SIMULATION OF POTENTIAL GENETIC CHANGE IN INDONESIAN FOWL

> Thesis for the Degree of M.S. MICHIGAN STATE UNIVERSITY MARIA ASTUTI 1976

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ABSTRACT

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By

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The effect of degree of truncation selection and level of heritability in simulated populations of poultry subjected to selection was studied.

The trait simulated was body weight at sexual maturity of native chickens in Indonesia.

Populations were simulated for all possible combinations of three levels of heritability (.1, .3 and .4) and three intensities of selection by upper truncation of the distribution of phenotypes (25%, 50% and 75%).

The only genetic variance contributed to the variability was the additive variance.

The size of offspring population in each generation was 600, 300 males and 300 females, with random mortality assumed to occur so that breeding size after truncation was constant at 6 males and 60 females.

Selection was performed for ten generations.

For each parameter combination, 100 replications (populations) were simulated. Two types of mating systems, random and assortative, were simulated.

The results from random mating and assortative mating showed the same pattern. The test of difference in slopes of regressions of the phenotypic means on generation number for the two types of mating was statistically significant in most cases but the difference was biologically trivial.

The best response to selection was obtained in populations with heritability = .4 when the proportion selected for mating was 25%. The least response to selection was for populations with heritability = .1 when the proportion selected was 75%.

Under the same level of truncation, the response to selection is proportional to heritability.

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IN INDONESIAN FOWL

By

Maria Astuti

A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Department of Dairy Science

ACKNOWLEDGMENTS

I am deeply indebted to Dr. John L. Gill, my major professor for his patient assistance and invaluable suggestions in the preparation of this manuscript. I would like to express my appreciation for his guidance and encouragement in my graduate program.

I am grateful to Dr. Clinton E. Meadows and Dr. Theo H. Coleman for their suggestions and participation in my graduate program, to Dr. Roger R. Neitzel for his assistance in computer programming and to Dr. William T. Magee for his sound advice and suggestions.

I am also grateful for the leave of absence provided by the Gadjah Mada University, for the financial support provided by the Midwest Universities Consortiums for International Activities (MUCIA, Inc.) and for the facilities provided by the Department of Dairy Science at Michigan State University.

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INTRODUCTION

Many pairs of genes may be involved in the expression of traits that have economic value. Such traits are known as quantitative traits or characteristics involving "multiple factors," and most of them are greatly influenced by environmental conditions.

Breeders try to improve economic traits through mating systems and selection. It is known that selection will change gene frequencies, and through continuous selection over several generations, the accumulated changes result in permanent change in the mean of the trait selected.

The expected response and improvement made by selection can be computed and always depends upon accuracy of selection and selection intensity. However, different combinations of mating systems and intensity of selection give different accuracy of selection and selection response, and cause different results in rate of improvement.

Because substantial investment of money and time is necessary to achieve major genetic change, considerable thinking must be done before one makes any decision about choice of improvement program. But quite often an improvement program will return different results from the expected after the program has been carried out for several years. If breeders can be given more accurate prediction of the

result of any improvement program, this problem can be overcome to some degree.

The general method of prediction is mathematical, in which the existing genetic theory is applied. Some modifications in the theory may be suggested from the results of experimental studies with laboratory animals. Relatively recently a new method that has been called the Monte Carlo method was developed as an aid to prediction.

The random mechanisms of genetics are simulated via pseudorandom numbers which are generated by digital computers. By incorporating known Mendelian laws, statistical distributions, or both, this method can indicate what kind of result should come from different possible combinations of systems of mating and intensities of selection, and establish which combination is likely to give optimum genetic improvement.

This study involves simulation of the effect of degree of truncation selection and level of heritability in simulated populations of poultry subjected to selection for a single quantitative trait. The main objective was to determine:

- 1. the change in phenotypic and genotypic mean in each generation,
- how response to selection in each generation will deviate from the expectation, and
- which selection intensity is optimal for genetic progress at different levels of heritability in populations of a given structure.

LITERATURE REVIEW

The genetic constitution of animals has been changing more rapidly since they have been domesticated, as men with artificial selection play a more important role than natural selection. It has been shown that breeders with artificial selection and breeding systems have succeeded in changing the conformation and performance of many species.

With the development of science and the spread of knowledge, breeders not only seek to change animals, but also wish to predict the amount of change and want to know how to achieve maximum change.

Breeders have always dealt with quantitative traits, but many theories in selection to improve these traits have not been applied. Also, there are problems in animal breeding that have not been solved.

In order to apply the theories, to answer the questions, and to get new results, actual selection experiments in the field must be conducted, but time, labor, money, and facilities sometimes do not permit controlled experiments of a size sufficient for the accuracy required of predictions.

Laboratory animals have been used and it has been proven that they can answer many questions about selection. Relatively recently the Monte Carlo method of computer simulation has been used to address

questions for which suitable answers have not been obtained by other methods. This method makes it possible to simulate genetic processes by using repetitive sequences and pseudo-random numbers generated by computers.

This review is mainly concerned with several selection studies with laboratory animals and with the use of simulation procedures to solve problems involving selection.

Selection Experiments With Laboratory Animals

Chapman (1951) summarized the effectiveness of selection studies involving laboratory animals. Laboratory species that have a short generation interval can be used to answer many questions about livestock improvement. Some results of laboratory animal experiments have indicated that selection with or without inbreeding was effective in producing changes in quantitative traits in both positive and negative direction over many generations. Crosses between individuals from positively and negatively selected lines will produce intermediate offspring.

Within selected lines, the coefficient of variation usually remained almost constant over many generations of selection. Several experiments showed correlated response and one experiment showed a reduction in heritability in later generations. Genetic variability in foundation stock will be used effectively by selection and environmental influence might limit the effectiveness of selection in positive direction but not the other.

Wilson et al. (1965) studied the pupa weight of <u>Triboleum</u> <u>castaneum</u> as measured at 19 days after the egg was laid. Two replicates were used, each replicate consisting of mass selected and randomly selected groups. Within each group five mating systems were applied. The selection experiment was conducted for 6 generations.

An analysis of variance of the regression coefficient of generation mean on generation number, averaged over selection methods and replications, revealed significant differences among selection methods (P < .05). The test of effect of different mating systems was conducted within the selection methods and the results showed no significant effect of mating system among the randomly selected lines but a slight indication of differential response among the mass selected lines. Tests of variances showed decline over generations of phenotypic and genotypic variation in mass selected lines regardless of mating system. In randomly selected lines there was a tendency for a decline in phenotypic variance but not for the genetic variance.

Another experiment with <u>Tribolium castaneum</u> was also reported by Enfield et al. (1966). Enfield et al. conducted an experiment similar to that by Rahnefeld et al. (1963). The selection experiment was for heavier pupa weight of <u>Tribolium castaneum</u> measured at 21st day after the egg was laid. The two populations to be selected were obtained from crosses of two highly inbred lines. The S-populations were selected for heavier pupa weight and the C-populations were control lines. Two replicates were used in this experiment. Thirty six males and 72 females which were selected each generation in each population became parents for the next generation. Individual

parents were selected on an intra-half-sib family basis. In Spopulations parents were selected from each half-sib family and in C-populations parents closest to the family mean were selected from each half-sib family.

There was a linear response to selection over twelve generations, but no reduction of additive genetic variance was observed. The average unadjusted selection differential in the S-populations was 212 μ g, and after adjustment for differences in reproduction of the individuals selected as parents, the average selection differential was 208.5 μ g.

The regressions of the difference in mean pupa weight between S-populations and C-populations on generation time for two replicates were 60.3 + 4.8 and 61.8 + 4.9.

McBride and Robertson (1963) carried out an experiment with <u>Drosophila melanogaster</u> and combined selection for bristle numbers with random mating and assortative mating. Three samples of flies were obtained and three paired comparisons were made between random mating and assortative mating. In two sets of lines, individual score was used for selection and as the basis for the assortative mating. In the third set, an index of individual and family score was used. Selection intensity was the same in all lines. The results showed that in all comparisons assortative mating gave a greater selection response than random mating and the largest effect of assortative mating was in the selected lines using index of individual and family score. They concluded that the greater selection response

was partly due to an increase in heritability and partly due to an increase in selection differential.

Frankham et al. (1968) also reported an experiment with <u>Drosophila melanogaster</u>. In this experiment a Canberra strain was used and selection was for the number of abdominal bristles. Selection was carried for 12 generations and the objective of the experiment was to investigate the joint effects of population size and selection intensity. Three population sizes and five selection intensities, with one to five replicates per combination, were used in the experiment. The results indicated a considerable response and on the average agreed well with the expectation from estimated base population heritability, although large differences between replicates were shown. For the same population size higher selection intensities produced more response and for the same selection intensity the effect of population size was not clear, but still there was a trend for the larger population to give more response.

McArthur (1949) conducted a mass selection for small and large body size in the house mouse. He noticed that from the first the body size increased in mice selected for large size and diminished in those selected for small size. After 14 generations, females two month old of the small race averaged less than 12 grams and from the large race 31 grams. In seven more generations the difference of 19 grams between the two races was increased to 23 grams. Males were about 20% larger than females.

The genetics of body size in mice was studied by Chai (1956). In his experiment he crossed large and small strains of mice to

produce F_1 , F_2 and backcross generations. Analysis of means and variances of 60 day body weight in the different genotypic groups was carried out. Backcross and F_2 generations had means slightly above their respective theoretical value, F_1 and F_2 means were halfway between the parents, and the backcross means were halfway between the respective parents. Hybrid F_2 had the largest variance, the second largest was the first backcross generation, and the smallest variances were from F_1 hybrids and the large and the small strains. He reported that the genes involved in this cross acted additively on a logarithmic scale rather than arithmetic scale, and the dominance effect contributed to the total variability, if any, was considered to be trivial.

Miller et al. (1963) conducted an experiment to estimate the extent of nonadditive hereditary variance in traits of mice. Five traits were involved in the study: (1) litter size, (2) 12 week weight of a litter of six mice, (3) individual weight at 3 weeks, (4) individual weight at 6 weeks, and (5) gain from 3 weeks to 6 weeks. Diallel mating was used and all possible combinations of matings were made among m males and d females. The male by female interaction component of variance from the factorial analysis was used to estimate the nonadditive hereditary variance. The results from 2879 mice showed no evidence of any nonadditive hereditary variance with respect to three and six weeks body weights. Data on litter size, obtained from 1161 litters, showed evidence of nonadditive hereditary variance, estimated to be 28% of the total variance.

Dalton and Bywater (1963) conducted an experiment with mice. In their experiment generation zero included offspring produced after subsequent mating of the stocks that had been produced by four-way crosses. Mice were placed on two different diets, "control" and "diluted" diets. The first selection was made between the young of generation 2 which became parents of generation 3. At weaning they selected the whole litter of the litters that were high in either litter size or weight. Random mating was practiced, but matings between litter mates were avoided. No selection was practiced in the control group. Only first parity data were collected and they observed that litter size and litter weight were not affected by selection over 14 generations for mice on either diet.

In the next experiment Dalton (1967) investigated effect of selection for growth in mice on two diets, full diet and diluted diet, where growth was measured as live weight from weaning to subsequent mating. Selection was continued for 13 generations per year with no overlapping generations. In each diet group mice were (1) selected for high growth, (2) selected for low growth, and (3) randomly selected for control. The response was expressed as deviations from controls. All lines within each diet, except for the line selected for high growth on diluted diet were significantly different from control diet.

Rahnefeld et al. (1963) performed an experiment with two populations of mice, the S lines from the reciprocal crosses of two inbred lines and the A line from standard laboratory inbreds. No overlapping generations occurred in the S line but in the A line

generations were overlapped. Rahnefeld observed that mass selection increased postweaning growth measured at 18 to 42 days of age. Selection was continued through 17 generations. Mean postweaning growth was increased 4.9 grams and the average total selection differential in the S population for males and females was 26.21 grams. He reported that mean postweaning gain was increased about six times the additive genetic standard deviation and about 43% of the original mean growth.

Sutherland et al. (1968) evaluated the effectiveness of selection in mice when combined with assortative or disassortative mating in comparison with random mating. The characteristic measured was body weight at 6 weeks of age. Three mating systems and three directions of selection were applied in this experiment. The results indicated that the mating systems had essentially no effect on the progress from selection in either direction. This result was similar to the result obtained with <u>Drosophila melanogaster</u> by McBride and Robertson (1963) and with <u>Tribolium castaneum</u> by Wilson et al. (1965). Furthermore, Sutherland drew a conclusion that assortative mating in livestock will give little benefit compared to random mating, as very few economic characters in livestock appear to be highly heritable.

Hanrahan et al. (1973) investigated the joint effects of population size and selection intensity for postweaning gain in mice after 14 generations of selection within full-sib families. The mating populations contained 1, 2, 4, 8, or 16 pairs. The selection intensities were 100% (C), 50% (I), or 25% (M) saved for breeding. The experiment was replicated. Within each population size the

response per generation was significantly (P < .01) larger at the 25% selection intensity than at 50% selection intensity. Little difference in response was found between M_8 and M_4 and between I_8 and I_4 . The genetic gains in I_{16} and M_{16} lines were significantly (P < .01) larger than in the smaller populations at corresponding selection intensity. The larger response could be attributed only in small part to greater cumulative selection differentials. The results suggest that in populations of relatively small effective size, the effects of genetic drift may cause a reduction of selection response.

Eisen (1975) examined the effects of population size and selection intensity on long-term selection response for postweaning gain in mice. A replicated experiment was conducted using 4, 8, or 16 pairs of parents, and selection intensities were 100% (C), 50% (I), or 25% (M). The effects of selection for 14 generations were reported previously by Hanrahan et al. (1973). In generation 14 the reciprocal crosses were made between populations of 16 pairs of parents to determine if realized heritability would be greater when selection was applied to crosses of selected lines than in the selected lines themselves. After one generation, each line was selected at 25%. То observe the effect of genetic drift and inbreeding depression at the termination of selection experiment, replicates of M_4 , M_8 , and M_{16} lines were crossed with C_{16} line. The joint effects of population size and selection intensity on long-term response to selection for postweaning gain in mice were similar to the results obtained for short-term selection. Within population sizes, more intense selection pressure led to greater total response. Within each level of

selection intensity, total response increased as effective number increased. Discrepancy was observed between observation and theory. In that experiment the total selection response did not increase linearly as the product of effective population size and selection intensity increased. Response to selection diminished markedly as generation number progressed, for lines with both low (I) and high (M) selection intensity, tending toward a plateau.

Kyle (1953) conducted an experiment for the purpose of comparing the theoretical effectiveness of selection for ovarian response to a gonadotrophic hormone. Rats were selected for low and high response on the basis of the ovary weights of full sisters injected with a standard dosage of gonadotrophic hormone over 14 generations in five mating systems. To predict the average ovary weight of each litter of offspring from the average ovary weight of sisters of each parent, a regression equation derived from a path coefficient analysis was used, and the estimate of source of variation in ovary weight was obtained from the foundation stock. The results of this experiment, over all generations and mating systems, showed observed and predicted average ovary weight from 270 litters of offspring from parents selected for low response were 61.0 and 58.6 mg, respectively. The difference was significant, but the observed and predicted average ovary weights of 314 litters of offspring from parents selected for high response were 75.4 and 76.4 mg, respectively, and were not significantly different.

The papers reviewed in this section showed that selection for many quantitative traits in laboratory animals was very effective

either for positive direction or negative direction. Selection pressure and population size affected the response to selection whether it was long term or short term selection but there were only trivial differences in response to different mating systems.

Selection Experiments With Simulated Populations

Scientists in various areas of research have taken advantage of the development of high speed electronic digital computers to get solutions for complex numerical problems at a relatively low cost. The use of computers as sophisticated and economical tools for geneticists became wider since Fraser (1957a) introduced simulation of genetic systems. Fraser showed how a computer can be used to carry out the gene by gene simulation by using binary arithmetic. Furthermore, Fraser (1957b) used the computer to simulate the effect of linkage on rates of advances under selection. The result showed that linkage in large populations caused a correlation of rate of advance with degree of linkage. The effect can be neglected if the recombination is greater than .5 percent. However, in small populations the effect of linkage is considerably exaggerated.

Scheinberg (1968) divided the use of computers in genetics into four basic categories: (1) for the design of efficient field and laboratory experiments, (2) for the statistical analysis of data, (3) for the numerical solutions to mathematically formulated problems, and (4) for the simulation of real and model biological systems using available statistical techniques. Scheinberg reported that no information is available on the utilization of computers for the

construction of efficient optimum designs for genetics experiments. The aid of computers eliminates most difficulties in analyzing an experiment with a vast amount of data and complex computations. Obtaining empirical solutions of complicated formulas or equations by the use of computers has long been demonstrated. In the last decade the utilization of computers for simulation of genetic systems has been advanced. This simulation technique has been termed the Monte Carlo method and many results have been reported.

Kemp and Magee (1966) used the Monte Carlo technique to simulate selection for production traits in two breeds of swine. The first breed was selected for feed efficiency and daily gain, the second breed was selected for backfat probe. Crossing was made before the first and after five generations of selection. Each trait was affected by genes at 20 loci. The genetic correlations of daily gain with feed efficiency and backfat probe were set at 0.6 and 0.2 respectively. Heritability for daily gain and feed efficiency was 0.3, for litter size 0.1, and for backfat probe 0.5. The results showed that each breed improved in the traits selected. Improvements were observed in the cross, for daily gain 0.73 to 0.75 kg/day, feed efficiency 0.32 to 0.33 kg gained/kg of feed, litter size 8.0 to 8.2 pigs per litter, and backfat probe 3.99 to 3.66 cm.

Bereskin et al. (1969) have also conducted simulation studies with swine parameters. Three different sizes of breeding groups were maintained in each generation. Group 1 had 16 replicates with 1 sire and 10 dams, group 2 had 8 replicates with 2 sires and 20 dams, and group 3 had 4 replicates with 4 sires and 40 dams. The traits

selected were litter size and growth rate with heritability of .12 and .34 respectively. Each individual had 64 independent loci, 48 affecting both traits, eight loci affecting only the first trait, and eight loci affecting only the second trait. Mean genotypic value for litter size declined substantially in group 1, less in group 2 and very little in group 3 over 10 generations. For growth rate the genotypic mean was maintained in group 1, but in each generation of groups 2 and 3 there were increases, averaging .25% and .50%, respectively. There was no indication of reaching a plateau by generation 10. Inbreeding increased at drastic rates for group 1 with the coefficient of inbreeding .76 at generation 11. Inbreeding for group 2 and group 3 were .57 and .40, respectively. Bereskin concluded that in small populations selection is ineffective against random drift while in large populations random drift effect is less and selection has more importance.

In a later paper Bereskin (1972) reported accumulated inbreeding and selection effects from generation 1 to 11 for litter size in group 1 were -10.90 ± 1.48 units and 4.63 ± 5.78 units, in group 2 were -7.24 ± 1.78 units and 3.77 ± 2.62 units, and in group 3 were -4.33 ± 0.73 units and 3.11 ± 3.59 units. For growth rate he found accumulated effects of inbreeding were -9.95 ± 1.28 units, $-5.96 \pm$ 1.04 units, -2.04 ± 0.10 units for group 1, 2, and 3 respectively, and accumulated selection effects were 10.68 ± 6.41 units, 13.30 ± 3.54 units, 15.49 ± 2.33 units for group 1, 2, and 3 respectively. Bereskin showed how small population size influenced the effectiveness of selection. The net result after 10 generations indicated a slight

gain in mean genotype for growth rate in group 1, and average total gains of 2.6 and 4.8% were obtained in group 2 and group 3 respectively. He concluded that for traits with heritability between 0.15 and 0.35, substantial long term genetic gains are possible even with rates of inbreeding as high as in group 2, where a 6% loss of heterogosity occurred per generation. The average genetic gain of individual replicates in group 2 was 5% per generation. This response to selection was attributed to the continued availability of adequate additive genetic variance, despite inbreeding.

Parker (1966) did a Monte Carlo simulation to examine selection response and genetic correlation through 30 generations of simulated selection. The trait selected for was expressed in both sexes and each was controlled by 48 loci with equal effect at every locus. The gene frequency was 0.5. The size of the populations of parents was constant, 48 in each generation. The design of his experiment was 3^4 factorial, allowing all possible combinations of 3 degrees of genetic correlation, 3 levels of selection and 3 levels of environmental variation for either trait. Parker considered two models of gene action, the additive model and a complete dominance model. In the first model he found that truncation selection caused a decrease in the genetic correlation, but it was more dependent on the level of heritability of the selected trait than on the degree of truncation selection if the latter was not intense. The correlated response was directly proportional to that in the selected trait and depended on the genetic covariance between the traits. In the complete dominance model, Parker reported that when selection was by upper truncation

the change in the genetic correlation essentially followed the same pattern as for the additive model.

Gill (1965a, b, c) presented a series of three papers on simulation studies. In the first paper, he reported that in a restricted size of population, nonrandom mating will occur and cause an accumulation of inbreeding effect although inbreeding is not intentional. He discussed the effect of population size upon the results of selection under nine different models of gene action, three of them having epistasis, conditional upon gene frequencies. The characteristic measured was expressed in both sexes and was determined by the genes at 40 loci equally spaced over eight chromosomes, two alleles per loci with equal genetic effect at all loci. The effective population sizes were 8, 12, 16 and 32 parents and selection intensities were specified as 1/2, 1/4, 1/6, or 1/8. The environmental variation was specified at 0, $1/3\sigma_G^2$, σ_G^2 or $3\sigma_G^2$ and linkage was specified for recombination probabilities of 0.005, 0.05, 0.2, or 0.5.

The populations with nonoverlapping generations were mating at random. Gill assumed no effects of mutation or natural selection. After 20 generations the mean genetic progress with complete dominance showed that populations of 32 had the greatest mean, all pair differences were statistically significant except for populations of 16 versus 12. Through 30 generations with overdominance, comparison of the means of all pairs of population of different size showed statistically high significance. Under epistatic models, except conditional epistatic, the rate of fixation was rapid and relatively invariant with population size from 8 to 16 parents. When selection

intensity and heritability were high the effect of inbreeding was larger than the amount calculated from population size. The additiveby-dominance conditional epistatic model showed a situation where inbreeding uplifted the genetic mean instead of depressing it.

In the next of his series of papers, Gill (1965b) reported the effects of selection on genetic progress of finite populations. He pointed out the evidence of ineffectiveness of prediction where population size is finite, whether the predictions are linear or assymptotic to the selection goal. Further he reported that both random genetic drift and selection have great influence in changing the values of genetic parameters.

Furthermore, Gill (1965c) reported that due to small population size random drift hindered the progress made by selection in populations with complete dominance, complementary factors or duplicate factors. Selection was effective in advancing the genetic mean of small populations under all models of gene action in which the genotype of highest merit was homozygous. However, selection was ineffective for a character that involves only heterozygous genotypes as optimum in small population under mass selection. Difference in the amounts of environmental variation between populations was important in affecting the total response only when the mean was changing rapidly because of intense selection. After the first few generations genetic merit, gene frequency, and fixation essentially were unaffected by different levels of linkage.

In other studies by Gill and Clemmer (1966) the effects of selection and linkage on degree of inbreeding were simulated. They

created bias in estimates of the degree of inbreeding in population of a given size. The joint effects of tight linkage and selection can increase the rate of inbreeding severely in just three or four generations. Selection in the absence of linkage appears to have little effect on the variability of degree of inbreeding.

Young (1966) has also presented the results from his simulation studies on the rate of decay of the additive genetic variance due to selection, and the resulting change in heritability. He simulated 1000 offspring each generation. The trait being selected was controlled by ten loci, with two alleles per locus with the initial gene frequency at each locus was .5. The design of the experiment was a 3^3 factorial design and the three factors were selection intensity, heritability value and tightness of linkage. The selection intensities were 80%, 50% and 10% of the offspring population saved for mating. Selection was by upper truncation. The heritability values were .9, .4 and .1. The population was in linkage equilibrium and the recombination values were .5, .2 and .05 between adjacent loci. Selection was for thirty generations for each of seven genetic models for all parameter sets, making a total of 189 populations.

In this paper, the first of a series, he presented only the analyses of the additive and complete dominance models. In the additive model the predicted and realized responses were in closer agreement in the early generations when the initial heritability was high than when it was low. The discrepancies between the realized and predicted responses began to occur later in the populations with

high heritability but became larger than the discrepancy in the populations with low heritability after six generations. Linkage had no apparent effect on prediction. When expected response was calculated on the basis of the preceding generation heritability the agreement between the realized and predicted response was close in all cases, but the prediction was less accurate for the combination of high selection intensity and low heritability. The rate of decay of the additive genetic variance was most rapid when selection intensity was high and the heritability was high. Under the dominance model predictions of genetic advance were less accurate. Under both models, high selection intensity with high heritability tended to overestimate genetic advance. On the other hand with low selection intensity and low heritability genetic advance was underestimated. Further, there was no fixation of undesirable alleles under high selection intensity, and linkage was found to have no appreciable effect on genetic advance.

Nishida and Abe (1974) used simulation to investigate the relationship between the skewness in the distributions of genotypic and environmental value and the linearity of heritability in terms of the regression of genotypic values on phenotypic values. Two different approaches were made: (1) a deterministic approach to study the geometric shape of heritability, and (2) computer simulation. The results obtained from computer simulation agreed well with the results obtained from the deterministic approach. They showed that curvilinearity in heritability is caused by the skewness of distribution of genotypic and environmental values. When the distributions of

the second second

genotypic and environmental values were not symmetric, the "linear heritability" (ratio of $\sigma_{\rm G}^2/\sigma_{\rm p}^2$) with the bigger value (i.e., .7) indicated a greater deviation more from linearity compared to the "linear heritability" with the smaller value (i.e., .5 or .3). When selection has been practiced for many years in a closed population and distribution of environmental values is symmetric but the distribution of genotypic values is expected to have a negative asymmetry, the genetic gain predicted by the linear heritability under high intensity of selection for the upper tail will be an overestimate as the heritability will be concave downward. Further he suggested that a practical way to use the curvilinear heritability is to divide the data into several groups and fit a linear heritability in each group separately.

Up to this point, results from various simulation studies have been reviewed. The results reported by Gill (1965a, b, c) and Bereskin (1969, 1972) were similar to the results obtained from laboratory animals reported by Frankham et al. (1968), Hanrahan et al. (1973) and Eisen (1975).

Gill (1965a) and Young (1966) have shown that simulation studies offer the possibility to study the effect of combination of various parameters under different models of gene action.

The above review leads to the conclusion that further development and application of Monte Carlo methods in quantitative genetics studies becomes more and more important as animal breeders attempt to study complex interactions or to predict the potential response to breeding systems before applying them to real populations.

Various Mating Systems and Their Effects

Many kinds of mating systems have been developed in the fields of plants and animal breeding. Random mating, phenotypic assortative mating and varied forms of inbreeding and outbreeding have been used.

Li (1955) and Falconer (1960) have given formal definitions of random mating. In the case of bisexual organisms, any one individual of one sex is equally likely to mate with any individual of the opposite sex. In other words, the frequency of a certain type of mating is dictated by chance.

Generally the Hardy-Weinberg Law is mentioned whenever random mating is discussed. The law points out that under the system of random mating a large population will be in equilibrium if mutation, migration, and selection do not occur. Equilibrium means that there is no change in gene frequency and genotypic proportions from generation to generation. Also, in random mating populations the frequencies of the genotypes in the progeny produced by such matings are determined solely by the gene frequencies among the parents.

Phenotypic assortative mating is based on the somatic resemblance or phenotypic likeness of parents and can be either positive or negative. Varied forms of inbreeding and outbreeding are the result of mating individuals because of their consanguinity (relationship) or nonconsanguinity. Mating systems based on consanguinity and phenotypic likeness differ in several ways. They will be discussed by reviewing ground work laid by Wright and Lush.

In assortative mating the phenotypic likeness may not be genic. If no linkage exists, all gene pairs act independently of each other

in consanguine mating and the number of loci does not affect the results, whereas in somatic assortative mating gene by gene similarity is dependent on the number of loci. Furthermore, somatic assortative mating produces correlations between nonallelic genes which affect the same trait, thus affecting the variability of the population, whereas consanguine mating does not. In consanguine mating the genetic structure of the population is not affected by heritability, but that is not the case with assortative mating. Some experimental studies showed that consanguine mating will cause a degree of inbreeding that can be accumulated and may cause a depression on performance.

Small population size brought about chance consanguine matings and increased the coefficient of inbreeding in simulation studies done by Bereskin et al. (1970) and by Gill and Clemmer (1966).

Several studies on inbreeding in swine have been reported. Dickerson (1949) observed a linear decline in performance with increased inbreeding for different strains of inbred swine. Bereskin et al. (1968) reported that as inbreeding of the litter and dam increased, litter size became smaller, pig mortality increased, and growth rate was slower.

Berruecos et al. (1970) noted that inbreeding depression was found significant for weight of pigs at 130 days and for backfat thickness.

Inbreeding with cattle was also reported by several authors. Rollins et al. (1949) studied the effect of inbreeding upon growth in Jersey cattle. Inbreeding caused a decrease in height, weight and

heart girth and there was a linear regression on percent of inbreeding. Records were made on 322 cattle, with average inbreeding of 15%. Significant decrease was shown in birth weight. The effect of inbreeding varied with age and characteristic. The maximum effect occurred at 6 months of age where an increase of 1% inbreeding caused a decrease of 0.4% in mean weight, 0.15% in mean heart girth, 0.16% in mean height. At 4 1/2 years this figure changed to 0.10% in mean weight, 0.01% in mean heart girth, and 0.01% in mean height. Further, they noted that until six months of age inbred animals grew more slowly than out-crossed animals but between 6 and 12 months they grew more rapidly and continued to do so for the rest of the period studied.

Nelms and Stratton (1967) found that inbreeding in Hereford calves caused a decrease of .465 kg for each percent increase in coefficient of inbreeding for 180-day weight.

Dinkel et al. (1968) have also reported that inbreeding of calf and inbreeding of dam effects are of more importance on weaning traits than on postweaning traits and the two sexes of calf showed different response. Further, they reported that growth was more affected than conformation by inbreeding.

The effect of inbreeding on production in Holstein cows was examined by Von Krosigk and Lush (1958). For each increase of 1% inbreeding intra-sire regressions were $-1.74 \pm .57$ lb. of butterfat, -54 ± 17 lb. of milk, and $+0.003 \pm .003\%$ of butterfat, when the average of each cow's records was used.

Shoffner (1948) studied the reaction of the fowl to inbreeding. Using 9 lines he found that the general effect of inbreeding was
depression, but that the performance trait depressed most differed from line to line. The greatest reduction in performance has been in hatchability, egg production, viability, and sexual maturity. There were no changes in body weight nor egg weight. With inbreeding up to 60%, the regression of hatchability of fertile eggs on coefficient of inbreeding (F_x) was -.436 ± .132. Egg production was measured as the number of eggs laid by an individual until she is 500 days of age. The within sire regression of the mean egg production of sister group of mean inbreeding was -.926 ± .068. The regression of sexual maturity (days from hatching to first egg) on F_x was .597 ± .111, the regression of body weight (pounds at 300 days of age) on F_x was -.004 ± .003, the regression of average weight of ten eggs was -.002 ± .008.

MacLaury and Nordskog (1956) studied the effect of inbreeding on mortality in the domestic fowl. Regression of mortality percent on inbreeding was 0.33 in the brooding period, 0.15 in the range period and 0.21 in the laying-house period. Some of the disadvantageous effects of inbreeding were shown. In general the effect of inbreeding was the reduction of phenotypic mean value of some characters.

Lush (1948) and Falconer (1960) pointed out that one can employ the effect of inbreeding as a tool to obtain heterosis. No reduction in chicken body weight due to inbreeding was reported by Schoffner (1948), and other reports by Martin et al. (1953), Brunson et al. (1956) and Kan et al. (1959), showed that body weight was an additive trait. In this case there was agreement as inbreeding depression should not occur with additive traits.

On the other hand if dominance involved in body weight, as stated by Siegel (1962) and Yao (1959), inbreeding depression will occur and mating two inbred-lines offers a possibility to obtain heterosis.

Somatic assortative mating is as Falconer (1960) describes it, when mated pairs tend to be of the same genotype more often than could occur by chance. Normally the mating so described is called positive assortative mating. Less often negative assortative mating is used, in which the tendency is toward the mating of genetic opposites.

In Lush's (1948) review, he stated that mating like phenotypes tends to bring together mates whose genes have similar effects but need not be allelic to each other. The likeness between the phenotypes can be high while yet the likeness between mates gene by gene can be very low. As the number of gene pairs that control a trait increases, less and less of phenotypic correlation comes from likeness in allelic genes and more and more of it comes from the nonallelic genes. Positive assortative mating tends to throw the population toward the two extremes and to diminish the frequency of the intermediate types, and negative assortative mating will show the opposite results. Moreover assortative mating can be practiced only for characteristics which can be seen and measured. It is effective in increasing variance for certain characteristics only if they are highly heritable and controlled by few genes. Some experiments with assortative mating have been done with laboratory animals.

Wilson et al. (1965) studied Tribolium, Sutherland et al. (1968) mice, and McBride and Robertson (1963) Drosophila melanogaster.

The review of these studies has been made in the previous section with the conclusion that assortative mating gives some advantage when the trait selected for is highly heritable.

Selection for Body Weight in Chickens

In chickens for broiler production, body weight is the most important trait, and profit will be more if breeders can improve this trait through selection.

Various results from selection for body weight have been reported. Godfrey and Goodman (1955) reported that selection, within line, for small and large body size in Silver Oklabar after 5 generations showed differences in six and 12 week body weights of 0.6 and 1.3 pounds, respectively. Heritability average was about 0.26 at both 6 and 12 weeks of age. Phenotypic variation was 14% for the large line and 19% for the small line, but genic variance of the large line was greater than that of the small line.

Siegel (1962) reviewed heritability studies for body weight in chickens. He noted that 176 published heritability estimates of body weight obtained for chickens 6 to 12 weeks of age gave the quartile range of .29 to .54 with the median of .41. Siegel (1962) conducted a selection experiment for body weight at 8 weeks of age in White Plymouth Rock chickens. He reported that 30% of the total variation was due to additive genetic variation, and epistatic deviations appeared to be unimportant. Siegel found that dominance and maternal effects influence body weight, as was reported by Yao (1961). There was an indication of sex-linked gene effects as reported by Brunson et al. (1956) and by Thomas et al. (1958).

Martin et al. (1953) reported that variance in body weight was due to additive genetic variance and random environmental factors, and that dominance effects did not show statistical significance.

Brunson et al. (1956) found that variances in body weight due to genetic differences were 41% for additive genes, 2% for nonadditive genes, and 10% for sex-linked genes. The effect of sex-linked genes may be considered important as it was also reported by Thomas et al. (1958).

Yao (1959) reported that dominance effects were found to be significant in several incrosses and in crossbreds. In a later study Yao (1961) found that maternal effects had an influence on 10 week body weight.

Kan et al. (1959) performed selection studies on nonadditive gene effects on six broiler traits. Results showed trivial, if any, nonadditive gene effects on body weight at either 4 or 9 weeks of age or on gain in weight from 4 to 9 weeks, but nonadditive effects were important contributors to variation in shank length, keel length, and body depth. Heritability for body weight was quite high (Siegel, 1962), and the variance of body weight was mainly due to additive genetic variances. Further, Martin et al. (1953) indicated nonadditive genetic variance has little or no effect. The result was confirmed by Brunson et al. (1956), and by Kan et al. (1959), so mass selection should be successful to bring an improvement in body weight.

METHODS AND PROCEDURES OF SIMULATION

Computer processes were used in this study to simulate the base parental population. A repetitive pseudo-random number generator was utilized in simulating the probabilistic genetic mechanisms.

Two mating systems were used, random mating and positive phenotypic assortative mating. Individuals in generation one in both systems were generated from random mating of the base parental population.

To obtain the data for this study FORTRAN programs with several subroutines were written and used in a CDC 6500 computer, at Michigan State University.

The programs in detail were too lengthy to be listed. Only a brief explanation of how the populations were simulated will be given.

The population simulated in this study was the native chicken population from the author's country (Indonesia) and selection was only for body weight at sexual maturity. Body weight of the native fowl is easy to measure, is likely to be moderately heritable, and is economically important in Indonesia.

The native chickens are raised widely but not intensively in the villages in Indonesia and their characteristics have not been studied thoroughly. However their potentiality in contributing to

the animal protein resource is great. Up to now no purposeful selection has been practiced and no research information has been obtained.

This simulation process is based on reviews of literature concerned with other populations of fowl. It has been assumed that the variance of body weight at sexual maturity is only due to additive genetic variance and environmental variance, i.e., that dominance and epistasis play no more than a trivial role in the determination of variation in body weight.

The design of this experiment is 3² factorial. Populations were simulated for all possible combinations of three levels of heritability and three intensities of selection by upper truncation of the distribution of phenotypes.

In each base population the parameters used for mean and standard deviation of body weight were 1.4 kg and .2 kg, to closely approximate the real conditions in Indonesian villages.

The three levels of heritability selected were .1, .3 and .4, and as the additive variance was the only genetic variance contributed, the corresponding value of environmental variance can be calculated easily.

The three levels of selection by truncation were 25%, 50% and 75% of young birds saved for breeding. For each population, selection was practiced for ten generations and 100 replication populations were simulated for each combination of heritability and selection intensity.

The FORTRAN program was made general for all populations by permitting variable "input" in each run for the heritability value and level of selection.

The size of offspring population in each generation was 600, 300 males and 300 females.

In the process of growing until birds reached sexual maturity, mortality was assumed to be random with respect to genetic potential for body weight. Random mortality here was defined as the reduction of the population size in the real condition because of weakness, diseases, predators, slaughter or sale.

After the appropriate level of selection by truncation was applied the numbers of males and females available for mating was always 6 and 60, respectively.

The process of simulation can be summarized as follows:

(1) Each run of the program started by reading the heritability value and the level of selection.

(2) A library program, RANF, was available at MSU for the generation of uniformly distributed random numbers.

In this study uniformly distributed random numbers in the range $0 \le r_i \le +1$ were generated by the RANF program.

The variance of a uniformly distributed variable is equal to the square of the range divided by 12.

Therefore, $V(r_i) = (1)^2/12 = 1/12$

Twelve random uniform numbers (r_i) were added together to form a random sum in the range 0 to 12. Then, the variance of the sum was equal to $12 \frac{(1)}{12} = 1$, so the standard deviation of the sum also was 1.

Upon subtracting six from any sum of twelve r_i , one obtains random numbers in the range, $-6 \le e_j \le +6$, and the e_j are normally distributed with a mean of zero and standard deviation of 1, providing standard normal random deviates.

A sample of random deviates so generated was examined and found to conform closely to the standard normal distribution.

(3) A subroutine that calculated the genetic and environmental deviation was called in the main program.

Six males and 60 females were simulated as the base population.

The genotypic and phenotypic values were calculated as follows: genotypic value = population mean + genetic deviation; phenotypic value = genotypic value + environmental deviation, where genetic deviation was calculated as (Std. Dev. of additive genetic values) (Random normal deviate) and environmental deviation was calculated as (Std. Dev. of environmental effects) (Random normal deviate).

(4) The second subroutine, which generated the offspring from randomly mating each male to ten females was called next. From those matings the first generation for selection was obtained.

Random matings produced 5 males and 5 females each, to insure that the numbers of males and females were equal. The total offspring in the first generation consisted of 300 males and 300 females. The genotypic values of offspring were calculated as:

Genetic value of sire + Genetic value of dam 2

+ random deviate from Mendelian sampling, and the phenotypic values were computed from genotypic value of offspring + environmental deviation, where the Mendelian deviate was calculated as $\sqrt{.5}$ x (Std. Dev. of additive genetic) x (Random normal deviate).

Next, a subroutine was called to simulate random mortality, which was assumed to occur before the offspring reached sexual maturity.

The numbers of male and female individuals that survived were determined by the desired level of truncation selection, so that after the selection was practiced the numbers of offspring saved and retained to be parents for the next generation were always 6 males and 60 females.

In this process a random number was generated and multiplied by 300, producing a number in the range of 0 to 299.999, which by the addition of 1 gave a number in the range of 1 to 300.999. This number then was truncated to integer value resulting in a random integer in the range 1 to 300. The same process was followed for the random survival of female individuals.

(5) The last subroutine was called for sorting individuals in descending order of phenotypic value, so that they were ready for selection. For both random mating and assortative mating the simulation process was the same until this point in the program. In assortative mating the top male was mated with the ten top females, the next top male to the next of the ten top females, etc. But in random mating another subroutine put the individuals for mating back in random order.

(6) To obtain ten generations of offspring a "do loop" was made in the main program following generation of the base population. Another "do loop" that was built into the main program, after the process of reading heritability value and the level of selection, made it possible to obtain 100 replications (simulated populations).

(7) Results were stored on magnetic tape to avoid excessive printing.

A second program was made for the statistical analysis of data stored on tape. The results printed from this program were the phenotypic and genotypic means and variances of 100 replications (populations) in each of 10 generations. Computing time for this simulation program was approximately one hour for each set of 100 populations.

RESULTS AND DISCUSSION

For each type of mating system (random and assortative), nine combinations of heritability and level of truncation selection were used. For each combination 100 populations (replicate runs) were simulated.

In each run the base population was generated at random using a repetitive pseudo-random number generator. Each population was permitted to pass through ten generations of selection and mating.

The final results that were printed out were the phenotypic and genotypic means and variances across 100 replicates (populations) in each generation.

Effect of Heritability on the Change of the Phenotypic Mean

The change in the phenotypic mean under random mating is shown in Figures 1, 2 and 3, where phenotypic mean is plotted against the generation. The change in the phenotypic mean under assortative mating is shown in Figures 4, 5 and 6.

The results when the proportion selected for breeding was 25% (Figure 1 for random mating and Figure 4 for assortative mating), showed that the highest heritability, .4, gave the greatest change in the phenotypic mean from one generation to the next and gave the



Fig. 1: Change in the mean when b=25% with random mating (b = proportion selected)



Fig. 2: Change in the mean when b=50% with random mating (b = proportion selected)



Fig. 3: Change in the mean when b=75% with random mating (b = proportion selected)





Fig. 4: Change in the mean when b=25% with assortative mating (b = proportion selected)



Fig. 5: Change in the mean when b=50% with assortative mating (b = proportion selected)



Fig. 6: Change in the mean when b=75% with assortative mating (b = proportion selected)

highest response at the end of the selection studies for either mating system.

Figures 2 and 5 show the results when the proportion selection was equal to 50% and Figures 3 and 6 show results when the proportion selected was equal to 75%, for random and assortative mating, respectively, at each level of selection.

Results under random mating and assortative mating showed the same pattern, that the higher the heritability the higher will be the change, i.e., the greater improvement by selection. Differences between the two mating systems were minor.

In the two mating systems of this study, the standard error of the phenotypic mean was obtained by the following calculations. The computer printout gave only the phenotypic variance of all individuals. The calculation of standard error of the mean is:

$$Y_i$$
 = individual value (result)
 Y_2 = mean value of 600 individuals in one population (replication)
= $\begin{pmatrix} 600 \\ \Sigma \\ i=1 \end{pmatrix} Y_i / 600$

Y₃ = mean value of 100 populations (60,000 individuals) V(Y₁) = variance of all individuals = 0.04

 $V(Y_2)$ = variance of mean of 600 individuals (one population)

$$= \frac{600}{\Sigma} (0.04/360,000)$$

$$= \frac{600 (.04)}{360,000} = .000067$$

$$V(Y_3) = \text{variance of the mean of 100 populations}$$

$$= \frac{100}{\Sigma} (.000067)/10,000$$

$$i=1$$

Standard error = $\sqrt{\frac{.000067}{100}}$ = .0008

In both systems of mating the percent of improvement in the phenotypic mean at generation ten was calculated as:

The values are presented in Table 1.

For 25% selection under random mating the improvements at generation 10 were 14.3%, 39.5% and 53.6% for heritability equal .1, .3, and .4. When 50% were selected the corresponding improvements were 9.4%, 25.4%, and 32.6%, and when 75% were selected improvements were 4.6%, 14.5%, and 18.1%.

	Ran	dom Mati	Mating .ng	g Type Assor	tative M	ating
	25%	50%	Proportion 75%	n Selected	50%	75%
	230	500	750	250	500	750
h = .1	14.3	8.4	4.6	14.0	9.2	4.6
h = .3	39.5	25.4	14.5	41.3	26.9	14.4
h = .4	53.6	32.6	18.1	54.3	34.8	18.6

Table 1.--Percent of Improvement at Generation 10 Under Random Mating and Assortative Mating.

For assortative mating improvements were 14.0%, 41.3%, and 54.3% when 25% were selected, 9.2%, 26.9%, and 34.8% when 50% were selected, and 4.6%, 14.4%, and 18.6% when 75% were selected, for heritability equal to .1, .3, and .4 in each case.

These results showed good agreement with the theory that the response to selection can be predicted and depends on the intensity of selection, heritability, and phenotypic standard deviation of the trait selected.

Falconer (1960) gave the prediction equation of response to selection as:

$$R = ih^2 \sigma_p$$

where i is the intensity of selection, h^2 is the heritability value and σ_p is the phenotypic standard deviation. The value of i for different proportions selected for mating can be obtained from tables presented by Lush (1956) and by Nanson (1967). Under the same selection intensity and the same phenotypic standard deviation the response to selection will be proportional to the heritability.

It was shown that the highest heritability (.4) gave the highest response at the end of selection. There have been no reported research studies on heritability of body weight of the native Indonesian chickens. Siegel (1962) reported the median heritability estimate of body weight for chickens 6-12 weeks of age is .41.

If the heritability of body weight in native chickens at sexual maturity were assumed to be .4 instead of .3 or .1, then, the improvement that can be achieved in 10 years can be estimated accordingly. Under random mating with 50% of population saved for breeding in 10 years, the heritability .4 will create a population mean difference in improvement of 106 grams above that for heritability .3. Between the heritability .4 and heritability .1 the difference will be 343 grams.

Effect of Level of Truncation Selection on the Change of the Phenotypic Mean

The effect of selection intensity on the change of phenotypic mean in each generation for heritabilities .1, .3, and .4 is presented in Figures 7, 8, and 9 for random mating and in Figures 10, 11, and 12 for assortative mating.

As expected the results showed that the higher the level of truncation (the smaller the population selected for breeding), the greater the change in each generation and the more the response at the



Fig. 7: Change in the mean when heritability = .1 under random mating



Fig. 8: Change in the mean when heritability = .3 under random mating



Fig. 9: Change in the mean when heritability = .4 under random mating





Fig. 11: Change in the mean when heritability = .3 under assortative mating



Fig. 12: Change in the mean when heritability = .4 under assortative mating end of selection. This was true both for random mating and for assortative mating.

These results showed good agreement with those of Frankham et al. (1968), Hanrahan et al. (1973), and Eisen (1975).

For either random mating or assortative mating under the same level of truncation, the response to selection is proportional to heritability.

The best response to selection at the end of selection was obtained in populations with heritability = .4 and the proportion selected for mating was 25%. The least response to selection in this study was for populations with heritability = .1 and proportion selected was 75%.

Each combination of heritability and proportion selected for mating gave different response. An analysis of variance was made to see if the level of truncation and the heritability level gave a significant contribution to the variability of response to selection at the termination of studies. Data for this analysis of variance were phenotypic mean values at generation ten under random mating.

The analysis of variance table is presented here:

Source of variation	df	S.S.	M.S.	F
Heritability	2	. 203378	.101689	1517.746**
Truncation level	2	.161588	.080794	1205.881**
Her. x truncation level	4	.397318	.0993295	1482.530**
Error	891		.000067	
Total	899			

The F statistics were tremendously large, the heritability, truncation level and the interaction between them being highly significant in contributing to the variability of response to selection. The mean differences between each level of truncation within the same level of heritability were tested with the Bonferroni t statistics. The Bonferroni t statistics gave the confidence interval of the mean difference.

C.I. = \pm (3.280)(.0011575) = \pm .0038 for α = .1, and the test of the mean difference between level of truncation within each level of heritability was significant.

The best response to selection was shown to be where 25% population was saved for breeding. That was true for all values of heritability applied in this study.

With random mating, after ten years selection the difference of the phenotypic mean if 25% population is saved for breeding instead of 50% amounts to 289 grams (assuming that the heritability = .4). Between 50% and 75% the difference is 204 grams. The difference in amount of progress shown is meaningful but in the practical situation 50% or 75% level of truncation seems more likely to be achievable than 25%. Some reasons can be given.

- 1. The idea of truncation selection is new to the village people; it needs a careful introduction with the least possible risk.
- When truncation selection is applied the natural condition will be changed.

- 3. People will be more likely to accept the smaller change. In this case it will be easier to accept the idea to save 50% or 75% of the population for breeding than 25%.
- Reinforcement of the value of selection will be slow, i.e., selection takes a long time before the major results can be observed.
- 5. Natural selection still exists and disease control is minimal. The risk will be lesser if the population saved is bigger, so that populations can be continued.
- 6. Fertility in native chickens probably is low. The more that can be saved, the more assurance for the continuation of selection.

If the level of truncation were 50%, the expected progress in 10 years would be 459 grams, nearly double the progress made by 75% truncation (255 grams).

Considering that the raw material of selection is genetic variation, to apply 50% level of truncation seems suitable when the population is considered large enough, but when the population is smaller, 75% level of truncation will be preferable.

Response to Selection with Random Mating and Assortative Mating

The response to selection when mating was assortative was nearly the same as when mating was random. Figures 13, 14, and 15 show phenotypic means under random mating and assortative mating, plotted against generation numbers, for 25, 50 and 75 percent truncation selection, respectively. The differences in slopes of regressions of







Fig. 14: Change in the mean under random mating and assortative mating when b=50%



Fig. 15: Change in the mean under random mating and assortative mating when b=75%

the phenotypic means on generation number for the two types of mating was statistically significant in most cases but the difference was biologically trivial except when selection intensity and heritability were high. In that case a small advantage may be noted for assortative mating. In this study statistical significance has little meaning. The difference that can be detected is very small because of large sample size (60,000 individuals per mean).

Sutherland et al. (1968) reported that assortative mating gives little benefit compared to random mating if the trait is not highly heritable. The results of this study agree with that. When the heritability was .1, assortative mating and random mating gave nearly the same results regardless of level of truncation selection. When the proportion selected for mating was 75% the results from both types of mating were very close for each of the three levels of heritabilities. Possibly, assortative mating in small populations tends to produce more genetic variation than in the case of random mating, but when the population saved for breeding is relatively large (as in the case of 75% selected), then the genetic variation may be nearly the same for both types of mating. In general, it appears that there is little or no benefit to assortative mating over random mating. Furthermore, in the practical situation with which this study is concerned, it would be very impractical if not impossible to conduct assortative mating. The native chickens in Indonesian villages are not raised in confinement, so even if assortative mating gave a meaningful benefit, still such matings could not be adopted unless

tremendous effort was made to change the traditional conditions in the villages.

The Genotypic Means and Variances

The genotypic means and the changes from one generation to the next, for each of the two types of mating systems, were very close to the results observed for the phenotypic means. The differences were trivially small if not zero.

The closeness of these results was expected for the trait simulated because the average environmental effect was expected to be zero.

Both phenotypic and genetic variances increased slightly from one generation to the next, but the genetic variance increased slightly more than the phenotypic variance. That caused heritability to increase somewhat over time. The heritability values increased more with assortative mating than with random mating when selection was not intense (75% or 50% saved for breeding), for each of the three initial levels of heritability. For more intense selection (25% saved), the changes in heritability were similar for the two types of mating.

The standard errors for the genotypic means were between .0003 and .0006.

Table 2.1 and 2.2 show the phenotypic and genotypic means and variances obtained by random mating and assortative mating, respectively. As in general there is little or no difference in practical benefit between assortative mating and random mating, only random mating will be discussed further.

	Heritability			.1					б.					4.		
Proportion Selected	Generation	Me Phen.	ean Gent.	Varia Phen.	ance Gent.	h ²	Me. Phen.	an Gent.	Vari Phen.	ance Gent.	$^{\rm h}$	Mei Phen.	an Gent.	Varia Phen.	ince Gent.	h ²
	1	1.400	1.400	.040130	.003917	0.98	1.400	1.399	.039195	.011608	. 296	1.398	1.398	.040031	.016014	.400
	2	1.425	1.424	.040138	.004042	.101	1.468	1.467	.038622	.010924	.283	1.496	1.495	.038515	.014326	.372
	ю	1.448	1.447	.039927	.004111	.103	1.530	1.531	.038829	.010944	.282	1.578	1.577	.038740	.014762	.381
	4	1.467	1.466	.039589	.004210	.105	1.596	1.595	.039034	.011351	.291	1.665	1.665	.039693	.015616	.393
75%	S	1.488	1.489	.040171	.004366	.109	1.655	1.654	.039223	.011449	.292	1.749	1.749	.039641	.015782	.398
0.07	6	1.508	1.508	.040477	.004633	.114	1.711	1.710	.039936	.012048	.302	1.831	1.831	.040387	.016216	.402
	7	1.528	1.528	.040821	.004807	.118	1.772	1.772	.040091	.012186	.304	1.908	1.908	.040844	.017099	.419
	ø	1.552	1.553	.041307	.005207	.126	1.832	1.832	.040152	.012332	.307	1.988	1.988	.041337	.017323	.419
	6	1.578	1.577	.041429	.005345	.129	1.892	1.893	.041012	.012894	.314	2.067	2.066	.042480	.018226	.429
	10	1.600	1.601	.041549	.005462	.131	1.953	1.953	.041091	.013584	.331	2.148	2.147	.042988	.018839	.438
	1	1.399	1.399	.040318	.004123	.102	1.398	1.399	.040023	.011914	.298	1.402	1.402	.040063	.016157	.403
	2	1.416	1.416	.040023	.004084	.102	1.443	1.443	.038933	.011181	.287	1.458	1.458	.038438	.014627	.381
	3	1.429	1.429	.039817	.004015	.101	1.482	1.482	.039697	.011905	.300	1.510	1.510	.038544	.014585	.378
	4	1.444	1.444	.039936	.004078	.102	1.521	1.520	.039795	.011979	.301	1.564	1.564	.038851	.015090	.388
508	S	1.456	1.456	.040410	.004317	.107	1.561	1.560	. 040065	.012052	.301	1.611	1.611	.038817	.015034	.387
4.OC	6	1.468	1.469	.040398	.004484	.111	1.598	1.598	.040293	.012283	.305	1.660	1.660	.039095	.015360	.393
	7	1.481	1.481	.040705	.004635	.114	1.637	1.636	.040618	.012578	.310	1.713	1.713	.040183	.016180	.403
	80	1.490	1.491	.040826	.004890	.120	1.674	1.675	.040693	.012534	.308	1.762	1.762	.040897	.016863	.412
	6	1.502	1.503	.040978	.004876	.119	1.713	1.713	.041347	.013253	.321	1.807	1.807	.041201	.017242	.418
	10	1.516	1.518	.040724	.004839	.119	1.753	1.751	.041782	.013628	.326	1.859	1.859	.041499	.017358	.418
	1	1.398	1.399	.040082	.004015	.100	1.400	1.399	.040364	.012289	.304	1.401	1.401	.039968	.015751	.394
	2	1.408	1.406	.039871	.004164	.104	1.426	1.426	.040200	.012087	.301	1.432	1.433	.039285	.015108	.384
	3	1.414	1.414	.040402	.004311	.107	1.452	1.453	.039663	.012015	.303	1.458	1.459	.039315	.015252	.387
	ব	1.422	1.421	.040436	.004537	.112	1.474	1.474	.040051	.012376	.309	1.486	1.486	.040005	.015620	.390
75%	S	1.430	1.429	.040746	.004657	.114	1.495	1.494	.041233	.012919	.313	1.516	1.515	.040543	.016501	.400
	9	1.433	1.433	.040505	.004770	.118	1.515	1.515	.041132	.012965	.315	1.544	1.543	.041255	.016715	.405
	-	1.440	1.439	.041178	.004980	.121	1.539	1.539	.041490	.013544	.326	1.576	1.575	.042240	.018120	.429
	00 (1.446	1.445	.040663	.004999	.123	1.560	1.560	.041787	.014281	.342	1.601	1.601	.043191	.019317	.447
	6	1.454	1.454	.040711	.004986	.122	1.582	1.583	.042826	.014739	.344	1.627	1.627	.043732	.019991	.457
	10	I.463	1.463	.040915	.005074	.124	1.603	1.604	.043340	.015483	.357	1.655	1.655	.044347	.020097	.453

Table 2.1.--The Change of the Phenotypic and Genotypic Means and Variances, and the Change of Heritability Value Under Random Mating.
Proportion	Heritability	Ŵ	Ľ	.l Varia	nce		Mea	5	.3 Varia	ece		Ne	5	.4 Varis	eou	
Selected	Generation	Phen.	Gent.	Phen.	Gent.	h ²	Phen.	Gent.	Phen.	Gent.	հ ²	Phen.	Gent.	Phen.	Gent.	ћ ²
	1	1.402	1.400	.039779	.003955	660.	1.399	1.398	.039898	.011851	.303	1.407	1.407	.040082	.016071	.401
	2	1.422	1.424	.040023	.003891	.093	1.472	1.471	.039048	.011419	.292	1.500	1.501	.038881	.015111	.389
	3	1.446	1.445	.040097	.003933	.098	1.536	1.536	.039647	.011628	.293	1.593	1.594	.038947	.014745	.379
	4	1.467	1.465	.040260	.004215	.105	1.603	1.604	.039362	.011461	.291	1.670	1.671	.039002	.014912	.382
15%	S	1.488	1.488	.040942	.004564	.111	1.667	1.667	.039878	.011781	. 295	1.754	1.753	.039846	.015735	.395
4 .C 7	Q	1.511	1.511	.040880	.004620	.113	1.730	1.731	.039897	.011946	. 299	1.836	1.837	.040666	.016710	.410
	7	1.529	1.530	.040970	.004847	.118	1.794	1.792	.039794	.012226	.307	1.921	1.921	.041054	.016943	.412
	œ	1.551	1.551	.041029	.004874	.119	1.855	1.855	.040903	.012905	.316	2.004	2.004	.041357	.017450	.422
	6	1.573	1.574	.041058	.004877	.119	1.915	1.916	.041532	.013507	.325	2.089	2.091	.041495	.017479	.421
	10	1.598	1.597	.041129	.005015	.122	1.977	1.978	.041241	.013691	.332	2.171	2.172	.042319	.018111	.428
	1	1.399	1.400	.040217	.004067	101.	1.404	1.404	.040036	.012209	.305	1.399	1.399	.039856	015909	399
	- 2	1.414	1.414	.040352	.004035	.100	1.449	1.448	039697	.011662	294	1.458	1.459	.039772	.015694	395
	1 10	1.429	1.429	039914	.004113	.103	1.490	1.490	038987	.011527	. 296	1.520	1.519	039886	015949	400
	4	1.442	1.443	.040445	.004385	.108	1.531	1.531	.040099	.012235	.305	1.570	1.570	.039852	.016031	.402
a C L	S	1.459	1.458	.040116	.004342	.108	1.574	1.574	.041019	.012833	.313	1.626	1.626	.039856	.016204	.408
\$0¢	6	1.470	1.470	.040054	.004643	.116	1.615	1.615	.041471	.013648	.329	1.674	1.675	.041650	.017154	.412
	7	1.484	1.485	.040849	.004938	.121	1.659	1.659	.042223	.014323	.339	1.728	1.727	.041574	.017725	.426
	80	1.499	1.499	.040811	.005080	.124	1.700	1.699	.043059	.014973	.348	1.780	1.779	.042878	.018887	.440
	6	1.513	1.514	.041134	.005061	.123	1.743	1.742	.043372	.015450	.356	1.836	1.836	.043075	.018785	.436
	10	1.527	1.527	.041057	.005344	.130	1.782	1.781	.044134	.016276	.369	1.886	1.886	.042824	.019005	.444
	1	1.399	1.399	.040419	.004162	.103	1.402	1.401	.039549	.011853	.300	1.405	1.404	.039703	.015592	.393
	2	1.404	1.405	.040454	.004090	.101	1.423	1.423	.040432	.012580	.311	1.427	1.429	.040589	.016391	.404
	3	1.413	1.412	.040001	.004175	.104	1.447	1.448	.041280	.013131	.318	1.456	1.456	.040485	.016959	.419
	4	1.422	1.422	.040420	.004407	.109	1.471	1.471	.041809	.013880	.332	1.480	1.480	.042629	.018671	.438
75%	S.	1.431	1.430	.040555	.004465	.110	1.495	1.494	.042385	.014415	.340	1.511	1.511	.043686	.019999	.458
	01	1.436	1.437	.040397	.004851	.120	1.517	1.517	.042133	.014618	.347	1.546	I.540	.044385	.020354	.458
	~ 0	1.445	1.440	.040000	100500.	125	1.520	1.235 1 541	.042433	01/210	705.	1/2.1	1.570	044509	0000000	204.
	0 0	1 458	1.455	040/040.	.00505	961	1 582	1.587	00/010	0//210.	368	1.632	1 633	.044009	530220	403
	ء 10	1.464	1.465	.040953	.005391	.132	1.604	1.605	.045027	.017270	.384	1.666	1.666	.046887	.022970	.490

Table 2.2.--The Change of the Phenotypic and Genotypic Means and Variances, and the Change of Heritability Value Under Assortative Mating.

Estimated Accumulation of Inbreeding

Wright (1931) pointed out that when population size is restricted, nonrandom mating will occur although it is not intended and this will cause an accumulation of inbreeding, or average likeness by descent of the two alleles at a given locus.

In this study the breeding size was restricted to 60 females and 6 males in each generation. Wright (1931) derived the equation used to predict inbreeding:

$$F = F' + \frac{N_{m} + N_{f}}{8 N_{m} N_{f}} (1 + F'' - 2 F')$$

where F is the expected inbreeding when F' was the inbreeding of the previous generation and F" was the inbreeding two generations previous.

The numbers of breeding males and females are N_m and N_f .

This equation was used to estimate inbreeding each generation. The results are presented in Table 3. The expected value of inbreeding was 19% at the end of selection and the average increase each generation was 2%. The amount of inbreeding was increased, but the response to selection as the generation progressed showed no inbreeding depression. This was expected because in this simulation study the trait was determined only by additive effects of genes. Kempthorne (1957) has shown that inbreeding depression does not occur without dominance.

Generation	% F Estimated
Base	0
1	0
2	2
3	5
4	6
5	9
6	11
7	13
8	15
9	17
10	19

Table 3.--Percent Estimated Inbreeding by Generation.

The Accuracy of the Prediction of the Phenotypic Mean

The observed and expected phenotypic means are shown in Table 4 and in Figures 16, 17, and 18. The expected phenotypic means were calculated by using the formula presented by Falconer (1960b), $R = nih^2 \sigma_p$, where R is response to selection, n is generation number, i is selection intensity, h^2 is heritability and σ_p is phenotypic standard deviation. The phenotypic mean in generation n was estimated as P_n and $P_n = P_0 + R$, where P_0 is phenotypic mean in base generation.

The selection intensity was obtained from the table presented by Nanson (1967) for effective population size less than 50. By interpolation, the selection intensities were 1.19, .71 and .39 for 25%, 50% and 75% proportion selected for mating, respectively.

The results showed that for the three levels of truncation the observed and the expected responses agree well throughout the generations when the heritability value is .1, but when the heritability values are .3 and .4 the discrepancies between the observed and expected responses began to occur after the 5th generation of selection with the expected values greater than the observed values, except for the population with 75% proportion selected where the observed and estimated responses agree well. The larger discrepancies were observed for the heritability .4 than for heritability .3. This was similar to results reported by Young (1966).

Estimation of Realized Heritability

Realized heritability was estimated using the method presented by Hill (1972), where the equation for the estimation was:

Heritabilitv	Generation	~	25%	Proportic	n Selected 0%		2% 2%
		Observed	Expected	Observed	Expected	Observed	Expected
	1	1.400	1.400	1.399	1.400	1.398	1.400
	2	1.425	1.424	1.416	1.414	1.408	1.408
	3	1.448	1.448	1.429	1.428	1.414	1.416
	4	1.467	1.471	1.444	1.442	1.422	1.424
-	S	1.488	1.495	1.456	1.457	1.430	1.432
۲.	Q	1.508	1.519	1.468	1.471	1.433	1.439
	7	1.528	1.543	1.481	1.485	1.440	1.447
	ø	1.552	1.567	1.490	1.499	1.446	1.455
	6	1.578	1.590	1.502	1.513	1.454	1.462
	10	1.600	1.614	1.516	1.528	1.463	1.470
	1	1.400	1.400	1.398	1.400	1.400	1.400
	2	1.468	1.471	1.443	1.443	1.426	1.423
	3	1.530	1.543	1.482	1.485	1.452	1.447
	4	1.596	1.614	1.521	1.528	1.474	1.470
r	S	1.655	1.686	1.561	1.571	1.495	1.494
c.	9	1.711	1.757	1.598	1.613	1.515	1.517
	7	1.772	1.828	1.637	1.656	1.539	1.540
	ø	1.832	1.900	1.674	1.698	1.560	1.564
	6	1.892	1.971	1.713	1.741	1.582	1.587
	10	1.953	2.043	1.753	1.783	1.603	1.611

Table 4.--Observed and Expected Phenotypic Means Under Random Mating.

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Heritabilitv	Generation		25%	Proportio 5	n Selected 0%	.~	75%
		Observed	Expected	Observed	Expected	Observed	Expected
	1	1.398	1.400	1.402	1.400	1.401	1.400
	2	1.496	1.495	1.458	1.457	1.432	1.431
	2	1.578	1.590	1.510	1.514	1.458	1.462
	4	1.665	1.685	1.564	1.570	1.486	1.494
•	S	1.749	1.781	1.611	1.627	1.516	1.525
4.	Q	1.831	1.876	1.660	1.684	1.544	1.556
	7	1.908	1.971	1.713	1.741	1.576	1.587
	80	1.988	2.066	1.762	1.798	1.601	1.618
	6	2.067	2.162	1.807	1.854	1.627	1.650
	10	2.148	2.257	1.859	1.911	1.655	1.681







Fig. 17: Observed and expected phenotypic mean with random mating and b=50%



Fig. 18: Observed and expected phenotypic mean with random mating and b=75%

$$b_{c} = \sum_{i=0}^{t} (S_{i} - \bar{S}) (X_{i} - \bar{X}) / \sum_{i=0}^{t} (S_{i} - \bar{S})^{2}$$

In this equation b_c is realized heritability estimate, S_i is the cumulative selection differential to generation i, X_i is the mean response at generation i, and \bar{S} and \bar{X} are the means of the S_i and X_i over i=0, ..., t generations.

The variance of the estimated value was calculated as:

$$\hat{V}(b_{c}) = \mu(b_{c}) + \frac{2(3t+4)}{5\bar{s}^{2}(t+1)(t+2)} \hat{\sigma}_{d}^{2}$$
where $\mu(b_{c}) = h\left[\left(\sum (x_{i} - \bar{x})^{2} - b_{c} \sum_{i=0}^{t} (S_{i} - \bar{s})(x_{i} - \bar{x}) \right] / \left[(t-1) \sum_{i=0}^{t} (S_{i} - \bar{s})^{2} \right]$

$$\hat{\sigma}_{d}^{2} = \hat{\sigma}^{2} \left[b_{c} (1 - b_{c}) / N + b_{c}^{2} / M \right]$$

and t is generation number.

$$N = \left[\frac{1}{4 N_{m}} + \frac{1}{4 N_{f}}\right]^{-1}$$
$$M = \left[\frac{1}{4 M_{m}} + \frac{1}{4 M_{f}}\right]^{-1}$$

 M_m and M_f is the number of males and females recorded and N_m and N_f is the number of males and females selected for mating.

The results of the estimated realized heritability by this formula are presented in Table 5. The estimated realized heritability values were smaller than the values estimated by variance components for this simulation in all cases (Table 2.1). The differences can be explained as in this study the value of the heritabilities were changed

h ²	25%	50%	75%
.1	.08 ± .003	.08 ± .005	.08 ± .009
.3	.24 ± .007	.24 ± .009	.26 ± .020
.4	.33 ± .008	.32 ± .011	.34 ± .019

Table 5.--The Estimated Value of Realized Heritabilities.

due to the change in the genetic and phenotypic variance. Hill (1972) discussed the theory of realized heritabilities, but assumed that the heritability does not change during the experiment. The heritability did change in this study, and the estimated realized heritability values differ from the heritability values computed from components. However, near the beginning of selection, the differences were small and can be neglected.

SUMMARY AND CONCLUSIONS

The effect of degree of truncation selection and level of heritability in simulated populations of poultry subjected to selection was studied. The trait simulated was body weight at sexual maturity of native chickens in Indonesia.

The CDC 6500 computer at MSU was used to generate the populations.

The design of the experiment was 3² factorial. Populations were simulated for all possible combinations of three levels of heritability (.1, .3 and .4) and three intensities of selection by upper truncation of the distribution of phenotypes (25%, 50% and 75%). The parameters used for mean and standard deviation of body weight were 1.4 kg and .2 kg and the only genetic variance contributed to the variability was the additive variance.

The size of offspring population in each generation was 600, 300 males and 300 females, with random mortality assumed to occur so that breeding size after truncation was constant at 6 males and 60 females. Selection was performed for ten generations. For each parameter combination, 100 replications (populations) were simulated. Two types of mating systems, random and assortative, were simulated.

The results from random mating and assortative mating showed the same pattern. The test of difference in slopes of regressions of

the phenotypic means on generation number for the two types of mating was statistically significant in most cases but the difference was biologically trivial. A small advantage was noted for assortative mating when selection intensity and heritability were high.

Under the same level of truncation, the response to selection is proportional to heritability. The best response to selection was obtained in population with heritability = .4 and the proportion selected for mating was 25%. The least response to selection was for population with heritability = .1 and proportion selected was 75%.

Discrepancies between observed and expected response were noted after the fifth generation of selection when heritability was .3 or .4, with the expected value greater than the observed value.

No inbreeding depression was observed but the estimated accumulation of inbreeding due to restricted population size averaged 2% each generation. The heritability values increased somewhat over time and increased more with assortative mating than with random mating when 75% or 50% of a population was saved for breeding, but when 25% was saved increases were similar for both mating systems.

The estimated realized heritability calculated with the formula presented by Hill (1972) were smaller than the values estimated by variance components in all cases, because the genetic and phenotypic variances changed over time in this study.

Assortative mating should not be preferred over random mating, as the small differences in results are not biologically meaningful.

Also, in Indonesian villages the native chickens are not raised in confinement and cannot be without major changes in

traditional practice. Therefore, only selection with random mating should be taken under practical consideration.

Although selection of only 25% of the population should produce greater improvement than selection of 50% or 75% for any level of heritability, in practice such strong selection should not be recommended.

There are several reasons, but most importantly it will be difficult to encourage the village people to save only 25% of the population.

Disease control is still minimal, natural selection still plays a significant role in mortality, and the risk of losing an entire population will be greater than if the population saved were bigger. Saving 50% to 75% of the population for breeding should be recommended.

Saving as much as 75% of the population should be preferable for villages which maintain relatively small populations.

To apply this study in the field a preliminary survey should be taken to estimate parameters of the Indonesian environment and to determine other conditions that might alter the results predicted by this study. Selection works better if the environmental conditions permit the quantitative trait to be fully expressed. The scarcity of food, lack of disease control and lack of cooperation of rural people are a few among many factors that may hinder potential improvement.

It is important to study the characteristics of the native chickens as they have adapted to village conditions and developed great resistance to disease. The idea of introducing a "new" breed (exotic breed) to the villages is still questionable, primarily because of the questionable adaptability to the Indonesian environment.

This study has shown that without introducing any blood from other breeds, selection along with random mating within the native chicken population can bring a significant improvement.

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