INBREEDING FOR THE GENETIC ANALYSIS AND IMPROVEMENT OF POULTRY POPULATIONS

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The use of inbred lines in poultry breeding was the subject of several investigations during the late Twenties and early Thirties. In many ways this work represented the first attempts to utilize new systems of breeding based on genetic principles and on the experiences of plant breeders who were then developing inbred lines of corn. It soon turned out that rapid inbreeding of chickens by brother × sister matings or by somewhat less intensive systems lead to the elimination of most lines within a few generations (Dunn, 1923; Jull, 1929, 1933; Hays, 1940). Other experiments resulted in the establishment of experimental inbred lines which apparently were lost or discarded after publication of their history (Goodale, 1926; Schultz, 1953). One possible reason for the loss of inbred lines in the above investigations may have been the fact that they were developed primarily to illuminate the process of inbreeding and not for the express purpose of obtaining viable highly inbred lines. Several attempts of the latter kind have however been made and have been successful. Thus, Waters and Lambert (1936), at Iowa State College were able to breed 6 highly inbred lines beginning in 1925 continuing over at least 12 years, one of them under continued sib-mating for 9 generations. Similarly, Dudley and Pease (1948) reported the successful establishment of 5 inbred lines under continued sib-mating from 10 to 22 generations. One of these lines-(I) had been obtained by Pease in 1938 from Iowa State. Some of these lines are still in existence, at calculated inbreeding levels exceeding 98%, (Somers, 1971).

Still another successful attempt at the breeding of highly inbred lines was initiated by Waters in 1940, with the goal of establishing genetically homogenous
stocks differing in their susceptibility to avian leukosis. Beginning with 99 matings from 9 different White Leghorn flocks Waters bred 15 lines, using strong initial selection between families for high hatchability followed by up to 4 generations of sib-matings, and later inbreeding at less intensity in larger groups. Of these 15 lines 3 (lines 6, 7 and 15) are still alive and are being used extensively at the East Lansing Poultry Disease Research Laboratory, at inbreeding levels in excess of 95%. Each of them now exists in the form of several sub-lines with modified susceptibility characteristics. It would appear that Waters applied at East Lansing many of the experiences of his inbreeding work at Iowa. Especially noteworthy is the reliance on strong initial selection for reproductive ability within and between lines.

It has thus been shown that highly inbred lines in chickens can be established and maintained indefinitely. Some of the most highly inbred lines also have found excellent use in the elucidation of the genetic control of resistance to lymphomatosis (Crittenden et al., 1972a, 1972b), and Mareks disease. Furthermore the use of inbreds for the production of commercial laying hens is a well established practice, although inbreeding levels in commercial lines are below 70% (Briles, Allen and Millen, 1957; Briles and Allen, 1961).

The aforementioned empirical studies of inbreeding and the successful use of inbred lines in biological work have been conducted with a minimum of theoretical considerations, and without a great deal of emphasis on the possibility of using the inbreeding process as a tool for the analysis of quantitative genetics of populations. Our own work on inbreeding was, therefore, initiated in 1956 in order to analyze the genetics of chicken, turkey and quail populations maintained
at the Davis Experiment Station. Of particular interest was a chicken population which had been under selection for egg production over about 20 generations (Berkeley Production flock, described by Lerner, 1958). After rapid selection response in the early generations this population had shown tendencies towards reduced genetic gains and was considered at a selection plateau when the current studies were initiated. In spite of reduced gains from artificial selection these populations showed genetic variance of almost unreduced magnitude and our investigation of non additive gene action began as a consequence of this apparent contradiction.

A considerable body of theoretical knowledge on the inbreeding process had been developed by the mid-fifties, when our own studies on inbreeding were initiated. Among the best investigated systems of breeding was that of continued brother x sister matings, where theoretical expectations for the change in mean performance, the variance within and between inbred lines derived from the same parent population as well as predictions of performance of crosses had been made (Robertson, 1952).

**Genetic Considerations and Experimental Design**

Perhaps the simplest genetic models that could account for reduced genetic gains under selection without a reduction in genetic variance would be the control of the characters involved by unfavorable recessive genes with individually small effects and at generally low gene frequencies. Such a situation is likely to prevail after long periods of directional selection during which favorable dominant alleles have been brought close to fixation, especially for genes with large effects. It is perhaps not unrealistic to assume that this may have happened within the population considered which had been under intensive artificial selection for 20
generations and with marked selection response. This simple dominance model of gene action can be contrasted in its implications with a model of heterotic (overdominant) genes where all homozygotes are assumed to be inferior to heterozygotes. Continued selection in a large population for high performance would lead to a genetic equilibrium where both inferior homozygotes as well as superior heterozygotes persist, without changes in the population mean. Genetic variance at equilibrium would then be of the dominance type with zero additive variance.

The work I wish to report today falls into two main parts. The first entails the use of sib-matings within relatively large populations as a means of eliminating deleterious recessive genes and is thus aimed at a reduced inbreeding depression of egg production and reproductive traits. The second experiment deals with the feasibility and problems of establishing highly inbred lines with high reproductive performance by means of continued full-sib mating.

I. Intermittent full sib mating within chicken populations under selection for egg production.

The problem of eliminating deleterious recessive genes has arisen in our work with a population of White Leghorns in which irradiation with X-rays was used as a means of increasing genetic variability (Abplanalp et al., 1964). This experiment, as far as the present report is concerned, consisted of two populations derived from a common line of Leghorns selected for egg production since 1932. After their inception in 1952 one of the lines (X) was irradiated with 8000 roentgen X-ray of semen over 7 generations, while the other line was reproduced at random. An estimated effective population size of about 80 was maintained during this initial phase of the experiment as well as in subsequent generations. Since all irradiation was applied to semen from about 30 males each generation it can be assumed that
induced mutations were present at frequencies of not much less than 1 percent.

After the irradiation phase of the experiment both populations were subjected to 7 generations of artificial selection for egg production to about 40 weeks of age with an index designed to give optimum weight to family means. Both populations were divided into two sublines. In each case one of the sublines was held under cage management, the other in large floor pens. Furthermore an attempt was made to maintain constant egg size in the floor replicates, while no restrictions were in effect for hens in cages.

In 1963 replicates of each population were crossed and inbreeding, by sib-mating, was initiated as a test for deleterious genes. (Abplanalp et al., 1964; Lowry and Abplanalp, 1970).

Selection response during the second phase of the experiment was evident in all populations but those with a history of irradiation showed no advantage over the controls as one would expect if additive genetic variability had been induced. Since the X-lines had shown reduced reproductive performance at the end of irradiation they ended the selection phase still well below controls in egg production and hatchability. Surprisingly, however, they exhibited better viability and higher egg weight than the controls throughout phase II. Furthermore, it was shown in analyses of variance that the irradiated lines had increased genetic variability for egg size (Abplanalp et al., 1964). Egg production on the other hand showed substantially increased variance components for individuals and full sib families, while variability of half sib groups remained unchanged. Such a result would be expected if radiation induced variability in egg size were of the genetically additive type while induced mutations affecting production were deleterious and primarily recessive. This conclusion was strengthened by preliminary observations of inbreeding effects in the two populations: Egg production
showed a greatly increased decline under sib mating in irradiated lines as compared to inbreeding depression in controls. Egg size declined somewhat in X-ray lines and very little in controls. These findings together with our interest in the study of inbred lines suggested the procedures for phase III of the study.

Our objectives for work in phase III were quite simple, namely: First to obtain more substantial information on non additive gene action from full-sib matings; second to apply artificial selection within and between inbred families in order to permanently reduce inbreeding depression; and third, to use for selection an index designed to increase egg production while holding egg weight constant, rather than a system of empirical culling levels employed in phase II.

The general plan for this study (Fig. 1) was applied to each of two populations established in 1964 by subline crosses: The X-line with a history of irradiation followed by selection; and the C-line, its non irradiated control.

Within each population (Fig. 1) three sublines were formed in 1964:

1. A selected control subjected to index selection only (subline R);
2. A subline in which full-sib matings were alternated with crosses of these inbreds, with index selection applied each generation;
3. A subline in which two generations of sib-mating were followed by crosses of inbreds, with index selection each generation.

Additional inbreds were produced each generation from the subline R flocks as a control for inbreeding depression. These test-inbreds were, however, not used for selection of parents for subline R. Test inbreds were produced by adding to each mating pen two sisters of the selected sire. Special care was taken to equalize the selection applied to these dams and the remainder of mated hens.
This procedure tended to reduce selection intensity in the control subline below the maximum possible; but it actually made controls more comparable to the cyclical sublines where inbreeding reduced the number of available offspring.

The R sublines were reproduced with 15 sires, each mated to 5 dams with approximately 300 pullets available for selection. In the cyclical sublines 40 pair-matings were made each generation, with approximately 240 offspring.

Selection was based on index values calculated for each pullet separately; family averages of indexes were then considered for selection of males. While these procedures are not optimal they were considered more comparable between populations than index procedures designed for optimum response within populations.

Phase III of the radiation experiment covered 8 generations of controls and four cycles of inbreeding and crossing in the two-year cycle and two complete cycles of doubly inbreds, followed by some additional inbreeding in the X-ray lines.

Selection response in the R sublines of populations X and C for egg production to 40 weeks is shown in Fig. 2 from 1958 to 1972, covering the entire selection period since irradiation of the X-line. Clearly both lines increased their egg production, but the X-line remained below its control throughout. However, this is not the entire story. When egg weight is considered, which was specifically included in the selection index since 1963 it can be shown that the X-line improved in egg size, while the C-line remained more or less constant for this trait. Thus, in total egg mass response over the last 8 generations the X-line actually improved faster than the control.

The presence of X-ray induced deleterious genes can be inferred from inbreeding depression of the X-line when compared to that of the control, using sib matings within each generation from the selected control sublines. These results are
shown in Table 1 for the years 1963-67, for egg production and egg weight. The evidence is that the loss in egg production due to 25 percent inbreeding was almost twice as great (13 eggs) for the irradiated line as for the control. Similarly egg weight in the X-population dropped considerably (1.4 g) while only mild depression is seen for the control. These results thus support preliminary observations and demonstrate that radiation induced deleterious recessive genes affecting both egg production and egg weight. The latter result is perhaps a little surprising, since egg size has a high heritability and has been shown to be unaffected by inbreeding in some of the older studies. Our results suggest that long term selection for egg number may also bring out genetic effects of recessive genes upon egg weight.

In the non-irradiated lines the initial generation of inbreeding in the subline with alternating sibbing and crossing turned out to have unexpectedly high egg production, exceeding the control, and in contrast to all other sets of inbreds obtained in the experiment (Fig. 3). While this initial result remains unexplained it can be seen that subsequent generations of inbreeding in both cyclical sublines fell regularly and substantially below control levels. Both generations of doubly inbred pullets also fell below singly inbreds obtained from controls and cyclics within the same year. A comparison of singly inbreds in the two-year cycle with singly inbreds from the control subline shows a consistent superiority in the cyclics. This observation would support the assumption that recessive deleterious genes were either eliminated under selection with inbreeding or reduced in frequency. Inbreeding depression in singly inbred pullets following a cross of doubly inbreds on the other hand fell below the control inbreds in both years when this comparison was made (1967 and 1970). This result at first sight appears to indicate a lack of selection
response against inbreeding effects; but a calculation of inbreeding coefficients under the double inbreeding plan shows F-values for the once-inbreds of 25.0 in the first cycle of inbreeding, 34.3 in the second and 35.7 percent for the third cycle. These last two values are considerably higher than the relative inbreeding of 25% expected for inbreds from controls, and observed inbreeding effects thus appear not out of line with those of controls. Similarly the doubly inbreds (II) in 1965 and 1968 seem to show relatively less inbreeding depression than controls when their relative inbreeding coefficients of 42.2 and 43.1 are taken into account.

Cyclical inbreeding also appears to have resulted in selection response expressed in crosses of singly and doubly inbreds. All crosses performed better than comparable generations of the selected control subline. This response is likely to be due to additive genes. Since crosses did not increase their relative advantage over the generations one might also assume an exceptionally lucky sampling at the first establishment of the two cyclic lines.

In the irradiated lines selection response differed markedly from that of the control sublines (Fig. 4). Here the first generation of inbreds used to establish both cyclic sublines appears exceptionally low in production (-26 eggs compared to control). However inbreds thereafter showed marked improvement from generation to generation to a point where the fifth inbred generation for cycles with singly inbreds almost equaled controls in 1972. Doubly inbreds also showed improvement. This was especially apparent when control inbreds also were carried to a second inbreeding generation, but without selection (1971-1972). Thus in 1971 control inbreds (I) were some 10 eggs below doubly inbred cycles and in 1972 doubly inbred controls similarly lay below triple inbreds from cycles. The results of inbreds thus strongly suggest that selection under inbreeding was reducing inbreeding depression, possibly by eliminating radiation induced recessive genes with fairly
large effects.

The performance of crosses in cyclic X-ray sublines improved consistently for singly inbreds to a point where they equaled (1969) or exceeded control performance (1971). Random matings among selected crosses (R) also resulted in a population equal to or better than the control.

Increased selection response in cyclic inbreds should of course be attributable to increased genetic variability in these populations. Perhaps the least biased estimate of changes in genetic variance under inbreeding can be obtained from the first generation inbreds of control lines, where each selected sire was mated to two sisters besides the 5 selected and unrelated dams assigned to him for reproduction of the line. Taking only offspring from the sib-matings analyses of variance were performed for 8 generations in each population (Table 2). Under random mating the two selected control populations had almost the same amount of variability with rather high heritability for egg production of about 30% and of about 70% for egg weight. Under inbreeding the variance between sires increased consistently in both lines but not nearly as much as one would expect for additive genes where the sire component should increase from $1/4$ of the initial additive variance to $5/8$ of its value. In the control line variance due to dams declined; in the X-ray population however, the dam-variance component increased for egg production, and individual variability increased markedly for egg production and increased to a lesser extent egg size. These results appear to be in reasonably good agreement with the assumption of relatively rare recessive genes affecting the performance of egg production and to a lesser extent, egg weight. Theoretical expectations of genetic variance due to additive and deleterious recessive genes are shown in Figs. 5a, 5b and 6. The results in Fig. 6 are particularly relevant to the case
considered since a gene frequency of the recessive deleterious gene was set at a fairly low value of 0.1. Under these conditions the genetic variance within lines would more than double in the first generation of inbreeding. Similarly the variance component due to sires would increase since it is confounded in our design with the between-line variance of Fig. 6, and an increase in variance due to dams would also be expected. Since the X-ray induced genes would very likely be present with frequencies below 0.1, individual variance would be expected to increase rather more than shown in Fig. 6. If allowance is made for environmental variability the results for egg production suggest that genetic variance between individuals increased almost fourfold under inbreeding (Table 2). It is therefore perhaps not unreasonable to propose that selection against recessives under cyclic inbreeding with sib-matings can be effective as suggested by the selection results.

II. The development of highly inbred lines by continued sib-mating.

As mentioned in the introduction there have been many attempts at the development of highly inbred chicken lines, but few of them have employed continued sib-mating. Furthermore only 4 or 5 lines with inbreeding over 90%, other than those to be reported here, are now in existence. It is fair to say that none of them would be considered to have good egg production, viability and hatchability by commercial standards. Our own experiments which were begun in 1956 had the objective to investigate the feasibility of breeding highly inbred lines of chickens with equal or better reproduction than the populations from which they were derived. Such an undertaking must by necessity involve a great deal of selection in order to allow sufficient opportunity for eliminating deleterious genes, most of them recessive and detectable only when homozygous.
The selection of high performance inbreds is not only of potential practical value but may answer a question which has been with us for a long time and for which so far no convincing quantitative answer has been found: How important are overdominant genes in causing inbreeding depression as compared to deleterious recessive genes? If overdominant genes were causing a great deal of the total inbreeding depression observed in egg production, hatchability and viability of chickens then it should be impossible to breed high performance lines; also, some heterozygosity might be maintained in highly inbreds indefinitely.

Our main approach to the problem has been a system of cyclical inbreeding in which an initial set of inbred lines was developed from a pair of base populations by sib-mating with fairly intensive selection, including elimination of many started lines. Such between-line selection is considered an important part of the plan, because it takes advantage of the fact that the variance between lines due to recessive genes increases rapidly in successive generations of sib-mating, especially when the genes are at low frequency in the base population, as shown in Fig. 6.

Long-term predictions showing the effects of between-line selection under cyclic sib-mating have been worked out by computer simulation, using a system of ten sib-lines, inbred for 5 generations each cycle with elimination of the five poorest performing lines at the fifth inbred generation and recrossing the remaining 5 lines to give a new set of 10 lines. Fig. 7 gives the results for a system of ten completely recessive genes all unlinked and at an initial frequency of 0.1 within the base population. Since the relative importance of each gene in this system is quite large the maximum limit of 20 units was almost reached within 4 cycles. Lower selection limits would be expected with more genes contributing to inbreeding
effects. The most important feature of this breeding plan is the consistent and marked improvement in inbred performance with a gradual decline of inbreeding depression each cycle.

A second gene model, consisting of 10 overdominant loci under the same breeding system is given in Fig. 8. In contrast to the recessive gene model there is no improvement, over cycles, with overdominant genes. Because only 5 lines were used to reconstitute each cycle the entire population of lines eventually lost heterozygosity by chance and declined in both inbred and cross performance. This distinction, among genetic models, will serve, among other things, as a criterion in judging the relative importance of overdominance in the development of highly inbred lines in our experiment.

The practical implications of the two genetic models are that with recessive deleterious genes as the major cause of inbreeding depression, it should be possible to select inbred lines free of such genes and hence at performance levels equaling the best crosses. For overdominant gene loci the best inbreds would never perform at the level of the best crosses. Of course, we can perhaps all agree that neither one nor the other genetic model is exclusively in control of reproductive performance and economically important characteristics of chickens. We also recognize that additive gene action must exist even for traits known to be subject to inbreeding depression. What does seem important, however, is the question of whether or not overdominant loci are sufficiently prevalent to preclude the breeding of high performance inbreds, or whether selection on dominant and additive genes can produce improvements sufficient to give high performance inbreds even in the presence of some overdominance.

Our experiment with highly inbred lines was an attempt to gain information on
this question, under a system of cyclic inbreeding. An outline of the experimental
design is shown in Fig. 9. In 1955 two base populations were available, both
derived from the Berkeley Production line mentioned earlier. Of these two lines
one (Line 1957) had been under continuous selection for egg production since 1932;
the other line (Line 1952) was taken off from Line 110 in 1952 as a randomly
selected control. Beginning in 1956 both lines were propagated with about 30 pair
matings under random selection except for the retention of maximum numbers of
families to reproduce the line.

Inbred lines were initiated by full-sib matings from each control population
in three successive years, beginning 1956 as shown in Table 3. Over the three
years a total of 279 sib matings were attempted, of which 203 left offspring. In
a few instances two full sib matings were derived from the same family but a total
of 120 independent lines were represented by live pullets and males at the end of
the first inbred generation, as shown in Table 3. In the second generation of
sib-mating 68 lines survived and at the end of the third generation 39 lines were
represented by live birds available for mating. The number of surviving pullets
in the first three generations of inbreeding were 431, 294 and 162, respectively,
for an average of about 4 surviving pullets per line. Thus about half of the lines
were eliminated in each of the first generations, and since each line was ultimately
propagated by only one pair mating a selection intensity of one out of four hens
was maintained within lines.

The principal mode of selection in the first three generations was the
elimination of families by natural selection due to poor egg production, low
hatchability and high mortality of chickens. Artificial selection was applied
through the use of duplicate or triplicate matings within full sib lines which
permitted the elimination of reserve families with low numbers of live chicks at the
end of the hatching season.

During the first three generations of inbreeding no attempt was made to keep specific lines alive. Eggs from only three week's production were accumulated for a single hatch and families evaluated after the chicks were sexed. This strategy was changed after three generations, when the hatch season was extended to 8 weekly hatches and an attempt was made to maintain all lines which were alive at that point. However, lack of egg production, poor semen production, extreme sex ratios and poor viability of embryos and chicks continued to eliminate many of the lines during subsequent generations. As the number of lines declined our efforts for keeping them alive were intensified, mainly by keeping reserve families for each line and by extending the number of reserve matings to six from the family selected to propagate the line. All these attempts really meant that selection between lines was gradually discontinued and selection within lines intensified as the experiment progressed.

An important consideration in planning the propagation of inbred lines by full sib mating is the loss of families by chance due to unbalanced sex ratios of survivors. This fact was not fully appreciated at the outset and much potential selection pressure was lost in the first three generations due to the chance elimination of lines because either all females or all males had been lost with ample survivors of the other sex. If the rate of egg production from mated hens, as well as the percent fertility, hatchability and viability of offspring are known then one can work out the probability of having at least one male and one female represent a family at mating time, given number of weekly periods over which hatches are saved. The results of this investigation are shown in Fig. 10, where the probability of family survival is plotted against the duration of the hatching season.
The four curves represent successively lower coefficients of reproduction (P) as measured by the probability of obtaining survivors from a one-day egg collection. For our control lines a P-value of .3 was computed, while for highly inbred lines a P value of 0.1 has been typical. The results show that a 4-week hatch period assures survival of 98 percent of non-inbred families while for highly inbreds the same period of egg saving would result in survival of only half the full sib families set up in matings. These odds are substantially improved however, when several reserve matings are planned within lines from which the best is chosen to propagate each line.

In retrospect it can be said that artificial selection during the first 3 generations of this experiment could easily have been doubled if a longer hatching season had been used.

Throughout the experiment the two random controls (100 and 110) were reared and housed together with inbreds and inbred crosses. In addition, reciprocal crosses between the random controls were made to obtain a control free of inbreeding. The performance of these lines in 40 week survivor egg production during the 16 years of their existence is shown in Fig. 11. It would appear that the two lines had comparable egg laying potential even though selection had been continued for 5 years in one of the lines (in Line 1957 from 1952-56) while Line 1952 was relaxed. The resulting initial superiority of Line 1957 was, however, lost soon after it too was relaxed in 1957. Crosses between controls had better laying ability than the lines themselves by some 5-10% showing that inbreeding had indeed lowered egg production in control lines. Year-to-year fluctuations in egg production of controls tended to be modest and without noticeable trend throughout the experiment.
Three-year averages of all inbred lines and the average of controls for 50-week survivor production is shown in Fig. 12. In the case of inbred lines the three-year averages are summarizing equal levels of inbreeding according to their year of origin as shown in data of Table 3.

It is quite apparent from the graph in Figure 12 that the decline of egg production was pronounced in the first generation of inbreeding but remained more or less unchanged thereafter. This result indicates that selection for large family size tended to counteract the rapid decline in egg number, except for the first generation of sib mating when the calculated level of inbreeding reached 25% (1956-58). Thereafter, selection of large families within lines and the drastic reduction in the number of surviving lines appeared to favor lines with high egg production. While the average decline of combined inbred lines allows the conclusion that selection operated to reduce inbreeding depression to less than expected levels we may now turn to examine how the best and lowest surviving inbreds performed. These results are summarized in Fig. 13. Histograms of 40-week survivor production are shown for one of the controls (Line 100, previously identified as Line 1952), the highest producing inbred (Line C) the lowest inbred (Line H), an intermediate line (I) as well as the backcross of a first cross between I and C (IC) on Line C (Backcross CCI). These results demonstrate the wide range in performance from some 35 eggs for Line H to 95 eggs of Line C as compared to the control with an average of some 85 eggs. Clearly the best inbred line outperformed the base population substantially, suggesting that overdominance cannot account for much of the initial inbreeding decline observed for egg production. If it did then none of the inbred lines should reach the performance level of the base population. This interpretation of results is however not entirely adequate,
because our base population had not in fact reached its maximum potential performance for egg production due to additive genes. This becomes apparent when egg weight of the lines is taken into account. While the egg size in the base populations remained unchanged throughout the experiment at about 55.0 gm, Line C is characterized by exceptionally small eggs averaging 46.5 grams, while Line H, the lowest producing inbred has an egg size of about 56.5 gm. What happened during the inbreeding and selection process was a strong selective change in some lines towards high egg number at the expense of egg size on the basis of primarily additive genes and in accordance with the well known negative genetic correlation between the two traits. Similar shifts in egg number at the expense of egg size presumably would have been possible in the absence of inbreeding as demonstrated in other studies involving the Berkeley production lines (Abplanalp, 1961). Nevertheless it is noteworthy that the absolute production level of our best inbred is very high with around 80 percent production. Until now no other highly inbred line with F in excess of 90 percent has been known to be capable of producing at such levels. Even higher rates of production have by now been attained by a back-cross of an I x C cross to Line C, at an inbreeding level in excess of 80 percent.

A somewhat different genetic situation appears to be in effect for viability of hens from hatch to 50 weeks of age (Fig. 14). While selection for large families apparently resulted in almost normal viability during the first 3 generations of sib mating a gradual increase in mortality took place thereafter to a level of about twice that of controls for the average of all inbreds. This change towards the worse in surviving inbreds undoubtedly reflects our efforts, beginning in 1960, of maintaining all 18 inbred lines alive at that point. Six out of the 18 lines
were lost in the following 5 years despite all reasonable efforts to keep them alive. For practical purposes, however, this meant almost complete cessation of between-line-selection after 1960. If one further considers the reduction in the expected genetic variances within lines due to additive as well as recessive genes then the deterioration of viability under continued inbreeding may be accounted for by a lack of effective selection to maintain viability in the face of continued exposure of deleterious homozygotes under inbreeding.

Indeed several of the surviving lines have by now been found to be afflicted with certain typical weaknesses in viability. Thus, Line C is characterized by an excess of females of 60:40 percent at hatching time, followed by very high brooder house mortality of chicks and high mortality of males thereafter. Close observation of chicks during the first days of brooding revealed a few years ago that Line C chicks tend to stay away from floor brooders and die of cold exposure. By brooding them in batteries this handicap has been largely overcome and low viability is no longer a major problem for that line. Another prevailing cause of mortality in the early brooding stages has been a tendency in many lines towards pasting of the chicks' vent resulting in mortality unless corrected by hand. Yet at least one of our highly inbred lines (I) appears to have excellent viability when compared with the base population and again leaves room for the assumption that heterozygosity and thus overdominance are not necessary prerequisites for good viability.

Further insights into the effects of inbreeding can be obtained by examining crosses among highly inbred lines. This was done at several stages during the experiment beginning in 1963. Fig. 15 shows the regression of 40 week survivor production in first crosses for average performance of inbred parents. In the case
of inbred lines three-year averages were used to minimize the effects of individual differences between hens. Thus, the regression observed can be assumed to be almost entirely due to the genetic average of lines. It should be noted that inbreeding levels in 1963, the first year crosses were made, ranged between 74 and 83 percent depending on the year of origin of lines. The results of this comparison are remarkable in that they show considerable depression of inbred performance to about 75 eggs, as compared to almost 110 eggs for crosses and about 85 eggs for controls (Fig. 11). It should also be noted that none of the mid-parent values reached the level of the best inbred (Line C) mentioned earlier. Best crosses, however, laid as many as 124 eggs to 40 weeks. A second, and surprising feature of Fig. 15 is the high regression of cross-performance on mid-parent values. This regression must be due almost entirely to additive genes, or epistatic interactions between additive gene effects. It would not be expected to arise as a consequence of recessive genes. Thus, egg production within the base populations appears to be controlled to a considerable degree by additive genes when examined by means of highly inbred lines derived from them. Again, however, a plausible explanation is found when egg weight is considered in conjunction with egg number. It appears that the divergence in average egg production among inbred lines is closely and negatively correlated with egg size, a trait known to be largely under control of additive genes. Thus, inbred lines and their line crosses with high egg number had all low egg size while the opposite was true for inbreds with high egg weight. This result also demonstrates a point made earlier, that selection for high performance inbreds for egg number results in surviving inbreds with generally low egg size. It would appear, however, that sufficient selection intensity for egg size as well as egg number of inbreds could avoid such an outcome of the inbreeding
process under practical conditions.

Yet another way to examine the genetic basis of the inbreeding process is through study of changes in the components of genetic variability both within and between lines, in comparison with expectations shown in Figs. 5 and 6. As mentioned earlier the variability between lines should increase linearly with inbreeding if additive genes were important and somewhat more rapidly if rare recessives controlled a given trait, or if overdominance were in effect. The within-line variance would decline linearly with inbreeding for additive genes but might increase for rare recessives up to the third generation of sib-mating. Thereafter genetic variances within lines for all above mentioned modes of gene action should go to zero in the long run. In Table 4 comparisons of variance components are made between the two randomly reproducing base populations (1952; 1957), and the series of inbred lines derived from them. For the inbreds the data are pooled over populations and years with comparable inbreeding levels (0.25; 0.38; 0.50), respectively, for each of the first three generations. Thereafter, inbred analyses were pooled for two five-year periods, 1961-65 and 1966-70, respectively, on the assumption that differences in variances of inbred lines within the 5 years were small enough to allow meaningful conclusions for each period. For the control lines data from the three years where inbreds were taken off were pooled. Also sire and dam components of variance are shown only in sum to avoid small numbers of degrees of freedom for these estimates taken separately. It should also be noted, that between-line variance cannot be estimated for controls, and that in the first three years of the inbreeding experiments mostly single pair matings were used to propagate lines, so that reliable estimates could not be obtained for within-line sire and dam components during that initial phase of the
The genetic variance within lines as estimated from sire and dam variance components was relatively high in the base population with a value of 330 corresponding to a heritability of 0.55. With inbreeding of lines from 0.59 to 0.89 the average variance between families within inbred lines dropped to about half the value of the base population, and a further drop in variance to 62.3 was observed for the lines surviving at inbreeding levels between 86 to 96 percent. These observations are not inconsistent with theoretical expectations which predict zero genetic variability within lines when inbreeding reaches 1.00.

The between-line variance of egg production under inbreeding followed a pattern which is not in strict agreement with the genetic expectations based on a model of rare recessive genes with small effects (Fig. 6). An initial increase in between-line variance in the first generation of sib-mating was followed by a drastic reduction of variability for the second and third generations, only to increase again about four-fold towards the end, when the lines were almost completely inbred. The apparently inconsistent decline in the variability of lines can, however, be explained if one takes into account that strong selection between lines was practiced in the first three generations of inbreeding. Thus, the first generation of inbreds represented offspring from a more or less random sample of control families, while lines surviving during the next three generations were strongly selected for reproduction, as shown by the decline in the numbers of surviving lines (Table 3). The decline in variability between lines thus closely parallels this selection phase of the experiment and can be explained if one assumes that the elimination of lines was due to the exposure under inbreeding of deleterious recessive genes with large effects such as lethals. When selection
between lines was discontinued their variability again increased to a magnitude consistent with a model of rare recessives.

The results reported for our highly inbred lines up to this point represent a first cycle of inbreeding and selection and demonstrate that selection between and within full-sib lines can be effective in establishing highly inbred lines. All these first-cycle lines, however, have some faults and only a system of breeding based on repeated cycles of inbreeding alternating with crossing of the best lines would appear capable of giving rise to high performance lines under sib-mating.

A second cycle of inbreeding was thus started after crossing surviving lines in pairs in the years 1963, 1964 and 1966, respectively. Following the crosses inbreeding by sib-mating was resumed within each of the new lines. Of these a total of 49 lines were leaving pullets in the first inbred generation, 27 survived two generations of inbreeding and 12 lines were left after 5 generations. As controls for the average performance of all these second cycle inbreds, corresponding years' data from the surviving first cycle inbreds, from repeated two-way crosses among first cycle inbreds as well as appropriate three-year averages of the cross between the two random controls (1952 x 1957) were calculated. These results are shown in Fig. 16 for survivor egg production to 50 weeks and expressed as deviations from the random control cross. The results suggest that neither the first cycle inbreds nor their crosses were subject to a great deal of change from one generation to the next. It is quite apparent, however, that the second cycle inbreds were undergoing genetic changes in the first 4 years of sib-mating. In the first generation the new set of inbreds was almost exactly intermediate in performance between two-way crosses and the first cycle inbreds, in accordance with expectation, since the coefficient of inbreeding for sib-matings from a two-way
cross should be a little more than half the inbreeding of the contributing highly inbred lines. After the first inbred generation further changes in average performance of surviving second cycle inbreds began to deviate from that expected of unselected lines, showing a gradual increase during the last two generations. Thus, the elimination of poor inbred lines resulted in survivors with performance in excess of that expected under inbreeding alone.

Similar relative improvement of reproductive performance of second cycle inbreds is shown for hatchability and viability of pullets in Table 5. When egg production is considered in conjunction with the preceding traits it is seen that total reproductive rate of second cycle inbreds in the 4th generation had dropped to almost a third the value of two-way crosses, but was still about twice the value of highly inbreds.

The results of this second cycle of inbreeding thus parallel those obtained with two and three generation cycles of inbreeding as reported in the first part of this paper. Selection against recessive deleterious genes, which account for inbreeding depression, has been effective in each case. It thus appears feasible to improve populations or sets of inbred lines, for their capacity to survive under rapid inbreeding. While overdominant genes may account for a part of observed inbreeding depression it would appear from the performance of our best inbred lines that such genes need not prevent the ultimate breeding of highly inbred lines with good reproduction.
Acknowledgements: It is a pleasure to acknowledge the cooperation of Mrs. Dorothy C. Lowry who conducted the experiments with radiation induced variability. Professor Elwood Briles and his wife Ruth have been most helpful in blood typing three generations of our most highly inbred lines for red blood cell antigens at 10 loci, demonstrating their high degree of homozygosity. Blood type information about our lines developed by them has convinced me that this quality control is essential for the maintenance of highly isogenic lines.


Table 1: The effects of one generation inbreeding by sib-mating (F + 0.25) in the control line and the irradiated line, respectively for egg weight at 32 weeks of age and survivor egg production to about 40 weeks of age.

**Egg Weight:**

<table>
<thead>
<tr>
<th>Year</th>
<th>Control Line F = 0.0</th>
<th>Control Line F = 0.25</th>
<th>Irradiated Line F = 0.0</th>
<th>Irradiated Line F = 0.25</th>
</tr>
</thead>
<tbody>
<tr>
<td>1963</td>
<td>47.3</td>
<td>47.5</td>
<td>50.7</td>
<td>49.8</td>
</tr>
<tr>
<td>1964</td>
<td>46.5</td>
<td>45.1</td>
<td>50.2</td>
<td>48.1</td>
</tr>
<tr>
<td>1965</td>
<td>47.5</td>
<td>46.9</td>
<td>50.6</td>
<td>49.1</td>
</tr>
<tr>
<td>1966</td>
<td>48.5</td>
<td>48.8</td>
<td>50.7</td>
<td>50.2</td>
</tr>
<tr>
<td>1967</td>
<td>48.8</td>
<td>47.9</td>
<td>52.0</td>
<td>50.5</td>
</tr>
<tr>
<td>Average</td>
<td>47.72</td>
<td>47.26</td>
<td>50.91</td>
<td>49.55</td>
</tr>
<tr>
<td>Inbreeding</td>
<td>---</td>
<td>-0.46</td>
<td>---</td>
<td>-1.36</td>
</tr>
</tbody>
</table>

**40-Weeks Survivor Egg Production:**

<table>
<thead>
<tr>
<th>Year</th>
<th>Control Line F = 0.0</th>
<th>Control Line F = 0.25</th>
<th>Irradiated Line F = 0.0</th>
<th>Irradiated Line F = 0.25</th>
</tr>
</thead>
<tbody>
<tr>
<td>1963</td>
<td>99.9</td>
<td>84.8</td>
<td>86.0</td>
<td>70.7</td>
</tr>
<tr>
<td>1964</td>
<td>92.1</td>
<td>88.0</td>
<td>81.9</td>
<td>68.2</td>
</tr>
<tr>
<td>1965</td>
<td>100.2</td>
<td>91.8</td>
<td>96.1</td>
<td>87.2</td>
</tr>
<tr>
<td>1966</td>
<td>102.3</td>
<td>100.4</td>
<td>100.6</td>
<td>90.4</td>
</tr>
<tr>
<td>1967</td>
<td>113.1</td>
<td>105.5</td>
<td>105.2</td>
<td>88.5</td>
</tr>
<tr>
<td>Average</td>
<td>101.5</td>
<td>94.1</td>
<td>94.0</td>
<td>81.0</td>
</tr>
<tr>
<td>Inbreeding</td>
<td>---</td>
<td>-7.4</td>
<td>---</td>
<td>-13.0</td>
</tr>
<tr>
<td>Effect</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>
Table 2: Variance components and degrees of freedom of egg weight (g) at 32 weeks of age and survivor egg production to 40 weeks of age for Sire (S), Dam within Sire (D) and Individual (I) under Random Matings and Brother-Sister Matings from the R sublines.

### Egg Weight (g) at 32 Weeks of Age

<table>
<thead>
<tr>
<th>Control Line:</th>
<th>Sire (S) df</th>
<th>Dam (D) df</th>
<th>Individual (I) df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Random Matings</td>
<td>1.91 (143)</td>
<td>1.73 (241)</td>
<td>5.17 (495)</td>
</tr>
<tr>
<td>Brother-Sister</td>
<td>2.40 (122)</td>
<td>0.33 (57)</td>
<td>5.38 (425)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Irradiated Line:</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Random Matings</td>
<td>1.86 (110)</td>
</tr>
<tr>
<td>Brother-Sister</td>
<td>2.71 (113)</td>
</tr>
</tbody>
</table>

### Survivor Egg Production to 40 Weeks:

<table>
<thead>
<tr>
<th>Control Line:</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Random Matings</td>
<td>19.3 (150)</td>
</tr>
<tr>
<td>Brother-Sister</td>
<td>46.1 (106)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Irradiated Line:</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Random Matings</td>
<td>22.4 (106)</td>
</tr>
<tr>
<td>Brother-Sister</td>
<td>36.8 (99)</td>
</tr>
</tbody>
</table>
Table 3. Numbers of matings attempted. Numbers of matings with at least one hen, number of lines with surviving pullets and number of pullets for the first three generations of full-sib mating.

<table>
<thead>
<tr>
<th>Year</th>
<th>From Population 1952</th>
<th>From Population 1957</th>
<th>Total Both Populations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of attempted matings</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1956</td>
<td>33 Total</td>
<td>54 Total</td>
<td>279 (S1)</td>
</tr>
<tr>
<td>1957</td>
<td>28 39</td>
<td>40 65</td>
<td>279 (S2)</td>
</tr>
<tr>
<td>1958</td>
<td>16 29 43 115</td>
<td>29 50 45 164</td>
<td>191 (S3)</td>
</tr>
<tr>
<td>1959</td>
<td>31 63 120</td>
<td>78 69 159</td>
<td></td>
</tr>
<tr>
<td>1960</td>
<td>20 67</td>
<td>17 124</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of Matings with Surviving Hens</th>
</tr>
</thead>
<tbody>
<tr>
<td>1956</td>
<td>19 Total 26 Total</td>
</tr>
<tr>
<td>1957</td>
<td>12 25 14 33</td>
</tr>
<tr>
<td>1958</td>
<td>11 21 30 74 22 40 37 96</td>
</tr>
<tr>
<td>1959</td>
<td>8 25 58</td>
</tr>
<tr>
<td>1960</td>
<td>11 30 11 55</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of Independent Lines</th>
</tr>
</thead>
<tbody>
<tr>
<td>1956</td>
<td>17 Total 26 Total</td>
</tr>
<tr>
<td>1957</td>
<td>7 18 11 29</td>
</tr>
<tr>
<td>1958</td>
<td>4 13 13 48 7 23 17 72</td>
</tr>
<tr>
<td>1959</td>
<td>4 9 29 13 5 39</td>
</tr>
<tr>
<td>1960</td>
<td>6 14 5 25</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of Surviving Pullets</th>
</tr>
</thead>
<tbody>
<tr>
<td>1956</td>
<td>48 Total 63 Total</td>
</tr>
<tr>
<td>1957</td>
<td>29 54 46 98</td>
</tr>
<tr>
<td>1958</td>
<td>24 42 75 177 40 102 93 254</td>
</tr>
<tr>
<td>1959</td>
<td>21 41 112 33 34 182</td>
</tr>
<tr>
<td>1960</td>
<td>23 68 21 94</td>
</tr>
</tbody>
</table>
Table 4.

Variance Components within and between inbred lines derived from the two base populations for survivor egg production to 50 weeks of age.

<table>
<thead>
<tr>
<th>Years</th>
<th>Inbreeding Coefficient</th>
<th>Variance Components and Degrees of Freedom</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Lines</td>
</tr>
<tr>
<td></td>
<td></td>
<td>VC</td>
</tr>
<tr>
<td>1956-58</td>
<td>0.00(Base)</td>
<td>--</td>
</tr>
<tr>
<td>1956-58</td>
<td>0.25</td>
<td>409.0</td>
</tr>
<tr>
<td>1957-59</td>
<td>0.38</td>
<td>216.6</td>
</tr>
<tr>
<td>1958-60</td>
<td>0.50</td>
<td>143.1</td>
</tr>
<tr>
<td>1961-65</td>
<td>0.59-0.89</td>
<td>248.6</td>
</tr>
<tr>
<td>1966-70</td>
<td>0.86-0.96</td>
<td>623.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Individuals</td>
</tr>
<tr>
<td></td>
<td></td>
<td>VC</td>
</tr>
<tr>
<td>1956-58</td>
<td>330.0</td>
<td>514</td>
</tr>
<tr>
<td>1956-58</td>
<td>921.7</td>
<td>311</td>
</tr>
<tr>
<td>1957-59</td>
<td>945.4</td>
<td>226</td>
</tr>
<tr>
<td>1958-60</td>
<td>1006.1</td>
<td>123</td>
</tr>
<tr>
<td>1961-65</td>
<td>568.6</td>
<td>481</td>
</tr>
<tr>
<td>1966-70</td>
<td>578.0</td>
<td>258</td>
</tr>
</tbody>
</table>
Table 5. Estimates of the reproduction index, $P$, and its components (rate of lay, hatchability, fertility and livability to mating age) in second cycle inbreds in contrast to contemporary data from first cycle inbreds. $P$ is the probability that a mated pair will leave mature offspring from one day’s collection of hatching eggs.

<table>
<thead>
<tr>
<th>Second Cycle inbreds:</th>
<th>$S_1$</th>
<th>$S_2$</th>
<th>$S_3$</th>
<th>$S_4$</th>
<th>$S_5$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rate of egg production</td>
<td>0.80</td>
<td>0.66</td>
<td>0.59</td>
<td>0.65</td>
<td>0.57</td>
</tr>
<tr>
<td>Fertility of eggs set*</td>
<td>0.80</td>
<td>0.80</td>
<td>0.80</td>
<td>0.80</td>
<td>0.80</td>
</tr>
<tr>
<td>Hatchability of fertiles**</td>
<td>0.73</td>
<td>0.60</td>
<td>0.57</td>
<td>0.62</td>
<td>0.52</td>
</tr>
<tr>
<td>Livability to mating age</td>
<td>0.90</td>
<td>0.76</td>
<td>0.69</td>
<td>0.70</td>
<td>0.64</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Second Cycle inbreds</th>
<th>Total reproduction $P$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.420 0.241 0.186 0.226 0.152</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>First Cycle inbreds:</th>
<th>$S_1$</th>
<th>$S_2$</th>
<th>$S_3$</th>
<th>$S_4$</th>
<th>$S_5$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rate of egg production</td>
<td>0.52</td>
<td>0.50</td>
<td>0.50</td>
<td>0.53</td>
<td>0.49</td>
</tr>
<tr>
<td>Fertility of eggs set*</td>
<td>0.80</td>
<td>0.80</td>
<td>0.80</td>
<td>0.80</td>
<td>0.80</td>
</tr>
<tr>
<td>Hatchability of fertiles**</td>
<td>0.48</td>
<td>0.48</td>
<td>0.47</td>
<td>0.50</td>
<td>0.46</td>
</tr>
<tr>
<td>Livability to mating age</td>
<td>0.54</td>
<td>0.47</td>
<td>0.47</td>
<td>0.42</td>
<td>0.47</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>First Cycle inbreds</th>
<th>Total reproduction $P$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.108 0.090 0.088 0.089 0.085</td>
</tr>
</tbody>
</table>

* Infertility due to complete lack of semen production as well as losses of matings due to lack of egg production are included under viability. Fertility of inseminated laying hens was then assumed relatively constant (0.80).

** Hatchability data are based on three week’s saving of eggs.
Fig. 1: Breeding plan for cyclic inbreeding used in each of the two populations originating from a Control Line and an Irradiated Line (X Line), respectively.

Fig. 2: Selection response in two populations (Control and X-ray, respectively) selected for high egg production with constant egg weight under random mating excluding close relatives.

Fig. 3: Selection for high egg production with constant egg weight in populations derived from the Control Line. The populations are:
1. A randomly mated control selected line (subline R).
2. Random sib matings from subline R.
3. A population with single cycles of sib mating followed by crosses among sib lines.
4. A population undergoing cycles of two sib matings followed by crossing of sib-lines.

Fig. 4: Selection for high egg number with constant egg weight in populations derived from the X-ray Line. For details see Fig. 3 and text.

Fig. 5: Theoretical expectation of genetic variances for a set of lines under continued full-sib mating derived from the same base population and for genes at initial gene frequency of $q = 0.5$. Generation 1 represents the base population. $V_B$ is the between-line variance, $S$ the variance due to sires within lines, $D$ the variance due to dams within sires, and $V_W$ the variance between full sibs within dams, sires and lines. This situation also reflects the variances of a set of sib-lines derived from a single cross between 2 completely inbred lines.

5a: Variances with additive gene action where $AA = 1.0; Aa = 0; aa = -1.0$.

5b: Variances with deleterious recessives. The sum of initial variances is
set equal to 1.0.

Fig. 6: Expectation of genetic variances with an initial gene frequency of $q = 0.1$ of completely recessive genes.

Fig. 7: Simulated selection response of a trait controlled by 10 recessive deleterious genes under cyclic inbreeding. Five generations of sib-mating, without selection of ten inbred lines is followed by the selection of the 5 best inbreds which are then crossed in all 10 possible pairs. Six such cycles are shown in the graph.

Fig. 8: Simulated selection response under cyclic inbreeding as explained for Fig. 7 with 10 overdominant loci where homozygotes are equally inferior to the heterozygote at each locus.

Fig. 9: Breeding plan for the first cycle of inbreeding and crossing under sib-mating with lines derived over 3 generations from each of two randomly propagated control lines (1952 Random Control and 1957 Random Control). See also Table 3.

Fig. 10: Expected probability of family survival (line survival in the case of pair matings) with at least one pair of mated full-sibs under various levels of reproductive potential ($P$). The latter is the probability of survival, to mating age, of progeny from one day's collection of hatching eggs from a typical pair mating. With inbreeding the reproductive potential falls from about 0.3 in the base population to 0.03 in some of the poorest inbred lines maintained in this experiment.

Fig. 11: Average survivor egg production of the two random lines and their cross. Note that for the 1957 random control all artificial selection was discontinued in 1956 so that the 57 generation was the first generation of
offspring from unselected parents. The same holds true for the 1952 Random Control, that 1952 was the first generation from unselected parents.

**Fig. 12:** Survivor egg production to 50 weeks of age for the two Random Controls (pooled) and all inbred lines derived from them. Averages for inbreds extend over three generations combining all generations with equal levels of inbreeding. Similarly the Control Lines are represented by three-year sliding averages. The 1955-57 period represents the initial non inbred parent populations from which first-generation inbreds were derived.

**Fig. 13:** Histograms of survivor egg production to 40 weeks of age for the 1952 Control (Line 100), the survivor line with highest egg production (C), the line with lowest egg production (H), an intermediate line (I) and a backcross of a two-line cross (I x C) onto the better inbred (C): CCI.

**Fig. 14:** Percent mortality of random controls (average) and all inbred lines averaged according to inbreeding levels over three years.

**Fig. 15:** Regression of 2-line crosses on average of inbred parent lines. For the mid-parent values unweighted egg production averages of 3 years (1963-65) was combined to obtain estimates relatively free of individual hen variability and year-line interactions.

**Fig. 16:** Comparison of egg production to 50 weeks of age for first-cycle inbreds, two-line crosses among first cycle inbreds, crosses of random controls and second cycle inbreds. Since the latter were originating over three generations (1963, 1964, 1966) corresponding averages were taken to allow unbiased comparisons of each level of inbreeding in the second cycle with the three types of controls.
PLAN FOR CYCLIC INBREEDING
R - RANDOM MATINGS
I - SIB-MATINGS
C - CROSS OF INBREDS

I I I I I I I I I
C C C C C C C C C
I I I I I I I I I
C C I I C I C I C
C C I I C I C I C

I - CONTROL
R - CONTROL
2-YEAR CYCLE
3-YEAR CYCLE

63 64 65 66 67 68 69 70 71
EGGS TO 40 WEEKS

CONTROL

IRRADIATED

SELECTION IN RANDOMLY MATED LINES
EGGS TO 40 WEEKS

CONTROL-C

SELECTION WITH SIB-MATING: X-RAY LINES

SIB-MATING IN CONTROL

I-C CYCLE
Fig. 10

LINE SURVIVAL

HATCH PERIOD WEEKS

0

1

2

3

4

5

6

7

8

9

10

P = 0.03

P = 0.07

P = 0.3
Fig. 12

EGGS TO 50 WEEKS

F = 25

38

50

59

67

73

79

83

86

89

91

SURVIVOR EGGS TO 50 WEEKS

INBRED LINES

RANDOM CONTROLS
Fig. 13

40 WEEK SURVIVOR EGG PRODUCTION
Fig. 14

% MORTALITY TO 50 WEEKS

- - - - -

1955-57
1956-58
1957-59
1958-60
1959-61
1960-62
1961-63
1962-64
1963-65
1964-66
1965-67
1966-67

10 20 30 40 50 60

F = 25 50 59 67 73 79 83 86 89 91

RANDOM CONTROLS

INBREDS

PERCENT MORTALITY TO 50 WEEKS
EGGS TO 50 WEEKS

SECOND-CYCLE INBREEDING FROM HIGHLY INBRED LINES

FIRST CYCLE INBREDs

SECOND CYCLE INBREDs

CROSS OF RANDOM LINES

FIRST CYCLE CROSSES
DR. HANS ABPLANALP - "INBREEDING FOR THE GENETIC ANALYSIS AND IMPROVEMENT OF POULTRY POPULATIONS."

HOWARD STONE: Do you feel that at high levels of inbreeding, the calculated theoretical inbreeding coefficient indicates a valid determination of the biological level of inbreeding?

ABPLANALP: With continued full-sib mating there is not much opportunity for preferential survival of heterozygotes, since only 4 genes are transmitted per locus and generation. Thus, I believe calculated inbreeding to be a good indicator of an average decline in heterozygosity especially when inbreeding exceeds about ten full-sib generations; at this point differences between succeeding generations become small.

CECIL McCARY: In discarding poorer performing inbred lines is it likely that you are eliminating the most highly homozygous lines and actually selecting the less homozygous lines, in regard to depressing genes?

ABPLANALP: Between-line selection may favor the more heterozygous lines, but continued inbreeding in surviving lines, especially those that can survive permanently, would eventually enforce homozygosity. Once a line is at calculated inbreeding levels of - say - 97% (17 generations of sib-mating) the theoretical delay of homozygosity by one or two generations will be of minor consequence in terms of inbreeding. Thus, between-line selection in the early stages of inbreeding will tend to become unimportant at high calculated inbreeding levels of surviving lines.

GERRY FRIARS: Do you feel that the amount of non-additive genetic variance present for egg size is coherent with the inbreeding depression encountered for that trait?

ABPLANALP: Only in the irradiated line (X) is there evidence of non-additive genetic variance for egg size as expressed in a larger variance within inbred full-sib.
families (table 2). The drop of egg weight in our highly inbred lines must be attributed to selection for high egg number which is negatively correlated to egg size through primarily additive genes. We find proof of this in the fact that single crosses of highly inbred lines had about the same egg weight as inbreds but vastly improved egg production.

ALAN EMSLEY: Recognizing that loss of reproductive performance is a major obstacle to maintaining a large gene pool, is there any merit in starting out inbreeding at a slower rate than for full-sib mating, and gradually increasing that rate as inbreeding increases and the damage from inbreeding depression is less -- or will this merely extend the time taken to reach maximum Fx.

ABPLANALP: Your last remark is correct. If inbreeding depression is indeed primarily due to recessive genes and if selection against them is to be used, then I would suggest that one should inbreed as rapidly as possible to a desired level of perhaps 25-50% where inbreeding effects show up strongly but without inhibiting selection and line survival, and where calculated genetic variances are expected at a maximum. By expanding lines at that point, selection against recessives could operate under optimal genetic conditions.

W. G. HILL: Is the method of cyclical inbreeding likely to be useful for overall economic performance, when some traits such as egg weight are nearly additive and inbreeding must reduce the rate of response?

ABPLANALP: Cyclic inbreeding in one form or another will necessarily enter into a breeding plan designed to produce high-performance inbred lines. This is so because fixation of deleterious genes cannot be completely prevented by selection under intense inbreeding, such as sib-mating. Thus, highly inbred lines will tend to be only partially cleared of recessives and need to be crossed at one stage or another
in order to allow recombination of fixed deleterious genes, thus allowing selection against them. Additive genetic gains must then be expected at rates less than optimum for large populations. You can't select additive and recessive genes at maximum rates simultaneously.

GORDON DICKERSON: Please explain why you feel that selection within inbred lines at about 50% level for several years is optimal use of inbreeding in selection programs against recessives.

ABPLANALP: If you consider the genetic variances for recessives under inbreeding by full-sib mating then both the within-line and the between-line genetic variances tend to be at high levels after about 2-3 generations as demonstrated in Fig. 6, provided gene frequencies of the recessive genes are low. This would only be true in the first inbred cycle from a large base population. If you were to inbreed after a single cross ($F_1$) of highly inbred lines (second cycle in our case) then maximum variances are encountered in the $F_2$ because now genes are all either present at frequencies of 50 percent or completely fixed (Fig. 5).