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Genetic Gains from Reciprocal Recurrent and Within-Line Selection for Egg Production in the Fowl*

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Summary. Selection for survivors percent egg production from first egg to 40 weeks of age was conducted for six generations. Within-line selection (WLS) on the basis of an index of individual records plus sire family and dam family means was compared with reciprocal recurrent selection (RRS) based on sire family selection among cross progeny. Genetically heterogeneous synthetic populations, the Cornell Control and the Purdue Pool strains were used.

The responses to WLS (3.84°) and RRS (2.57°) were both significantly greater than zero, but were not significantly different from each other. Nevertheless, the responses were proportional to their predicted values (.363 vs .340). The advantage of WLS was due to the mechanics of selection resulting in slightly greater selection intensity and an increased correlation between the criterion of selection and the trait being improved. On the contrary, the RRS method had a slightly larger realized heritability as would be expected in the presence of non-additive genetic variance. Four of five pure-lines selected under both methods had statistically significant declines in performance due to inbreeding depression effects. All of the results observed are comparable with known genetic theory.

Some problems in comparing genetic gains from different selection methods or selection criteria are discussed.

Introduction

Improvement of quantitative traits by selection depends upon increasing the frequency of desirable genes. The capability of selection among phenotypic measurements to change the gene frequency is dependent upon the regression of individual breeding values on their phenotypic estimates or the criteria of selection. This regression is a function of the heritability, or the proportion of the total phenotypic variance that is additive genetic. When heritability is low due to large environmental contributions to phenotypic variance, several methods of increasing the proportion of additive genetic variance, i.e., increasing the heritability, have been suggested. Selection criteria based on dam family means or sire family means, for example, average out environmental deviations.

The regression of the breeding values on the phenotypic values may also be low due to the presence of non-additive genetic variance. In this case the heritability may be increased by finding a new phenotypic selection criterion that has a greater correlation with the breeding value of the individuals. An example of such a criterion is the "test cross to the recessive" which results in differences in breeding values between tested individuals, masked by dominance deviations in their own phenotype, becoming additive and selectable when measured by the cross progeny means.

Shull (1914) coined the word "heterosis" to describe the phenomenon of heterozygote superiority associated with non-additive genetic variance. Among other schemes suggested to exploit heterosis for the genetic improvement of domestic plants and animals, reciprocal recurrent selection (RRS) in corn was proposed by Comstock, Robinson and Harvey (1949) to take advantage of all forms of genetic variance. Reciprocal recurrent selection in chickens was suggested by Bell, Moore, Bohren and Warren (1952).

Empirical comparisons of reciprocal recurrent selection and within-line selection have been made by Bell, Moore and Warren (1955), Rasmuson (1956) and Kojima and Kelleher (1963) in *Drosophila*, and by Bell and Moore (1972) in *Tribolium castaneum*. Saadeh, Craig, Smith and Wearden (1968) compared the effectiveness of within-line index selection and reciprocal recurrent selection for increased egg production in chickens.

The purpose of the present study was to compare the genetic gains from within-line selection (WLS) on an index of individual, dam family and sire family means (*ids*), with those resulting from reciprocal recurrent selection (RRS or *rr*) on sire family means, for the improvement of survivors percent egg production from first egg to 40 weeks of age in chickens.

Materials and Methods

Genetic Stocks: Two large populations were sampled to establish selected lines. One population was the Cornell Control White Leghorn Population (CC) which has been described by King, Carson and Doolittle (1959). The other population was the Purdue Pool Population (PP), which was established at Purdue University by crossing one strain each of Black Leghorn, White Minorca, White Leghorn, Mottled Ancona and two strains of Brown

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Leghorn. These control populations were maintained at the North Central Regional Poultry Breeding Laboratory in a manner to minimize inbreeding and converse stable gene frequencies as described by King *et al.* (1959). They provided both a highly heterogeneous genetic source for selection and the controls for comparison with selected lines.

Selection Populations: Five groups of parents were selected for the trait, survivors percent egg production from first egg to 40 weeks of age, in each of six generations. Selected populations were identified as follows:

CC_{ids}	Cornell Control foundation selected within line (WLS) on an index of individual record, plus dam mean and sire mean (*ids*).
PP_{ids}	Purdue Pool foundation selected within line (WLS) on an index of individual record, plus dam mean and sire mean (*ids*).
PC_{ids}	Foundation established from crossing PP and CC populations and selected within line (WLS) on an index of individual record, plus dam mean and sire mean (*ids*).
CC_{rr} and PP_{rr}	Pure line foundations selected on sire cross progeny means (*rr*), i. e., reciprocal recurrent selection (RRS).

Each WLS pure line was limited to 500 individuals measured while each RRS cross was limited to 250 individuals measured. Thus a total of 2,000 individuals were measured for selection each generation. The generation interval was one year for both methods. Otherwise, genetic gain was maximized as much as possible within the limits imposed by the methods. Differences between the genetic gains for the two methods reflect differences in the selection differentials, the heritabilities and in the regressions of the performance in the trait to be improved on the criteria of selection. All of these differences are direct consequences of the methods of selection used, so that the difference in the genetic gains reflect differences in the total effect of the two methods.

Line-Test Populations: In addition to the populations in which selection occurred, a set of 13 line-test populations was produced each generation by which genetic gains were measured. The identification codes of 12 of the strain-method test populations are shown in Table 1.

Table 1. *Strain-method class identificationa Capital letters indicate strain or cross while subscripts designate selection method*

Selection Methods		
Control (c)	Reciprocal recurrent (rr)	Individual, dam and sire family index (ids)
CC_c	CC_{rr}	CC_{ids}
PP_c	PP_{rr}	PP_{ids}
C_cP_c	$C_{rr}P_{rr}$	$C_{ids}P_{ids}$
P_cC_c	$P_{rr}C_{rr}$	$P_{ids}C_{ids}$

P Purdue Pool base population
C Cornell Control base population

A test population of PC_{ids} was also produced each generation. Capital letters represent strain or cross while lower case letters indicate the method of selection. For example, CC_{rr} represents pure Cornell Control selected by reciprocal recurrent selection. A total of 2,200 female progeny were measured each generation for estimating line means, with 170 being measured for each line-test population in each generation. These were placed in five pens, two at Purdue University in one house and three at the Regional Poultry Breeding Laboratory, each pen in a different house.

The trait measured was pen-mean hen-day percent egg production from 20 to 40 weeks of age. This trait was not the same as survivors' percent production to 40 weeks of age, on which the criterion of selection was based, but was a correlated trait. This measurement was used because the extra labor for trap-nesting the individual pullets in the test pens was not available.

Within-Line Selection: A total of ten breeding pens were used for within-line selection in the Cornell Control, the Purdue Pool and the cross-bred foundation (PC_{ids}) populations. Each sire was mated to seven dams. An effort was made to have available ten female and two male progeny from five of the seven dams mated to each sire. Thus, a total of 500 female and 100 male progeny were saved per generation in each pure line.

The criterion of selection for females was an index based on the sire and dam family means and individual records as presented by Osborne (1957a), and in males was an index based on sire and dam family means as shown by Osborne (1957b), both modified for finite numbers. One son was selected for breeding from each of the ten dam families with the highest indexes or from the best 20 percent of the dam families. Individual indexes of the 500 female progeny in each population were ranked and the best 70 pullets were selected for mating, or about 14 percent of the population.

The birds selected and mated to become parents of the next generation in which selection would occur, also produced progeny for line tests. The pure line-test progeny were used to produce both reciprocals of cross line-test progeny. Because of this delay in producing the cross progeny, genetic gain measured in the cross of the *ids* lines in any one year represented one generation less of selection than in the pure lines and *rr* crosses measured at the same time.

Foundation populations were sub-sampled each generation to provide pure-line control test groups. These were mass mated in the test pens to produce cross control populations for the next generation.

Selection in Cross Progeny: A total of 40 breeding pens were used for reciprocal recurrent selection, 20 for each reciprocal. Each pen contained one sire and seven dams of the opposite strain. For progeny test, 13 progeny were selected at random from each breeding pen to total 260 pullets measured for each reciprocal. To produce pure-line progeny of the reciprocal recurrent selected parents, sires were exchanged among breeding pens such that one sire and seven dams of the same strain occupied each breeding pen. From the pure-line progeny of each sire, 50 females and eight males were chosen at random providing a total of 1,000 female and 160 male progeny per reciprocal, each identified by sire. These pure-line progeny were held until the superior sire families could be identified from the performance of the cross progeny.

The criterion of selection was sire cross progeny mean. Sire means were ranked and the pure-line progeny of the best five of 20 sires in each reciprocal were selected. From each of the selected sires, 28 female and four male progeny were placed in breeding pens to produce both cross progeny ($P_{rr}C_{rr}$ and $C_{rr}P_{rr}$) for selection in the next generation, and line-test cross progeny populations. The remaining progeny of selected sires were mass mated to produce pure line-test pullets (CC_{rr} and PP_{rr}).

Prediction of Genetic Gains

To predict the genetic gain ($\Delta G_{T \cdot C}$) in any trait T from selection on any criterion C, the fundamental equation is

$$\Delta G_{T \cdot C} = \Delta P_C \beta_{G_T P_C} = \Delta P_C \varrho_{G_T P_C} \frac{\sigma_{G_T}}{\sigma_{P_C}}, \qquad (1)$$

where $\Delta P_C = \bar{i}\sigma_{P_C}$ is the phenotypic selection differential in the criterion, $\beta_{G_TP_C}$ is the regression of the breeding values for the trait T in which improvement is desired on the phenotypes of the criterion of selection C, $r_{G_TP_C}$ is the correlation between the breeding value for the trait and the phenotype of the criterion and σ_{G_T} and σ_{P_C} are the genetic and phenotypic standard deviations of the trait to be improved and the criterion of selection respectively.

When gain in one sex of progeny results from selection in both sexes of parents, the predicted genetic gain in the progeny is the average of the predicted breeding values for the trait T of the two sexes of parents when selected for the criteria $C_{♂}$ and $C_{♀}$, which may or may not be different for the two sexes. For example, predicted genetic gain in a trait T in female progeny from selection in male and female parents for the selection criteria $C_{♂}$ and $C_{♀}$ would be expressed as

$$\Delta G_{T_{♀}\cdot C_{♂}C_{♀}} = \frac{1}{2}\left[\Delta G_{T_{♀}\cdot C_{♂}} + \Delta G_{T_{♀}\cdot C_{♀}}\right]. \qquad (2)$$

Predicted Genetic Gain from Within-Line Index Selection (ids): The criteria of selection for female ($C_{♀}$) and male ($C_{♂}$) parents under *ids* were indexes ($I_{♀}$ and $I_{♂}$) based on individual record plus sire and dam family averages. For these criteria, equation (2) is expressed as

$$\begin{aligned}\Delta G_{T_{♀}\cdot C_{♂}C_{♀}} &= \frac{1}{2}\left[\bar{i}_{♀}\sigma_{P_{I_{♀}}}\beta_{G_TP_{I_{♀}}} + \bar{i}_{♂}\sigma_{P_{I_{♂}}}\beta_{G_TP_{I_{♂}}}\right],\\ &= \frac{1}{2}\left[\bar{i}_{♀}\sigma_{P_{I_{♀}}}R_{G_TP_{I_{♀}}}\frac{\sigma_{G_T}}{\sigma_{P_{I_{♀}}}} + \bar{i}_{♂}\sigma_{P_{I_{♂}}}R_{G_TP_{I_{♂}}}\frac{\sigma_{G_T}}{\sigma_{P_{I_{♂}}}}\right],\\ &= \frac{(\bar{i}_{♂}+\bar{i}_{♀})\,\sigma_{G_T}}{2}\left[\frac{\bar{i}_{♀}}{\bar{i}_{♂}+\bar{i}_{♀}}R_{G_TP_{I_{♀}}} + \frac{\bar{i}_{♂}}{\bar{i}_{♂}+\bar{i}_{♀}}R_{G_TP_{I_{♂}}}\right].\end{aligned} \qquad (3)$$

When standardized for the selection intensity and the genetic variance, the genetic gain is equal to the correlation, where the coefficients of the R values are the relative selection intensities applied to the two sexes.

For finite populations, the expected multiple correlations $\left(R_{G_TP_{I_{♂}}}, R_{G_TP_{I_{♀}}}\right)$ between the breeding values for the trait and the phenotypes of the criteria (indexes) for selection of female and male parents are similar to those derived by Osborne (1957 a, b), as presented by Kinney *et al.* (1970).

Predicted Genetic Gain from Reciprocal Recurrent Selection (rr): For this method, the criterion of selection was the sire family phenotypic average of cross progeny ($P_{\bar{S}}$) for the trait to be improved. Twenty sires of each line were mated to seven females of the other lines and approximately 13 cross progeny were measured. The purebred male and female progeny of five selected sires in each line were used for cross mating the next generation. The genetic gain in cross performance from one generation of selection is the average change in the crossbred breeding values of the pure lines resulting from reciprocal recurrent selection. Then equation (2) can be written as

$$\begin{aligned}\Delta G_{T_{♀}\cdot C_{♂}C_{♀}} &= \frac{1}{2}\left[\Delta G_{PP_{rr}} + \Delta G_{CC_{rr}}\right]\\ &= \frac{1}{2}\left[\bar{i}_{PC}\sigma_{P_{\bar{S}_{PC}}}\beta_{G_TP_{\bar{S}_{PC}}} + \bar{i}_{CP}\sigma_{P_{\bar{S}_{CP}}}\beta_{G_TP_{\bar{S}_{CP}}}\right].\end{aligned} \qquad (4)$$

It is assumed that these regressions and phenotypic standard deviations are the same in the two reciprocals, since reciprocal effects have been shown to be negligible. In this case, equation (4) reduces to

$$\begin{aligned}\Delta G_{T_{♀}\cdot C_{♂}C_{♀}} &= \frac{\bar{i}_{PC}+\bar{i}_{CP}}{2}\sigma_{P_{\bar{S}}}\beta_{G_TP_{\bar{S}}},\\ &= \frac{\bar{i}_{PC}+\bar{i}_{CP}}{2}\sigma_{P_{\bar{S}}}\varrho_{G_TP_{\bar{S}}}\frac{\sigma_{G_T}}{\sigma_{P_{\bar{S}}}}.\end{aligned} \qquad (5)$$

The regression of the breeding value in the cross (T) of a single individual in the pure line on the sire mean of the crossbred progeny ($\bar{S}$) is,

$$\beta_{G_TP_{\bar{S}}} = \frac{h_x^2}{4}\left[\frac{n}{1+(n-1)\,rh_x^2}\right], \qquad (6)$$

where the subscript, x, indicates that the heritability involved is that for cross performance and not that for pure line performance. The correlation between these two variables is then,

$$\varrho_{G_TP_{\bar{S}}} = \beta_{G_TP_{\bar{S}}}\frac{\sigma_{P_{\bar{S}}}}{\sigma_{G_T}} = \frac{h_x}{4}\sqrt{\frac{n}{1+(n-1)\,rh_x^2}}, \qquad (7)$$

which is the formula for the correlation between the genotype of an individual not included in the family average and the family average phenotype.

Calculated Heritabilities: Heritability for prediction purposes was estimated for each selected line based on the sire components from the usual hierarchal analysis of variance with unequal subclass numbers (Steel and Torrie, 1960). Where reciprocal recurrent selection was employed, only the sires were identified, so estimates of heritability were based on the sire components adjusted by the method proposed by Bohren, McKean and Friars (1965), for the situation where only one parent is identified. These estimates were averaged over six generations for each line and are listed as predicted heritabilities in Table 5. For the three populations selected within-line, the Cornell Control had the highest heritability and the Purdue Pool the lowest. The population selected on the within-line method from the crossbred foundation (PC_{ids}) had a heritability intermediate between the two parent populations. On the other hand, estimates of heritability based on sire components when the males were mated to females of the opposite line

($C_{rr}P_{rr}$ and $P_{rr}C_{rr}$) were about two percent higher than the estimates for either PC_{ids} or the average of the estimates for the two pure lines.

Assumptions for Prediction of Genetic Gains: Observed phenotypic response to selection, or realized response (ΔP), is estimated as the change in the phenotypic mean resulting from t generations of selection, and in closed populations of finite size consists of two parts. The first is that change in phenotype due to selection (ΔP_S), the value of which is assumed to be the genetic gain (ΔG), while the second part is the effect on the phenotype due to inbreeding depression, or $\Delta P = \Delta P_S + \Delta P_F$. In populations having many deleterious recessive genes, the inbreeding depression from homozygosity due to random drift could be larger than the genetic gain, yielding a negative phenotypic response to selection. The two terms are not independent. Homozygosity resulting from chance fixation rather than selection will reduce the gains per generation and the limits of selection by reducing the genetic variance (Robertson, 1961), which is a direct effect on the genotypic variance. On the other hand selection may hasten the fixation of undesirable recessive alleles linked to desirable alleles being selected, which would further reduce the effective population size below the actual number of parents, leading to even greater increases in homozygosity when compared to unselected controls (Robertson, 1960; Latter and Robertson, 1962).

No method of estimating the proportionate effects of genetic drift and inbreeding depression on the response of a single population is available, even when considering deviations from controls in the estimation of the response. Therefore, in predicting response to selection by equations (3) and (4), it is assumed that no inbreeding and no inbreeding depression occurs, and that the phenotypic correlation between family members is entirely due to the genetic correlation between them. The failure of these assumptions would result in overprediction of the observed response.

Results

The line test means for the selected populations and crosses and the cumulative realized genetic gains from the six generations of selection are presented in Table 2. Cumulative genetic gains to each generation are deviations from the control having similar genetic composition. These values are presented as angles rather than percentages because they more nearly approach a normal distribution on which selection theory is based.

The means for the twelve strain-method combinations shown in Table 1 were first subjected each generation to an analysis of variance similar to that reported by Saadeh *et al.* (1968) and presented in Table 3. The differences in results at the two stations could largely be attributed to difference in performance between the Purdue Pool population and the Rhode Island Red strain used in the Kansas Experiment. These analyses do not provide a good comparison of the selection systems because the comparison is based on the means of the two purebred and the two reciprocal crosses developed under each system (S_2 in Table 3) and no consideration is given to the expected responses. Since no replicated lines were measured, the error term in this analysis does not contain, the effect due to genetic drift, so that tests of differences between strain means would be more likely to be significant. Conversely, lack of statistical significance would be strong evidence that no real differences exist.

In spite of these deficiencies, several important points may be derived from this analysis. First, the similarity of the results in the two experiments strengthens the conclusions to be drawn. Secondly,

Table 2. *Line test population means and genetic gains (as angles in degrees) for six generations in pure lines and crosses selected for percent egg production by within line and reciprocal recurrent selection*

Generation	CC_{ids}	PP_{ids}	$\frac{(CC_{ids} + PP_{ids})}{2}$	PC_{isd}	$\frac{(C_{ids}P_{ids} + P_{ids}C_{ids})}{2}$	CC_{rr}	PP_{rr}	$\frac{(CC_{rr} + PP_{rr})}{2}$	$\frac{(C_{rr}P_{rr} + P_{rr}C_{rr})}{2}$
					Means				
1	54.31	45.10	49.70	49.07	51.30	49.71	45.92	47.82	49.80
2	54.59	45.07	49.83	47.08	49.35	45.59	42.54	44.06	47.30
3	53.85	40.72	47.28	45.82	48.28	47.99	40.44	44.22	46.76
4	58.49	45.63	52.06	48.35	54.56	49.94	41.77	45.86	50.48
5	53.52	41.49	47.50	43.83	50.46	45.78	40.83	43.30	48.16
6	52.98	39.75	46.36	44.86	50.41	44.12	37.50	40.82	49.14
					Deviations from controls (genetic gains)				
1	2.74	0.06	1.40	0.77	2.02	−1.86	0.88	−0.49	0.53
2	6.58	3.07	4.82	2.08	1.55	−2.42	0.54	−0.94	−0.49
3	4.73	2.14	3.44	1.97	1.08	−1.13	1.86	0.36	−0.44
4	6.52	−1.39	2.56	−1.14	2.79	−2.03	−5.25	−3.64	−1.29
5	6.13	−1.52	2.30	−1.37	4.25	−1.61	−2.18	−1.90	1.96
6	4.97	−3.50	0.74	−0.77	3.83	−3.89	−5.74	−4.82	2.56

Table 3. *Analysis of variance of hen-day percent production (as angles in degrees) after each of six generations of selection*

Source of variation	d.f.	Mean squares for generations and years					
		1 1961	2 1962	3 1963	4 1964	5 1965	6 1966
Strain-methods	11	40.0**	58.4**	100.0**	109.2**	72.8**	106.6**
Selection Systems (*S*)	2						
Control vs. Sel. (S_1)	1	10.0	20.4*	16.5*	.1	36.5**	4.5
ids vs. *rr* (S_2)	1	28.7**	152.8**	52.7	261.9**	105.6**	116.3**
Breeding Types (*T*)	3						
Strains (*A*)	1	317.8**	287.7**	812.3**	565.9**	380.8**	504.5**
Heterosis (*B*)	1	34.5*	51.4**	78.8**	148.4**	129.7**	295.5**
Reciprocal (*C*)	1	6.3	12.7	28.1**	29.7*	6.8	1.8
$T \times S$	6						
$S_1 \times A$	1	.1	.1	.1	52.5**	28.2**	44.3**
$S_2 \times A$	1	36.9**	52.3**	39.0**	28.6**	62.7**	54.8**
$S_1 \times B$	1	2.2	6.7	8.2	5.7	28.1**	91.5**
$S_2 \times B$	1	.4	34.6*	6.0	10.8	9.1	45.9**
$S_2 \times C$	1	.2	15.5	2.2	4.5	3.6	13.3
$S_2 \times C$	1	2.9	8.0	56.3**	92.8**	9.6	.2
Houses	3	14.6	4.6	31.9**	4.4	73.4**	24.3*
Houses × Strains	33	2.8	7.1	4.4	4.9	3.0	4.5
Within Houses and Strains	12	6.4	3.8	2.8	5.3	2.5	6.0
Total	59						

* Significant at the .05 probability level.
** Significant at the .01 probability level.

no significant differences were observed between reciprocal crosses, so only the average values of reciprocal crosses are presented. While heterosis, defined as the difference between the mean of the two pure lines and that of the two reciprocal crosses increased over generations, the interactions of selection methods by heterosis were not significant in either experiment until the last generation. This lack of interaction suggests that heterosis developed under the within-line selection method as rapidly as under reciprocal recurrent selection, which was the only method expected to select for heterotic effects. If reciprocal recurrent selection was increasing overdominant effects in the crosses, heterosis would be expected to increase most rapidly under this method. While the heterosis effects were somewhat larger under RRS, examination of the genetic gains in Table 2 indicate that this was due to a decrease in gains in the pure lines resulting from inbreeding depression, rather than as a consequence of greater gain in the RRS crossbreds due to overdominance.

It was intended to select as intensely as each method would permit. If the best 20 percent of the males and 14 percent of the females had been selected as planned under WLS, the expected standardized selection differential or selection intensity in males would have been $\bar{i}_{♂} = 1.4$ and in females $\bar{i}_{♀} = 1.59$ standard deviations. This would have resulted in cumulative selection intensities for six generations of 8.4 and 9.5 standard deviations in males and females, respectively. Similarly, if the best 25 percent of the sire progenies had been selected under RRS, the theoretical selection intensity would have been 1.27 standard deviations in one generation and 7.6 in six generations for each sex.

The realized or observed selection intensity was obtained by dividing the observed selection differential by the phenotypic standard deviation, the observed selection differential being the difference between the mean of the selected parents and the mean of the population from which they were selected. The cumulative selection intensities obtained in this manner along with the average phenotypic standard deviations for the selection criteria in all selected populations are shown in Table 4. The observed values are lower than the theoretical values, as expected. They are about 82 percent of the theoretical values and the reductions are about the same for the two methods.

Table 4. *Average phenotypic standard deviations for the selection criteria in each sex for each of the selected populations and the cumulative standardized selection differentials for the six generations of selection in each population*

	♂		♀	
	σ_{P_C}	$\Sigma\bar{i}$	σ_{P_C}	$\Sigma\bar{i}$
CC_{ids}	2.84	6.28	3.67	7.58
PP_{ids}	3.25	7.20	4.04	8.13
PC_{ids}	3.27	7.15	4.05	7.55
CC_{rr}	3.50	6.20	3.50	6.20
PP_{rr}	3.89	6.31	3.89	6.31

For six generations of selection, an average of 7.32 standard deviations of selection were applied in the within-line method and 6.26 standard deviations of selection were applied by the reciprocal recurrent

Table 5. *Predicted and realized genetic gains, correlations between the breeding value for the trait percent production and the phenotypes of the different criteria of selection, heritabilities and inbreeding (F) after six generations of selection. Confidence intervals (95%) are given for genetic gains and heritabilities*

	Genetic gains $(\Delta G)_T$			Correlation $(r_{G_T P_C})$		Heritability (h^2)		
Lines & crosses	Predicted (P)	Realized (R)	R/P	Predicted	Realized	Predicted	Realized	Inbreeding (F)
CC_{ids}	14.02	4.97 ± 2.65	.354	.5358	.1898	.148	.042 ± .032	0.114
PP_{ids}	12.51	−3.50 ± 1.96	−.280	.4855	−.1359	.101	−.022 ± .012	0.138
PC_{ids}	15.40	−0.77 ± 1.88	−.112	.5150	−.0575	.128	−.010 ± .013	0.132
$C_{ids}P_{ids}$ $P_{ids}C_{ids}$	10.56	3.83 ± 1.15	.362	.5110	.1842		.036 ± .011	0
CC_{rr}	7.70	−3.89 ± 2.80	−.505	.3452	−.1663		−.049 ± .035	0.117
PP_{rr}	7.39	−5.74 ± 2.85	−.777	.3313	−.2182		−.128 ± .064	0.123
$C_{rr}P_{rr}$ $P_{rr}C_{rr}$	7.55	2.57 ± 1.41	.340	.3385	.1046	.152	.056 ± .025	0

selection method. The within-line method is favored by 1.06 standard deviations over the six generations.

The predicted genetic gains based on substitution into equation (3) for the *ids* populations and into equation (4) for the *rr* populations are presented in Table 5. The realized genetic gains after the six generations of selection are also shown in Table 5 along with their 95% confidence limits, derived following the logic presented by Hill (1971) and including the effect of genetic drift. None of the confidence intervals included zero, except that for the PC_{ids} line. In general, the positive responses of CC_{ids} and the crosses are significantly different from those of the remaining four populations having negative gains. The confidence intervals for the three positive responses overlap, indicating that no significant difference between them exists. The same is true of the confidence intervals for the four negative responses.

The ratio of realized to predicted response (R/P) is negative for the four pure lines showing negative response. Of greater interest is the average ratio for the within-line (.363) and reciprocal recurrent selected (.340) cross populations. These values are not very different from each other or from the ratio for the within-line selected Cornell Control (.354). These figures are quite similar to that reported by Kinney *et al.* (1970) of .34 from another set of samples of the same CC_{ids} population as reported here. Since the latter figure is based on measurements of the selected trait, while the figure reported in this study is for the measurements on a correlated trait, the similarity of these ratios indicates that the correlation between these measurements was high, and use of the correlated measurement should not interfere with comparisons between the selection systems. These workers reported a higher ratio of realized to predicted gain of .71 for the case of individual selection in females for the same trait.

It is not possible to distinguish whether the low values of this ratio are due to restrictions on gains brought about by the effect of homozygosity resulting from random drift, inbreeding depression, or to the fact that the penotypic correlations between family members may include causes other than genetic relationship. Common family environmental effects would not be expected to be large for this trait in these populations since individuals were mixed at random for both selection and line evaluation. On the other hand, the calculated coefficients of inbreeding (Table 5) increased about two percent per generation. Also, the fact that response in four of the five pure lines was negative suggests that inbreeding effects were quite large. Crosses of selected pure lines with controls should be used to measure half of the response to selection, unbiased by inbreeding depression.

The realized correlations between the trait under selection and the criteria of selection ($r_{G_T P_C}$), along with their predicted values are presented in Table 5. These correlations, obtained from equations (3) and (5) are of particular interest as they are the responses in standard deviations of the trait (T) from one standard deviation of selection on the criterion of selection (C). The average correlation for the reciprocal crosses of the WLS group (.1842) was similar to that for the pure Cornell Control line (.1898) and larger than the average for the reciprocal crosses of the RRS populations (.1046), but the difference is not significant. Confidence intervals on these values resulted in interpretations similar to those for the unstandardized genetic gains.

Realized heritabilities and their 95% confidence intervals are also presented in Table 5. These were obtained from the correlations by substitution of the mean number of sires, dams and progeny measured into equations (3) and (7) and solving for h^2. The realized values are still much smaller than those predicted. Here the estimates from the RRS crosses average larger (.056) than those from the crosses resulting from WLS (.036) and much larger than the average of the two pure lines used in the crosses (.01). The estimate for the CC_{ids}, however, was intermediate between those from the two pairs of reciprocal crosses.

If reciprocal recurrent selection is superior to within-line selection, it would be a result of better utilization of non-additive genetic variance, particularly overdominance. Consequently, if large amounts of dominance or overdominance were present, and heritability was estimated on crossbred progeny performance, the heritability should be greater than if the heritability estimates were based on purebred progeny performance. The estimates based on sire variance components from cross populations are about three percent larger than the average of the estimates from the pure lines. The realized heritabilities are also somewhat larger from the reciprocal recurrent selection lines, but the differences are not significant since the confidence limits overlap.

Discussion

Several laboratories have conducted empirical comparisons of reciprocal recurrent and within-line selection. Different experimental designs at different laboratories have led to conclusions being based on somewhat different comparisons between selection methods. Rasmuson (1956) and Kojima and Kelleher (1963) compared the average of two within-line selected pure populations to the average of the two reciprocal recurrent selected crosses. Bell, Moore and Warren (1955) and Bell and Moore (1972) compared the response to reciprocal recurrent selection in two reciprocal crosses of two populations, each derived from four different laboratory stocks to response from within-line selection in a single population derived from the same eight laboratory stocks. On the other hand, when *ids* is compared with *rr* either in the report of Saadeh *et al.* (1968) or in the present study (S_2 in Table 3), the means being compared are the averages of four populations, the two pure lines and their reciprocal crosses in each breeding method. It is clear that the results of these and other studies are not comparable, and that the most appropriate comparison of the two methods should be considered.

Selection response in pure lines of small effective numbers would be reduced (Robertson, 1960) due to the effect of random gene fixation, not only at the limit, but in each generation. Shultz (1953) found that genetic gains were being made even when population means were declining due to inbreeding. The gains were able to express themselves only when the inbred lines were crossed. This may be a small effect for body weight in large populations of *Tribolium*, as claimed by Bell and Moore (1972), but could be a large factor for heterotic traits such as egg production in *Drosophila* and in poultry. Rasmuson (1956) found enough heterosis for egg production in *Drosophila* to more than offset the advantage found for reciprocal recurrent selection when the *rr* crosses were compared to the within-line selected pure lines. Some heterosis was found for egg production in the zero generation of the present study, and it developed rapidly under both methods of selection. An increase in heterosis was also observed by Saadeh *et al.* (1968). This suggests that when comparisons are made between the means of crosses from one method and the means of pure lines from the other method of selection, two things are being measured, (1) the difference in the real genetic gains due to selection, plus (2) the heterosis in the cross, or conversely the inbreeding depression in the purebreds.

If the same comparison is made in the present data from Table 2, as that made by Kojima and Kelleher (1963), the result is $\bar{X}_{rr}$ cross-$\bar{X}_{ids}$ pure values (Col. 9 − Col. 3) of 0.10, −2.53, −0.52, −1.58, 0.66 and 2.78 in the six generations. On this basis it would appear that by the sixth generation the *rr* method had caught up with and passed the gains made by *ids* selection, as predicted by Bell and Moore (1972). If comparison is made on the same basis as that used by Bell and Moore (1972) and Bell *et al.* (1955), the result is for $\bar{X}_{rr}$ cross − PC_{ids} pure values (Col. 9 − Col. 4) which are 0.73, 0.22, 0.94, 2.13, 4.33, and 4.28 over the six generations. In all generations the *rr* cross performance is superior and the superiority is increasing over generations. Again, however, the effect of heterosis and that of the selection systems is completely confounded.

On the other hand, if the *crosses* produced by both breeding methods are compared as $\bar{X}_{rr}$ cross − $\bar{X}_{ids}$ cross (Col. 9 − Col. 5), the differences of −1.50, −2.10, −1.50, −4.10, −2.30, and −1.30 for the six generations show little or no trend, even though the fourth and fifth generation differences are significant ($P < .05$). A similar comparison of $\bar{X}_{rr}$ cross −$\bar{X}_{ids}$ cross presented by Saadeh *et al.* (1968) yields 2.71, −4.53, −4.63, −1.85, −4.86, 0.20 for the six generations, again showing no trend in the amount of superiority of one method over the other. Clearly much of the superiority of *rr* to *ids* when comparing genetic gains in crosses with those in pure lines is due to inbreeding depression which places the within-line selected populations at a disadvantage.

While a number of comparisons between the two breeding methods are possible, only the comparison of the crossbred progeny produced by the two methods compares the genetic gains with a minimum of confounding with inbreeding or heterosis effects. In addition to the scientific validity of this comparison, it is also of practical interest, since commercial chicks are crosses. The desirability of comparing the means of the crosses produced by the two methods of selection has also been recognized, by Vinson, Eisen and Robison (1969) and by Biswas, Chapman, First and Self (1971). This same principle applies when comparing selected pure lines where the effective population sizes differ. In this case it is necessary to compare the crosses of the selected lines with a common tester line, such as the control, in order to get an estimate of the genetic gains unbiased by unequal inbreeding depression effects. This would have been a desirable procedure in the study of Kinney *et al.* (1970) in which the comparisons would have been between unbiased estimates of half of the genetic gains resulting from the different selection techniques.

Accurate extrapolation of the responses from these two selection methods to future generations seems unlikely. In the first place, the nature of the genetic variance present is not known, although some additive genetic variance must be present as shown by the gains in the CC_{ids} line and the *ids* crosses. Nonadditive genetic variance must also be present as indicated by the inbreeding depression in the Purdue Pool lines and the lack of response in the pure lines of the *rr* selection method. According to Comstock *et al.* (1949) reciprocal recurrent selection has the greatest advantage over within-line selection when genetic variance due to overdominance is present. While some overdominant loci may be present, no evidence of overdominant loci affecting egg production has been presented, and little evidence of any specific combining ability has been shown among selected strains and lines for egg production in the fowl (see, for example, Eisen, Bohren, McKean and King, 1967 a, b).

Secondly, in order to make additional genetic gains in the crosses by either selection method, genetic variance must continue to exist in the pure lines, and the pure lines must continue to be able to reproduce. The reproductive performance of the pure lines, particularly the Purdue Pool which was poor to begin with, has reached a point where it could have a limiting effect on gains from selection. It is doubtful whether the gains from the RRS system could overtake those for the WLS system before the reduced genetic variance and reproductive fitness in the RRS pure lines would become a limiting factor. The effective population size for the RRS system in this study was about half that for the WLS system (17.5 vs. 33.3). If total facilities had been equalized, the difference in effective population size would have been even greater (17.5 vs. 66.7).

A striking feature of these results is the negative genetic gains occurring in four of the five pure lines. Such a response in the pure lines might be expected under RRS if the regression of the pure line performance on the cross line performance was negative. But, this explanation would not apply to the negative response of the Purdue Poole or the PC_{ids} line under WLS.

A hypothesis of a large number of loci with complete dominance and being deleterious when homozygous recessive, seems to explain most of the facts observed in this experiment. Under within-line selection, both the PP_{ids} and PC_{ids} lines had negative gains while the CC_{ids} had the largest genetic gain of any selected population. The foundation lines of the *CC* population were all highly selected commercial strains and many undesirable recessive genes could have been eliminated. On the contrary, the Purdue Pool strain was developed from stocks relatively unselected for egg production, and several of the strains incorporated were of exhibition stock. Consequently, many undesirable loci were segregating and the initial performance of the Purdue Pool strain was low. Attempts to inbreed the Purdue Pool proved unsuccessful.

If the difference in the number of deleterious recessives was the only factor involved, the gains in the PC_{ids} line should have been intermediate between those for the PP_{ids} and the CC_{ids} lines. They were however, closer to the gains in the PP_{ids} line. This reduced gain in PC_{ids} could be due to the effect of initial linkage disequilibrium on response to selection, since selection was started in the initial cross of the two control lines. The deviation of these gains in PC_{ids} (−.77) from the exact intermediate value (.74) was not so large, however, that it could not be due to genetic drift.

Both of the pure lines produced by RRS had negative genetic gains. This type of response is sometimes cited as evidence of selection for overdominant gene effects in the cross. This could be the explanation in the present case. However, a similar result could occur in such small populations in the presence of only simple dominance, as hypothesized. Within-line selection would tend to maintain the frequency of the favorable dominant alleles at high levels in the pure lines, minimizing the number of homozygous recessive individuals in the population. Selection in the Purdue Pool line was not able to surmount the effects of the initial high frequency of undesirable recessive alleles and the changes in phenotype became negative after the third generation. Under reciprocal recurrent selection, the selection pressure was directed toward having at least one dominant allele at each locus in the cross, so there was less pressure to keep the frequency of the desirable dominant alleles high in the pure lines. In addition, after a dominant allele is fixed in one line, *no* selection would be applied to that allele in the other line. The gene frequency at such loci would drift at random and many would become homozygous for the undesirable recessive. The two pure lines declined about the same amount under RRS, and the facts that a decline occurred in the PP_{ids} but not in CC_{ids}, and that heterosis developed at equal rates under both selection methods argues for simple dominance and against overdominance as an explanation of this decline.

It is reasonable to conclude that the magnitude and direction of the differences observed in this experiment are explainable on the basis of genetic theory, in spite of the fact that some of the differences are not statistically significant. On this basis it could be concluded that, given equal selection intensity and identical selection criteria, RRS may be slightly superior to WLS for improvement of this trait because of the larger calculated and realized heritabilities in the cross populations, as expected when non-additive variance is present, even though this difference is not statistically significant. At the other extreme in a practical situation, however, the methods would be compared on the basis of equal facilities, such as equal numbers of breeding pens and or progeny holding capacity, in which to select two pure lines for subsequent crossing as proposed. Then the advantages of WLS would outweigh any apparent advantage of RRS because of the greater potential selection intensity, larger correlations between the breeding values and the possible criteria of selection, and because of having three to four times as large an effective population size in the pure lines. The latter would be a major deterrent to the relative long term progress by RRS due to reduction of genetic variance in the pure lines by random drift rather than by selection.

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