

THEORETICAL PREDICTION OF LONG-TERM SELECTION RESPONSE

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SUMMARY

A theoretical model to predict effects of long-term selection for one trait on population mean, heritability and distribution of breeding value was developed. The model was extended to predict the effect of long-term selection on genetic correlation and further extended to predict the effects of long-term index selection. For the generalization of this theory, some special assumptions used in this study to simplify the problem have to be deleted in future.

INTRODUCTION

Genetic improvement by means of long-term selection in a closed population has a fundamental importance in animal and poultry breeding. The genetic gain from one generation of selection ΔG can be expected as the selection differential i multiplied by the heritability h^2 , $\Delta G = ih^2$. Experimental data have shown that the response is usually maintained with little change over several generations (Falconer 1960).

On the other hand, Cochran (1951) showed that the mean, the variance and the heritability of the trait are all subject to changes with one generation of selection. He also stated that the frequency function is positively skewed to a marked degree if the heritability is high and the proportion of selection is small, otherwise skewness is only moderate. Rönningen (1970) studied the effect of one generation of selection on the frequency distribution of phenotypes and genotypes by computer simulation. The results are similar to that reported by Cochran.

Nishida and Abe (1974) confirmed that the skewness in the distribution of genotypic and environmental value can be a cause of curvilinear regression of genotypic value on phenotypic value, i.e. heritability. In practice, Beardsley (1950) encountered curvilinear heritability in dairy cattle, Robertson (1977a) in *Drosophila* and Nishida (1972) in mice.

A warning was given by Finny (1962) about the effects of selection in modifying the distribution of traits; when the distribution has become appreciably non-normal, any calculation of genetic gains from formulae based on normality will tend to over estimate. Harris (1977) pointed out we are seemingly at the very unsatisfactory point to predict "long-term" response to alternative selection schemes.

The present study was undertaken to develop a theoretical model for predicting long-term selection response.

A MODEL TO PREDICT EFFECTS OF LONG-TERM SELECTION FOR ONE TRAIT

If we suppose an orthogonal coordinate system with breeding value G as the ordinate and environmental effect E as the abscissa, the axis of phenotypic value P , $P = G + E$, is obtained from the following transformation of the coordinate system (Fig. 1).

- 1) Counterclockwise rotation of E axis around the origin at an angle of $\pi/4$ radian.
 $E' = G \sin(\pi/4) + E \cos(\pi/4) = (G + E) / \sqrt{2}$
- 2) Scale transformation which converts one unit of

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length on E axis to $\sqrt{2}$ unit on the rotated new axis.
 $\sqrt{2}E' = G+E = P$

If we write bivariate distribution with G and E as $F(G,E)$, the marginal distribution of G for selected part based on P is given by

$$f(G) = \int_S F(G,E) dE \quad (1)$$

where s means a restriction in the range of integral to selected part (Nishida and Abe 1980a).

Thus the mean \bar{G} , the variance σ_G^2 and the skewness SK_G of the marginal distribution in G are evaluated by the following equations.

$$\bar{G} = \frac{1}{P} \int_{g_1}^{g_2} G f(G) dG \quad (2)$$

$$\sigma_G^2 = \frac{1}{P} \int_{g_1}^{g_2} (G-\bar{G})^2 f(G) dG \quad (3)$$

$$SK_G = \frac{1}{P \sigma_G^3} \int_{g_1}^{g_2} (G-\bar{G})^3 f(G) dG \quad (4)$$

where p is the proportion of selection as $p = \int_{g_1}^{g_2} f(G) dG$ and g_1, g_2 are the lower and the upper limit in G respectively.

To obtain the joint distribution function $F(G,E)$ for the next generation, total probability in G of the selected part must be adjusted to unity as follows.

$$f'(G) = \frac{1}{P} f(G) \quad (5)$$

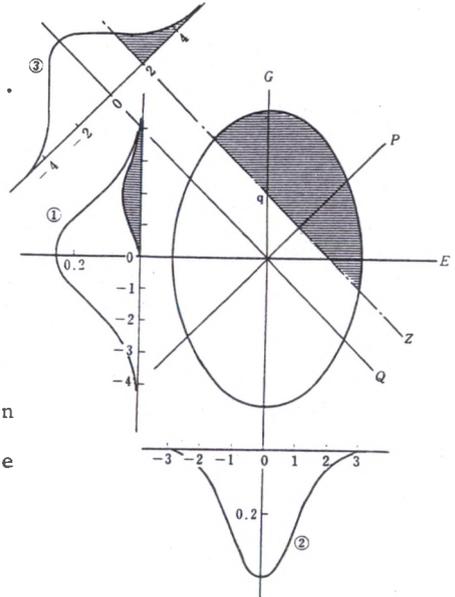


Fig. 1. Truncation selection based on phenotypic value. G: axis for breeding value. E: axis for environmental effect. P: axis for phenotypic value. Z: truncation line. shadowed area: selected portion. (1): marginal distribution in G. (2): marginal distribution in E. (3): distribution in P.

This brings us

$$\int_{g_1}^{g_2} f'(G) = 1.$$

When we obtain $F(G,E)$ for the next generation, repeated use of the equations from (2) to (5) should enable us to predict selection responses up to arbitrarily decided number of generation.

PREDICTION OF RESPONSE WITH CURVILINEAR HERITABILITY

An equation for predicting response to one generation of selection was derived when curvilinear heritability exists (Nishida and Abe 1980b). We write regression equation of G on P as $\hat{G} = F(P)$ and the derivative of F with respect to P as $\varphi(P) = F'(P)$, Predicted genetic gain is

$$\widehat{\Delta G} = i \int_k^{P_2} \varphi(P) f(P) dP / \int_k^{P_2} f(P) dP \quad (6)$$

where i is selection differential, k is truncation point in P , P_2 is the upper limit in P and $f(P)$ is frequency of P .

A MODEL TO PREDICT EFFECTS OF LONG-TERM SELECTION ON GENETIC CORRELATION

A theoretical framework for predicting effects of long-term selection for one trait was extended as shown in Fig.2 to predict the effect on genetic correlation (Nishida and Hayashi 1983). This enables us to predict genetic correlation in successive generations under long-term selection for one trait using the following equations.

$$f_{12}(G_1, G_2) = \int_s F(G_1, G_2, E_1) dE_1 \quad (7)$$

$$f_1(G_1) = \int_s f_{12}(G_1, G_2) dG_2 \quad (8)$$

$$f_2(G_2) = \int_s f_{12}(G_1, G_2) dG_1 \quad (9)$$

$$r_{G_1, G_2} = \frac{\int_s \int_s (G_1 - \bar{G}_1)(G_2 - \bar{G}_2) f_{12}(G_1, G_2) dG_1 dG_2}{\sqrt{\int_s (G_1 - \bar{G}_1)^2 f_1(G_1) dG_1 \cdot \int_s (G_2 - \bar{G}_2)^2 f_2(G_2) dG_2}} \quad (10)$$

where

F : three-variate distribution with G_1, G_2 and E_1

f_{12} : bivariate distribution with G_1 and G_2

f_1, f_2 : distribution of G_1 and G_2 respectively

s : restriction in range of integral to selected part

r_{G_1, G_2} : genetic correlation

A MODEL TO PREDICT EFFECTS OF LONG-TERM INDEX SELECTION

The theory was further extended to predict the effects of long-term index selection in a closed population (Nishida et al. 1984). We suppose that the purpose of our selection program is to improve P_1 and P_2 simultaneously using a selection index of $I = b_1 P_1 + b_2 P_2$. When we write the joint distribution with G_1, G_2 and E_1, E_2 as $F(G_1, G_2, E_1, E_2)$, the marginal distribution of G_1 and G_2 for the selected part is obtained by the following equations.

$$f_{12}(G_1, G_2) = \int_s \int_s F(G_1, G_2, E_1, E_2) dE_1 dE_2 \quad (11)$$

$$f_1(G_1) = \int_s f_{12}(G_1, G_2) dG_2 \quad (12)$$

$$f_2(G_2) = \int_s f_{12}(G_1, G_2) dG_1 \quad (13)$$

where

f_{12} : bivariate distribution with G_1 and G_2 for the selected part

f_1, f_2 : distribution of G_1 and G_2 for the selected part

s : restriction in range of integral to the selected part based on the selection index

NUMERICAL EXAMPLES

The following assumptions were made. 1) Additive genetic model 2) All the genetic properties are the same in selected parents and their progeny 3) The ranges of P, G and E are limited within an assigned level 4) E is always normally distributed within the range 5) G in base population is normally distributed within the range 6) G and E are uncorrelated 7) proportion of selection is always 0.5.

Selection for One Trait

The results are shown in Fig.3~6. The change in genetic variance caused by one generation of selection predicted by the model presented agreed well with that by Robertson's formula (1977). Since this model does not require the normality as a necessary condition, it is applicable to prediction of long-term selection response (Nishida and Hayashi 1980c).

Effect of Selection on Genetic Correlation

As a result of long-term computer selection experiment for one trait genetic correlation decreased towards zero.

Effect of Index Selection

The effects of long-term index selection were predicted. All the initial genetic correlations decreased towards -1.0. The total effects of long-term index selection are visualized in Fig.7.

DISCUSSION

To make numerical examples, we assumed all the genetical properties are the same in selected parents and their progeny. However, since the lost genetic variance by selection is partly restored by random mating in selected parents, this assumption is not strictly satisfied. It is necessary to investigate in future effects of mating in a long-term selection program for assuming random mating in selected parents.

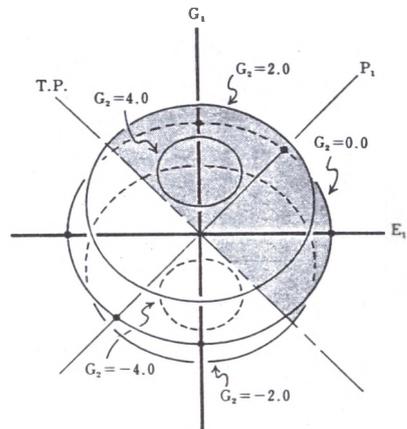


Fig. 2. The image of selection for P_1 at the base population. Initial heritability $h_0^2=0.5$, initial genetic correlation $r_G=0.5$, P_1 : axis for phenotypic value of trait number 1, G_1 : axis for the breeding value, E_1 : axis for the environmental effect, T. P.: truncation plane, Shaded area: selected part, Axis for G_2 should be supposed to intersect at right angles with G_1, E_1 plane through origin in this figure. Each ellipse shows intersection of plane denoted by " $G_2=\text{constant}$ " and limiting isoproability ellipsoid, $F=10^{-5}$. Intersections with dot are all on the G_1, E_1 plane. The ellipses illustrated as $G_2=-4.0$ and -2.0 are located behind the plane and the ellipse of $G_2=-4.0$ is at the bottom. The ellipses of $G_2=2.0$ and 4.0 exist in front of the plane and the ellipse of $G_2=4.0$ is at the top.

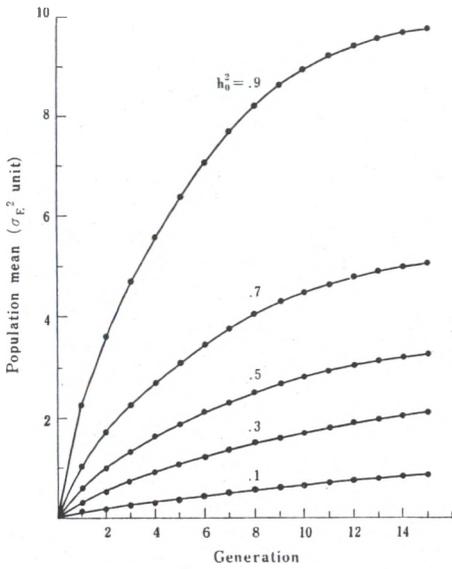


Fig. 3 Response curve of population mean to selection.

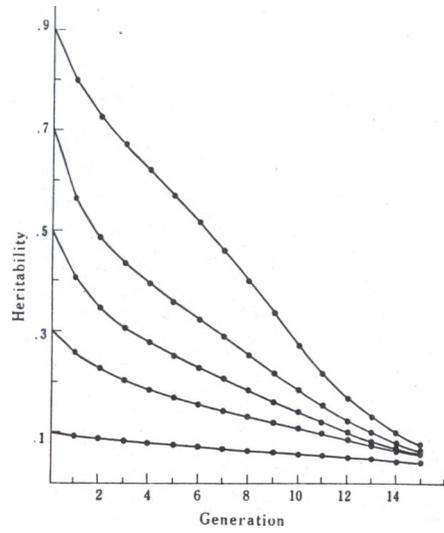


Fig. 4 Consumption of initial heritability with selection.

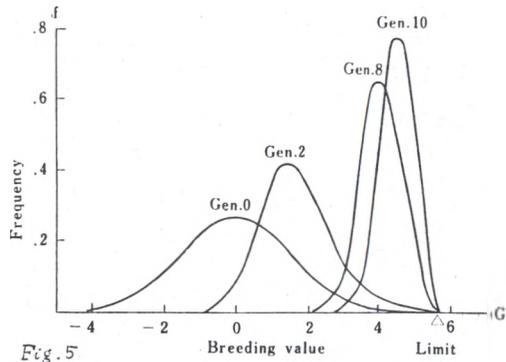


Fig. 5 Change in distribution of breeding value with selection

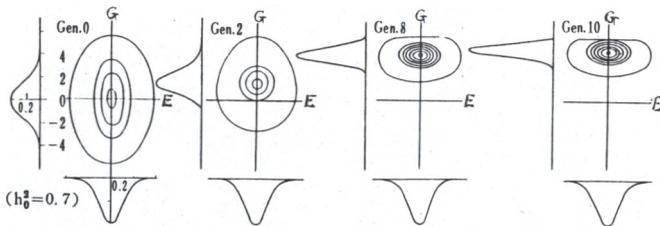


Fig. 6. Effects of selection on contours in joint distribution and on marginal distribution

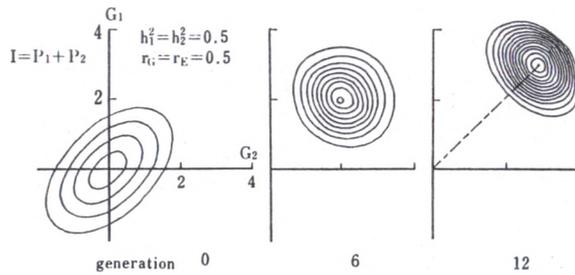


Fig. 7 The total effects of repeated index selection on the contour map of the bivariate distribution with G_1 and G_2 . The contour interval is 0.04. The dashed line indicates the direction of improvement.

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