COMPARISONS OF THE PREDICTED WITH ACTUAL GAINS FROM SELECTION OF PARENTS OF INBRED PROGENY OF RATS*

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DEDUCTION from genetic theory enables one to predict how much genetic gain ought to be made per generation from a known amount of selection. Knowledge of the extent of disagreement between the predicted and actual results and inquiry into possible reasons for any disagreement is of considerable importance in the field of animal breeding.

Even though there is a large body of literature on selection for various characters in animals and plants, little attempt has been made to compare the effectiveness of selection with that expected on the basis of the degree of selection and heritability.

Comparisons between the expected and observed results have been reported by DICKERSON and GRIMES (1947) for feed efficiency in swine, by LERNER and HAZEL (1947) for a production index in poultry, by KRIDER *et al.* (1946) for growth rate of swine, by FREY and HORNER (1955) on barley, and by DICKERSON *et al.* (1954) for growth rate within inbred lines of swine. These authors report no obvious discrepancy between the observed and expected in certain traits but less effectiveness than expected in others.

KYLE and CHAPMAN (1953) made a comparison of the theoretical effectiveness of selection with the actual results obtained experimentally for ovarian response to a gonadotrophic hormone in rats, using noninbred progeny only. Selection was made for high and low responses on the basis of full sister and progeny information. The average ovary weight of each litter was predicted from that of sisters of parents using the heritability for individuals derived from an earlier study by CHAPMAN (1946). This study indicated that in general the observed gains from selection for high and low responses were somewhat less effective than predicted.

The present investigation is an extension of the above study involving comparison of the predicted averages with the observed ovarian responses in inbred offspring.

MATERIALS AND METHODS

The technical details of the experiment are fully described by CHAPMAN (1946) and KYLE and CHAPMAN (1953). In the first of these studies it was found

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that 36 percent of the total variance of ovarian response was due to additive gene effects (heritability, g^2, in the narrow sense) in the random bred population which formed the foundation stock for the present selection experiment. Environmental factors common to litter mates (e^2) were found to be responsible for 22 percent of the total variance.

In the second study, on a selectively derived population, it was indicated that the earlier estimate of g^2 may have been too large and e^2 too small. This was suggested by the similarity in sizes of the correlations among full sister litter mates in the foundation stock and in the selected stock, and the lower aunt-niece correlation in the selected than in the foundation stock. When $g^2 = .22$ and $e^2 = .26$ were used in the predictions close agreement was obtained between the predicted and observed results on these same data. For this reason a heritability of .22 for ovarian weight of an individual rat was used in the present study of inbreds.

An inbred is defined here as an individual whose inbreeding coefficient (WRIGHT 1922) exceeds .0625. The comparisons of predicted with observed averages in the present study were made within inbred progeny produced by inbred parents, by "outbred" parents, and by "crossbred" parents. An "outbred" results from parents which are bred at random except for an attempt to avoid inbreeding of progeny. "Crossbred" refers to progeny from line-crossing (mating inbred, but unrelated animals), topcrossing (mating inbred males to unrelated outbred females), and bottomcrossing (mating outbred males to unrelated inbred females). The different kinds of "crossbreds" were combined for presenting results because of their similarity in degree of heterozygosity and the small number of matings available in each classification.

Since a preliminary study indicated an effect of progeny testing on gain from selection, the prediction equation should include this aspect of selection. Due to the difficulty of disentangling the progeny data used in prediction from those found in the observed results, the present analysis was confined to those litters of offspring whose parents were not progeny tested. The prediction equation for the present study was similar to that derived by KYLE and CHAPMAN (1953).[1] The predictions were made on the average ovary weights of offspring resulting from a given mating whether or not all offspring belonged to one litter.

Simple average of all offspring resulting from different matings were used as the observed values in the comparisons with the predicted ones. The test of signifi-

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[1] $\hat{A}_O = f\,(\bar{A}_M, \bar{A}_F, n_S, n_D, n_i, r_S, r_D, f_S, f_D, A_S, A_D, g^2, e^2)$

where:

$\hat{A}_O$ = Predicted average corrected ovary weight of a particular litter of offspring.

$\bar{A}_M$, ($\bar{A}_F$) = Unweighted average of the sister average ovary weights of all males (females) in sire's (dam's) generation.

n_S, (n_D) = Total number of sire's (dam's) sisters in all litters.

n_i = Number of offspring in a particular litter.

r_S, (r_D) = Relationship between full sisters of sire (dam).

f_S, (f_D) = Inbreeding of sire (dam).

A_S, (A_D) = Average corrected ovary weight of sire's (dam's) sisters.

g^2 = Heritability of individual's corrected ovary weight.

e^2 = Fraction of variance due to environmental factors common to litter mates.

cance of differences between the observed and predicted was made by means[2] of:

$$F = \frac{N(\sum_{1}^{N} W D)^2}{(\sum_{1}^{N} W)\ (\sum_{1}^{N} W D^2)}$$ with 1 and N degrees of

freedom where:

N = Number of pairs of comparisons.
W = Number of offspring on which the observed average was based.
D = Individual difference between the observed and the predicted values.

The comparisons were made by generation, on several generations combined, and over all generations within and over parental mating types. The detailed results by generation and by several generations are not presented here. The average numbers of generations of selection covering high and low response lines were 14, 12, and 6 for the parental groups of inbred, outbred, and crossbred, respectively.

RESULTS AND DISCUSSION

Inasmuch as this study was concerned with the prediction of ovarian response of inbred offspring in relation to actual response, an attempt was made, in a preliminary study, to evaluate the extent to which the character was affected by inbreeding. The average performance of inbred offspring was compared with that of their noninbred aunts, and the data were also examined for any association between the degree of inbreeding (WRIGHT 1922) and the average ovarian response. There was no indication of the trait being influenced by inbreeding.

The over-all predicted and observed results are presented in Table 1 with the averages of some of the factors involved in the predictions. The average values of sister performances, the population averages, the average "selection differentials," and the averages of numbers of sisters of the parents, and the inbreeding of the parents were weighted by the numbers of observations in each generation giving equal weight to the sisters of the sires and dams. The average of the population from which a particular parent was selected was taken to be the average of sister averages of all individuals of the same type of mating as the parent. "Selection differential" refers to the deviation of the average ovary weights of parental sisters from the population average in a given generation. Differences between the observed and predicted were expressed so that the negative sign indicates that the observed did not reach the predicted.

Inbreeding was negligible for the outbred and crossbred parents in the high and low groups whereas the average inbreeding of inbred parents was .19 for the high compared to .25 for the low response group. The average inbreeding of off-

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[2] The authors are indebted to Drs. M. Kimura and N. E. Morton for derivation of this formula.

TABLE 1

Averages of the observed and predicted ovary weights of inbred offspring from parents selected for high and low ovarian response under different mating systems and the averages of some of the factors involved in the predictions

Kind of parents	Numbers of matings	Sister averages	Population averages	"Selection differentials"	Numbers of sisters	Inbreeding of parents	Relationship of parental sisters	Inbreeding of offspring	Numbers of offspring	Observed offspring avg. (A_0)	Predicted offspring avg. ($\hat{A}_0$)	Differences†
HIGH RESPONSE												
		mg	mg	mg						mg	mg	mg
Inbred	95	93.4	73.0	20.4	2.8	.29	.68	.35	2.0	76.6	80.1	—3.5
"Outbred"	46	97.6	75.5	22.1	2.6	.04	.52	.19	2.6	85.7	80.8	4.9*
"Crossbred"	16	88.4	68.3	20.1	2.7	.06	.53	.25	2.2	76.8	73.2	3.6
All	157	94.1	73.2	20.9	2.7	.19	.62	.29	2.2	79.3	79.6	—.3
LOW RESPONSE												
Inbred	111	45.6	60.5	—14.9	3.5	.37	.72	.43	2.3	55.1	54.1	—1.0
"Outbred"	36	46.0	67.0	—21.0	3.0	.01	.51	.21	2.2	61.0	61.2	.2
"Crossbred"	19	44.5	67.4	—22.9	2.4	.03	.52	.23	2.1	52.0	61.5	9.5
All	166	45.6	62.7	—17.1	3.3	.25	.65	.36	2.2	56.0	56.5	.5

* $P < .05$.

† ($A_0 - \hat{A}_0$) for high response group and ($\hat{A}_0 - A_0$) for low response group.

spring over all mating types were .29 and .36 for the high and low response groups, respectively.

The average observed ovary weights for the high response group of progeny were 76.6, 85.7, and 76.8 mg as compared to 80.1, 80.8, and 73.2 mg for the predicted from inbred, outbred, and crossbred parents, respectively. The difference of 4.9 mg for offspring from outbred parents was found to be significant at the five percent level. However, the observed average 79.3 mg over all parental mating types was not significantly different from the over-all predicted average of 79.6 mg.

For the low response lines, the observed values were 55.1, 61.0, and 52.0 mg in contrast to 54.1, 61.2, and 61.5 mg for the predicted for offspring from inbred, outbred, and crossbred parents, respectively. The averages of the observed and predicted over all mating systems were 56.0 and 56.5 mg, respectively. None of the differences between the predicted and observed for the different mating systems or over-all in the low group was found to be significant.

No obvious trend was seen in the effectiveness of selection relative to number of generations of selection, nor was there any consistent trend with increase in inbreeding of the offspring.

In spite of the fact that the predictions of offspring performance were made on the basis of varying numbers of relatives of parents and with varying degrees of inbreeding and relationship in the relatives, these complicating factors appeared to have been taken into account adequately in the equations used to give statistical effect to genetic theory.

It is noted that the agreement between the observed and expected ovary weights of inbred progeny in the present experiment appeared to be better than in the noninbred stock studied by KYLE and CHAPMAN (1953). In comparing the present study with the previous one on the noninbred progeny, it must be remembered that the heritability for individuals of .22 was used here instead of the .36 used earlier, and that the effect of progeny on the prediction was taken into consideration in this analysis and not in the earlier one.

Considering all mating systems in this study and the earlier one, the general agreement between actual observation and prediction based on estimates of additive genetic variability ($g^2 = .22$) imply that nonadditive genetic variability was not playing an important role in causing differences in this particular character. The present experiment does not, of course, provide a very precise test of the presence of nonadditive genetic variability.

The effectiveness of mass selection, at least for early generations of selection, has been abundantly demonstrated for different traits of various organisms by WINTER (1929), MACDOWELL (1915, 1917, 1920), CASTLE (1919), GOODALE (1938, 1941), MACARTHUR (1944, 1949), ROBERTSON and REEVE (1952), FALCONER (1953), LEWIS and WARWICK (1953), and others. That the mere presence of additive genetic variability does not assure the effectiveness of mass selection after many generations of selection was shown by ROBERTSON and REEVE (1952) and REEVE and ROBERTSON (1953) in wing length in Drosophila and by DICKERSON *et al.* (1954) in several traits in swine.

The trait dealt with in this study is one for which there is no obvious adaptive value represented within the range of values observed. Likewise there was no indication from the analyses that litter size at birth or age at vaginal opening were genetically correlated with ovarian response. Following the argument of DICKERSON (1955) and others this character would not be one in which it would be expected that additive variability would have been exhausted or unavailable for selection due to previous selection pressure.

SUMMARY

Selection for high and for low response to a standard dose of gonadotrophic hormone was practiced in the rat for different numbers of generations under mating systems involving inbred progeny from inbred, outbred, and crossbred parents. Comparisons were made between the actual and predicted gains from selection. The predictions of the average ovarian responses of offspring were made from the averages of full sisters of parents based on a heritability of .22 for ovarian response of an individual.

In general, good agreement was obtained between the observed and predicted averages in both the high and low selection groups. Over all generations and mating systems of parents, the average ovary weights of the observed and expected were 79.3 and 79.6 mg, respectively, for the high selection line. The comparable values for the low group were 56.0 and 56.5 mg.

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