

## POPULATION GENETIC BEHAVIOUR UNDER LONG-TERM SELECTION\*

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### SUMMARY

A series of simulation studies on population behaviour under long-term selection were reviewed. Population genetic behaviour in population means, variance and distributions, heritabilities, effect of each allele and effect difference of two alleles in a locus, major loci and general loci effects, selection differential and selection response, symmetry of accumulative response in opposite direction and interaction among different kinds of genes was described and discussed. In most of cases these seemed to be in accordance with results of the long-term selection experiments on *Drosophila*, mice and farm animals. It would be suggested that further study must be put on a deeper understanding of biochemistry and physiology of the selected trait.

### INTRODUCTION

Long-term selection experiments have served as a major tool in our attempts to understanding the nature of genetic variation for quantitative traits, but a lot of expenditure is needed to do them, especially on farm animals. The objective of this paper is to review population genetic behaviour under long-term selection by computer simulations in order to apply them to improvement animals in practice.

### SIMULATION PROCEDURE

A series of formulas for calculating population distribution frequencies, mean and variance in base population and frequencies of genes in each locus and population mean in selected parents in trait controlled by additive or complete or overdominant or these three kind of genes were developed (see papers by Jiang et al, 1989). Magnitudes of effects and primary frequencies for all of alleles assumed were given for each simulation case. Individuals which performance is super to the population mean in each generation, were selected as the parents of next generation.

### RESULTS AND DISCUSSIONS

#### Population mean

Population mean in successive generations changes classically in two types-"Eisen" model, i.e., population mean appears as an initial linear change with generations of selection or cumulative selection differential followed by a gradual decrease of response until a selection limit is attained, just as Eisen (1980) described; and "S" model, i.e. population mean expresses as an initial gradual

\* The Project Supported by National Natural Science Foundation of China

\*\* Awardee of Fok Ying Tung Education Foundation

increase, then linear change and final gradual decrease of response with generations of selection until the selection limit reached. However, these changes depend on some factors, such as initial gene frequencies, gene action type, number of loci and selection differentials. When the initial gene frequencies are low, or the trait is controlled mainly by additive or complete dominant genes, changes of population mean in successive generations are inclined to "S" type; when the trait is determined mainly by overdominant genes, or number of loci which control the selected trait is enough large or enough little, or the selection differential in each generation is very large, trends of population mean are inclined to "Eisen" type. However, experiment on *Drosophila* (Yoo, 1980) showed that trends of population mean under the long-term selection are too variable to conform to any classical models described above, because there are many factors to affect the selection response in practical conditions. Certainly, long-term selection always leads up to population changes until the limit is attained.

#### Population variance and distributions

The simulation results showed that as the frequency of the desired genes changes in a large range, trend of population variance in successive generations occurs in a parabolical curve in the trait determined by additive or complete dominant genes with equal effects and equal frequencies. Population distribution moves from one side asymmetrical to normal and finally toward asymmetrical in other side. While in the trait controlled by overdominant genes, the population variance increases gradually with selection generation and finally fixes in a given value, population distribution in the case changes only from one side asymmetrical to the normal. When the trait is controlled by major additive, or major complete dominant genes or three kinds of genes, population variances in successive generations appear also in parabolical curve, but with fluctuations. Population distribution changes are more complicated than that mentioned above.

Some of experiments supported the theory from these simulations (MacArthur, 1949; Clausen et al, 1872; Jiang Zhihua and M. Sviben 1987). However, selection experiments for abdominal bristle number on *Drosophila* showed that long-term selection leads the population variance enlarged in opposite directions. There may be two reasons for this - different response for the 4th and 5th sternite although they are incorporated to one trait and existence of lethal gene for the trait (Clayton et al, 1975) and Yoo, 1980).

#### Heritability

When the trait is controlled only by additive genes, the heritability in any selection generation equals one, because only additive variance exists in this case. While the heritability will be less than one when the trait is controlled by complete dominant genes or overdominant genes or three kinds of genes because both additive and nonadditive variance are present, and it decreases gradually with increase of selection generations. These were supported by experimental results on mice (Eisen, 1975) and on Japanese quail (Marks, 1982). It was found that there is a difference between Falconer's heritability and the realized heritability, but not very large.

## Effect of each allele and effect difference of two alleles in a locus

Simulation studies showed that when the trait is controlled by additive or complete dominant genes, loci with same effect difference of two alleles, no matter how effect of each allele in a locus is, have same function to population mean, variance, response and other parameters. In case of overdominant genecontrolled trait, extra effect  $K$  acts as same as the effect difference of two alleles described above. However, it must be kept in mind that magnitude of desired gene effect contributes to population up-selection limit. while magnitude of another gene effect to down-selection limit in a population.

## Major loci and general loci

When the number of major loci is given, more generations are needed for either major or general desired genes to reach their limits with the increase of number of general loci which control the selected trait. In the trait determined by same number of major and general loci, the larger locus-effect difference is in major genes, the more fast the major and the more slowly general desired genes reach their own limits. Also the generation gain in frequencies of major and general desired genes decreases with increasing proportion of major loci in total genes controlled the selected traits. These mean that if locus-effect difference in major loci is enough large or number of major loci is too many, the major loci will loss their "major" effect.

## Selection differential and selection response

When the trait is controlled by additive genes, selection response in the offsprings equals selection differential in parents population, because the heritability is one. When the trait is determined by complete dominant genes, trends of selection differential and reponse in initial generations are variable, then decrease together until the limit is attained, but not in paralled way, the latter decreases more rapidly than the former, i.e. the heritability becomes smaller. In the overdominance trait, although selection response in near to zero just before selection limit is attained, the great selection differential also exists.

## Symmetry of accumulative responses in opposite directions

When the trait is controlled by additive genes, accumulative selection responses in opposite directions will be symmetrical as selection is taken in a base population with initial gene frequency 0.5. However, when the trait is controlled by complete dominant genes or overdominant genes, accumulative reponses of divergent selections are asymmetrical, even if the initial population mean is in medium of the up- and down-limit.

## Interaction among three kinds of genes

In the trait controlled by three kinds of genes, if major additive genes

exist, the population is easier to reach the limit and heritabilities decrease slowly in some initial generational; if major complete dominant genes occur, fluctuations will be showed in population variance, selection differentials and responses in initial generations; if there are some major overdominant genes, population reach the limit with very slow rate, and great selection differential appears but almost the selection response disappears in final generations. Among three kinds of genes, a great number of overdominant loci make the desired gene frequencies of each kind reach their own "limit" with the shortest generations selection, next does a lot of additive genes and with the longest generations a great number of complete dominant loci.

Simulation studies revealed population genetic behaviour under the long-term selection, which in most of cases are in accordance with results of the long-term selection experiments on *Drosophila*, mice and farm animals. However, it would be suggested that further study must be put on a deeper understanding of biochemistry and physiology of the selected trait.

#### References

- AL-MURRANI, W.K. 1974. ABA. 42, 587 - 592.  
BLAIR, H.T. 1986. Proc. 3rd World Congr. Genet. Appl. Livest. Prod. 12:215-220.  
CHAPMAN, A.B. 1951. J. Anim. Sci. 10, 3 - 8.  
CLAUSEN, H. ET AL. 1972. Beretn. Forsoogslab. 394.  
CLAYTON, G.A., MORRIS, J.A. AND ROBERTSON, A. 1957. J. Genet. 55, 131 - 170.  
EISEN, E.J. 1975. Genetics. 79, 305 - 323.  
Eisen, E.J. 1980. Z. Tierzuchtg. Zuchtgsbiol. 97, 305 - 319.  
FALCONER, D.S. 1960. Oliver and Bagd, Edinburgh and London.  
GOWE, R.S. AND R.W. FAIRFULL 1986. Proc. 3rd World Congr. genet. Appl. Livest. Prod. 12:215-220.  
HILL, W.G. AND BISHOP S.C. 1986. Proc. 3rd World Congr. Genet. Appl. Livest. Prod. 12:215-220.  
JIANG, Z.H. 1985. ph.D. Dissertation. Zagreb.  
MACARTHUR, J.W. 1949. Genetics. 34, 194 - 209.  
MARKS, H.L. 1982. Proc. 2nd World Congr. Genet. Appl. Livest. Prod. 5:84-92.  
SALMON ET AL, 1988. Genet. Res. 52, 7 - 15.  
VANGEN, O. 1980. Acta Agric. Scand. 30, 125 - 141 and 309 - 319.  
YOO, B.H. 1980. Genet. Res. 35, 19 - 31 and 1 - 17.