction would cause positive bias in the estimates of genetic change in the selected

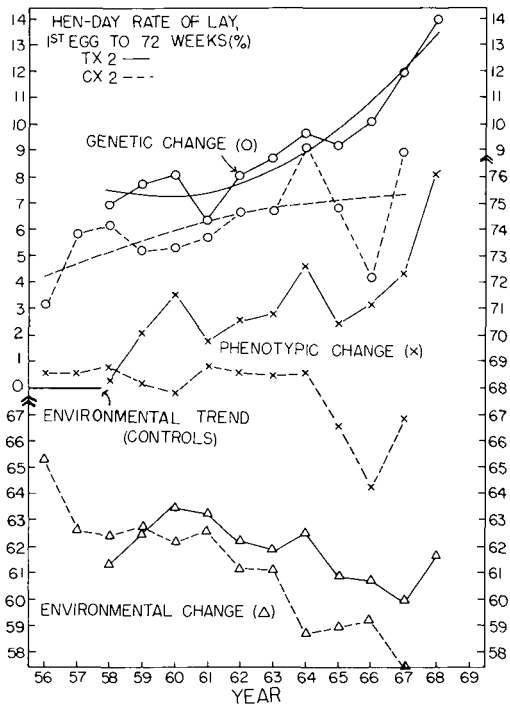

FIG. 6. Phenotypic (X), environmental (Δ), and genetic (o) changes in pedigreed TX2 (———) and commercial CX2 (-----) strain crosses for rate of lay. Smooth curves for genetic change are quadratic fit (PR72 in Tables 5 and 7).

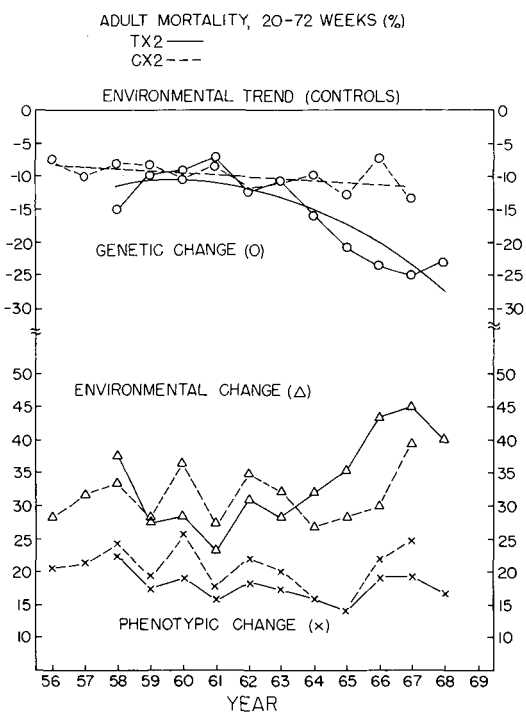

FIG. 5. Phenotypic (X), environmental (Δ), and genetic (o) changes in pedigreed TX2 (———) and commercial CX2 (-----) strain crosses for adult mortality. Smooth curves for genetic change are quadratic fit (AMRT in Tables 5 and 7).

crosses (i.e., in $\Delta P_{TX} - \Delta E_C = \Delta G_{TX}$). This concern about possible greater sensitivity of the pure strain control was the reason for shifting to the strain-cross repeat mating control after 1966. It is reassuring to note that genetic gains of TX crosses continued unabated from 1966 to 1969 inclusive when estimated environmental trend based on strain-cross controls was negligible for mortality, rate of lay, egg weight, and economic index (Figures 1 to 8). Another possible source of adverse bias in environmental trend was the removal of CC parents whose dams were not repeated because of death or reproductive failure.

Average Genetic Change. Estimated average genetic response per year (b_{GY}) in Tables 4 to 8) was much larger for the TX1 and TX2 crosses than for the corresponding CX1 and CX2 crosses or the control strain in economic index ($.16, .18 *vs.* .08, .11, and .10), adult mortality (-1.9, -1.6 *vs.* -.7, -.3, and -1.2%), rate of lay (.39, .60 *vs.* .08, .27, and .21%), eggs per hen housed (2.5, 3.3 *vs.* .5, 1.0, and 1.2 eggs),

and egg weight (.20, .17 *vs.* .11, .12, and .07 g). Early mortality declined -.5 to -1.0% yearly in all but the CX1 cross. Yearly gain was similar in all stocks for albumen score (.5 to .6 H.U.), shell color (-.04 to -.05 score), and shell shape (-.01 to -.03 score). Shell strength was maintained in crosses (.01 to -.04) but declined in controls (-.11), and little change occurred in mature shell texture (-.02 to -.07 score) or blood spot incidence (-.26 to .13%).

Standard errors for estimated average selection response were augmented to include expected cumulative error contributions of genetic drift and estimated environmental change (Bennett, 1980). Gains were highly significant ($P<.01$) in all five populations for economic index. In TX1 crosses, gains were significant at the .01 or .05 level for index, adult mortality, egg numbers, egg weight, shell shape and color, and albumen score, and at the .10 level for rate of lay and body weight. In TX2 crosses, gains were significant at the .01 and .05 level for index, early mortality, rate of lay, egg numbers, shell color, and albumen score, and at the .10 level for adult mortality, egg weight and shell shape. In CX1 crosses, gains were significant at the .01 or .05 level for only index, excitability score, shell color, and albumen score and at the .10 level for only shell shape. Commercial CX2 gains were at the .01 and .05 level only for index, shell color, and albumen score and at the .10 level for early mortality, excitability, and egg weight. Gains in the control strain were at the .01 or .05 level for only index, shell color, and albumen score, and genetic loss in specific gravity was at the .01 level of significance.

In general, significant genetic gains were found for the traits that received major emphasis in selection (Table 2). Response was small in relation to selection emphasis for rate of lay, probably because of its negative genetic association (-.3) with egg weight and shell strength (Emsley *et al.*, 1977). Yearly gains in total eggs amounted to 1.2 and 1.5% for TX1 and TX2 crosses, respectively, but were much less in the

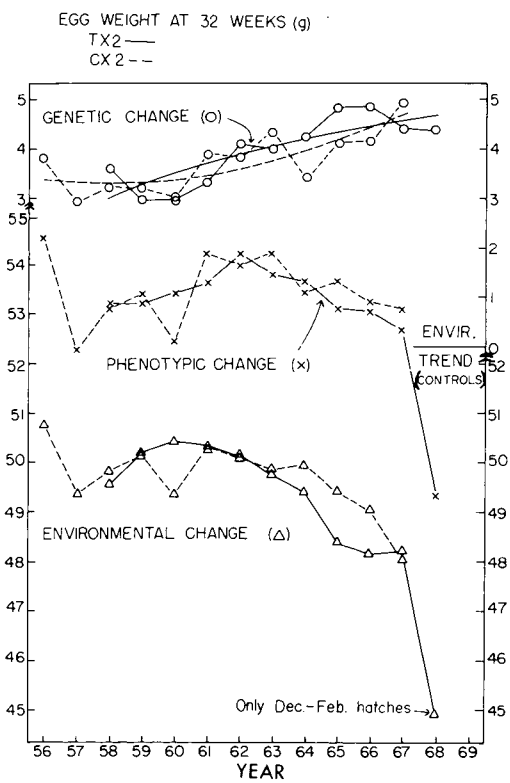

FIG. 7. Phenotypic (X), environmental (Δ), and genetic (o) changes in pedigreed TX2 (———) and commercial CX2 strain crosses for egg weight. Smooth curves for genetic change are quadratic fit (EGWT in Tables 5 and 7).

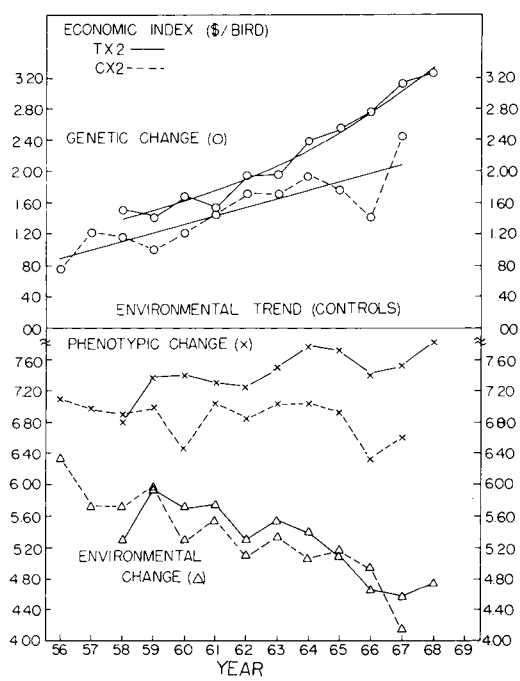

FIG. 8. Phenotypic (X), environmental (Δ), and genetic (o) changes in pedigreed TX2 (———) and commercial CX2 (-----) strain crosses for economic index. Smooth curves for genetic change are quadratic fit (ECON in Tables 5 and 7).

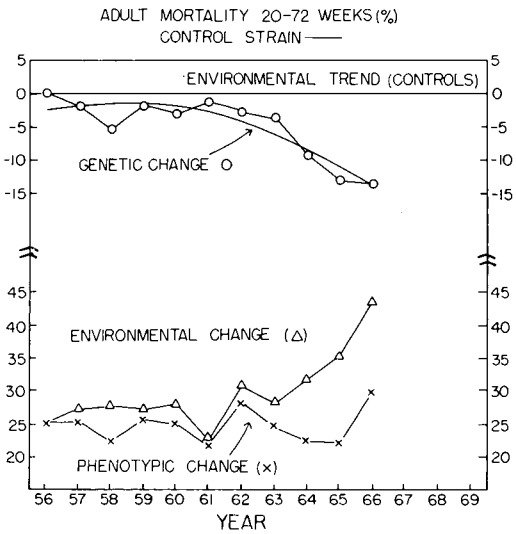

FIG. 9. Phenotypic (X), environmental (Δ), and genetic (o) changes in CC pure-strain control (———) for adult mortality. Smooth curves for genetic change are quadratic fit (AMRT in Table 8).

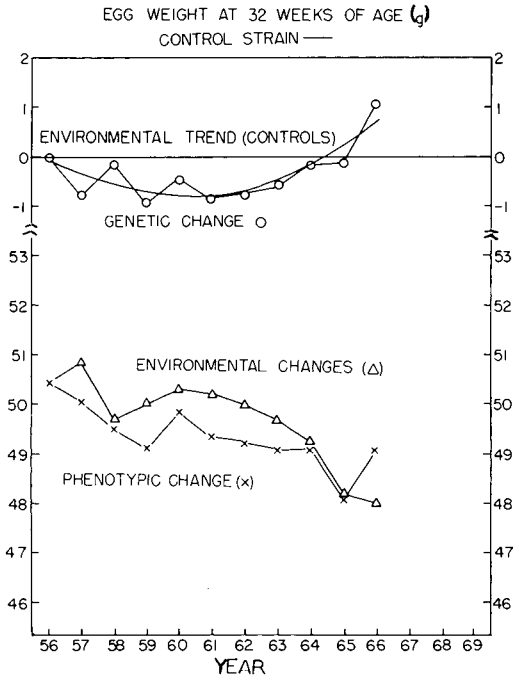

FIG. 11. Phenotypic (X), environmental (Δ), and genetic (o) changes in CC pure strain control (———) for egg weight. Smooth curves for genetic change are quadratic fit (EGWT in Table 8).

corresponding CX1 and CX2 crosses (.3 and .5%) and C strain (.6%). Gains in egg mass per hen housed amounted to about 1.5 and 1.8% yearly for the TX's, .5 and .7% for the CX's, and .7% for the C strain. Corresponding gains in economic index were 2.2 and 2.4% for TX's, 1.2 and 1.6 for CX's, and 1.6 for C strain.

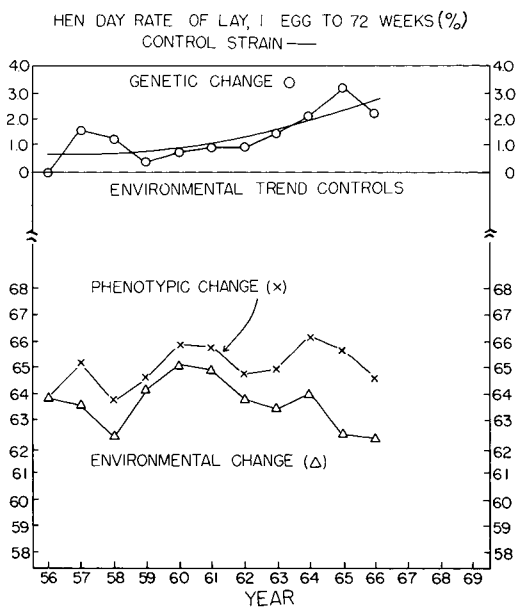

FIG. 10. Phenotypic (X), environmental (Δ), and genetic (o) changes in CC pure strain control (——) for rate of lay. Smooth curves for genetic change are quadratic fit (PR72 in Table 8).

Smaller genetic gains in field performance for C strain than for the TXs might be expected, because selection in C strain was based solely on pure strain performance to 60 weeks in the single floor-litter, trapnest environment of the centrol breeding farm, rather than on full-year strain-cross progeny performance under a range of field cage environments. Less than perfect genetic correlation between breeding farm and field environments would thus discount field effectiveness of selection in the central-farm environment. Another factor that presumably handicapped both absolute level and apparent genetic change in the commercial crosses (CX1 and CX2) as well as in the control strain (C) was the fact that they were progeny of unselected female parents. Thus, more female parents of CX and C pullets than of TX pullets were likely infecting their progeny with leukosis virus and thus reducing their mean level of performance by altering the environment in which their genetic potential was expressed (Spencer *et al.*, 1979).

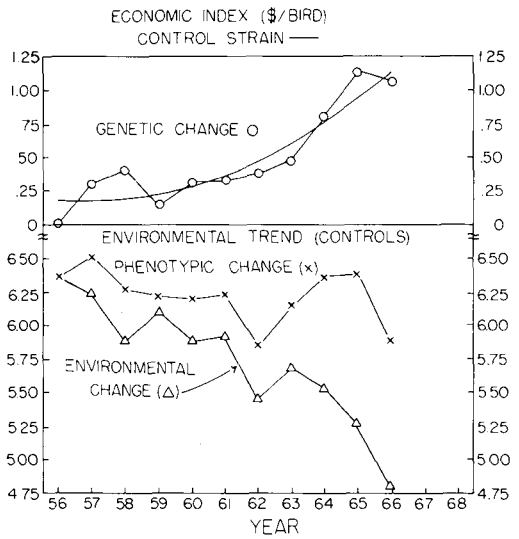

FIG. 12. Phenotypic (X), environmental (Δ), and genetic (o) changes in CC pure strain control (———) for economic index. Smooth curves for genetic change are quadratic fit (ECON in Table 8).

The yearly responses from pure-strain selection for part-year rate or total egg production of layers reported by Gowe (1977) were much larger than responses from C strain for full-year eggs per hen housed (4.9 and 4.4 *vs.* 1.2 eggs), hen-day rate (3.0 and 1.7 *vs.* 2%), and egg weight (.5 *vs.* .1 g). This greater response of selection may be related to such factors as vaccination for Marek's disease, rearing strains separately in multiple-bird, wire-floor cages and housing in single-bird cages to minimize horizontal transmission of disease and measuring responses in the same environment used for selection.

Other estimates of genetic gains in commercial egg production stocks have been based on time trends for deviations from an unselected control strain. Gains were evaluated for the same six commercial stocks (including the present CX1) in US Random Sample (RS) tests from 1958 through 1968 by Dickerson (1968) and from 1958 through 1970 in a single year experiment by Dickerson and Mather (1976). Similar estimates for four stocks in British Random Sample tests from 1968 through 1973 have been reported by Foster and Weatherup (1977). Von Krosigk *et al.* (1973) have reported multiple location but potentially biased (over) estimates of genetic change in pedigreed matings of a commercial cross, using contemporary comparison of strain-cross progeny from selected and unselected 1-year-old parents. These estimates of genetic change in commercial strain-cross layers are compared with those from the present study in Table 9.

The present California field trial estimates of yearly genetic change in CX1 and CX2 were smaller than those from the US RS tests and from the 1976 experimental studies for rate of lay (.2 *vs.* .6 and .8%), total eggs (.8 *vs.* 3.0 and 2.4), and age at first egg (.2 *vs.* -1.0 days), but greater for mortality (-.9 *vs.* -.3 and .2%), albumen score (.7 *vs.* -.5 and .4%), and shell thickness (0 *vs.* -.08 and -.03%). Estimates of genetic change in TX1 and TX2 field performance were very similar in rate of lay and egg size to those for all six commercial stocks in US RS tests and for the four commercial stocks in the British RS tests, but greater in mortality than either and greater in sexual maturity than the British stocks. The estimates of yearly gains by von Krosigk *et al.* (1973) are the highest of all for rate of lay and egg size. However, they are for performance to only 10 months of age and subject to positive bias because they were based on contemporary comparison of strain-cross progeny of selected *vs.* unselected 1-year-old parents and would include any temporary differences in direct maternal (e.g., virus transmission; Spencer *et al.*, 1979) or epistatic recombination effects (Dickerson, 1964).

Nonlinear Genetic Changes. The general nature of selection response in the TX crosses was to maintain actual livability and egg weight but to increase actual rate of lay and economic index during a period of environmental decline in livability, egg weight, rate of lay, and especially economic index as measured by repeated generations of the control strain. The environmental increase in mortality from 1963 to peak levels in 1966 and 1967 (Figures 1, 5, and 9) was associated with field outbreaks of Marek's disease.

Curvilinear selection responses (b'_{GY^2} in Tables 4 to 8) could be from the increased emphasis on selection for rate of lay, egg weight, shell color, defects, and shape and the decreased emphasis on mortality and other traits when index weightings were revised in 1962 and 1965 (Table 2). Genetic gains in TX1 crosses accelerated significantly (Table 4) for rate of lay (Figure 2) and egg numbers but slowed for excitability score, mature shell defects, and blood spots. In TX2 crosses, response again accelerated at near significant

TABLE 9. *Summary of average yearly genetic changes in pedigreed and commercial stocks of layers*

Source, stock, period	Mortality 0-500 days (%)	Hen-day production (%)	Eggs/hen housed	Age first egg (days)	Egg weight (g)	Albumen score (%) b	Shell thickness (%) b
Pedigreed crosses							
TX1, TX2 (1956-1969)	−2.5	.5	2.9	−.5	.18	.6	−.01
Commercial crosses							
CX1, CX2 (1956-1967)	−.9	.2	.8	.2	.12	.7	0
6 commercial stocks							
Dickerson (1968) RST (1958-1966)	−.3	.6	3.0	−1.0	.21	−.5	−.08
Dickerson and Mather (1976)							
Floor (1958-1970)	.3	.5	1.2	−1.2	.07	.3	−.03
Cage (1958-1970)	.2	.8	2.4	−1.1	0	.4	−.03
4 commercial stocks							
Foster and Weatherup (1977) RST (1968-1973)	.3	.4	1.2	.9	.23	.....	.08
Von Krosigk *et al.* (1973)							
TX3 (1964-1969) USA	−1.5[a]	1.5[a]	2.9[a]	−.4	.04	.....	.24
TX3′ (1964-1971) Germany	....	1.2[a]	....	−.8	.37	2.6	.02

[a]To 305 days, for contemporary superiority of crosses from selected *vs.* unselected 1-year-old parents.

[b]Percent change.

levels for rate of lay (Figure 6) and egg numbers but slowed for shell shape, shell color, mature shell defects, and albumen score and worsened for excitability score (Table 5).

The significant upward curvilinearity in TX1 and TX2 responses for rate of lay (Figures 2 and 6) began in 1962 and was strong after 1966. Trends in adult mortality (Figures 1 and 5), egg weight (Figures 3 and 7), and economic index (Figures 4 and 8) showed only nonsignificant deviations from linear response. The increased response in rate of lay after 1966 probably was from its increased emphasis in selection (Table 2) from 1965 on. Departure from linear response in the commercial crosses approached significance only for increasing early mortality in CX1 (Table 6) and decreasing shell defects in CX2 crosses (Table 7). Thus, the responses obtained provide little evidence of the accelerating response to reciprocal selection for increased heterozygosity of a strain cross expected from overdominance theory (Dickerson, 1952).

Actual trends in control strain progeny from selected parents (Table 8, Figures 9 to 12) were down in egg weight, steady for mortality and rate of lay, and slightly negative for economic index ($-.03/year) during a 10-year period when the field environmental trends were adverse for these as well as for shell color, albumen score, and blood spots and favorable for only shell strength, shell defects, and body weight. Genetic gains in field performance of the control strain from 1956 to 1966 accelerated significantly for egg weight (Figure 11), age at first egg, and economic index (Figure 12); slowed for body weight, albumen score, and blood spots; and recovered for shell strength. Non-significant acceleration for mortality and rate of lay also helped offset the slowing of response in other components to permit the significantly improved rate of response in economic index.

Comparison of Commercial and Pedigreed Crosses. Commercial crosses differed from pedigreed crosses in several ways that affect interpretation of both the absolute levels of performance and the estimates of genetic trend shown in Tables 4 to 7 and figures 1 to 8. The CX pullets were produced by unselected 1-year-old strain-cross parents, from largely unselected 1- and 2-year-old grandparents, but from great grandparents selected on strain-cross progeny or sib performance. Thus, CX pullets were genetically comparable with the TX pullets produced at least 2 years earlier, except that both parents and grandparents were unselected and their female parents were strain crosses. Therefore, some loss in direct maternal influence or from recombination of epistatic effects might be expected in the CX crosses in addition to the 2+-year lag in selection response.

The mean superiority of pedigreed over commercial crosses for all years in which both were represented ($\overline{\Delta}$) is shown for TX1 and TX2 crosses in Tables 4 and 5, respectively. Superiority of both TX1 and TX2 crosses per bird housed was large for economic index ($.50 and .48), adult mortality (-5%), total eggs (11 or 12), and rate of lay (2.5 and 2.2%) and mildly favorable for most other component traits except fertility. The 11 and 13% lower fertility for TX crosses of pure strain females than for the CX crosses of strain-cross females arises from female heterosis in fertility.

The proportion of the TX cross advantage ($\overline{\Delta}$) accounted for by the 2+-year lag in linear selection response of CX1 and CX2 commercial crosses ($2\,b_{GY}$, Tables 6 and 7) would be larger for economic index ($2 \times .08/.50 = 32\%$ and $2 \times .11/.48 = 46\%$) than for adult mortality (25 and 13%), total eggs (9 and 17%), and rate of lay (6 and 24%). For egg quality traits, which increase when egg numbers decline, the superiority of TX over CX crosses is less than two yearly increments of genetic change in the commercial cross. For example, in egg weight $.045 < 2(.11) = .22$ for CX1 and $.13 < 2(.12) = .24$ for CX2. Apparently, use of unselected breeders to produce both the parent stock and then the commercial chicks was associated with serious adverse effects on mortality and egg numbers, which were only partly offset by favorable effects on egg size and some egg quality traits. Because these large adverse effects were health related, a difference in direct maternal effects seems a more likely explanation than recombination loss of epistatic superiority.

Selection contributing to response in TX crosses was 2 years in advance of CX crosses, and TX responses were measured for 1 or 2 years longer. Thus, genetic trends in TX crosses represented more recent years of selection than trends in CX crosses (4 for TX1, 3 for TX2). These were the years of most rapid genetic gains in both sets of TX crosses for egg numbers and of continued linear gains in TX mortality, egg weight, and economic index. Hence, genetic

trends in the CX commercial crosses may have been considerably underestimated.

If we could assume that rate of genetic change for CX1 and CX2 commercial crosses would equal that of their constituent TX crosses if measured for the same period of selection applied (i.e., 2+ years later for the CX cross), the part of observed TX cross superiority ($\overline{\Delta}$) in Tables 4 and 5) explainable by the 2+-year earlier expression of selection response in the TX crosses would be much larger than that based on the linear b_{GY} observed in the CX crosses ($2b_{GY}/\overline{\Delta} = 65$ and 74% for economic index, 73 and 67% for adult mortality, 43 and 59% for total eggs, 31 and 54% for rate of lay). Then the proportional disadvantage of the CX1 and CX2 commercial crosses in relation to TX crosses still unexplained by lag in response would be only about -2.6 and -1.8% for economic index [e.g., (-.504 + .324) / (7.28 - .324) = -2.6% for CX1 (Table 4)], 9.8 and 10.6% for adult mortality, -3.1 and -2.1% for total eggs, and -2.6 and -1.4% for rate of lay. In absolute units, the adjusted CX cross disadvantage per bird housed would be $-.18 and -.13 for index, 1.4 and 1.6% for mortality, -6.7 and -4.7 for total eggs, and -1.7 and -1.0% for rate of lay. These differences are still important, associated with the loss of temporary maternal and epistatic effects of producing the TX crosses with young pure strain (rather than line-cross) breeders from families selected on their parents' strain-cross progeny tests and individual pullets selected for size and quality of eggs and for superior early rate of lay.

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