Possibilities to substitute the selection by independent levels with indirect selection

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SUMMARY

Selection on multiple traits diminishes the genetic progress on the generation for each one. In addition, adding some traits known later in the candidates' life increases the generation interval and participates at the greater diminution of yearly genetic progress. It is expected that in accordance with the correlation between characters to be a limit beyond which it is bigger the correlated effect of an indirect selections on an earlier character that would reduce the generation interval.

In this study the author establishes mathematical relationships that allow mathematical modeling of the problem investigated.

The results show that if we have two characters and it is possible to obtain the value 2 for the parameter k (simplifying the objective to a single character would bring in indirect selection of the second, or the doubling of the heritability or the halving of the interval of the generation) it is possible to renounce at the selection of the both characters on independent levels when the correlation between them is greater than 0.4. With k = 4 (indirect selection on a character with double heritability and generation interval halved) critical value of the correlation decreases to 0.2, and with a correlation of 0.5 indirect selection offers a double effect unlike the independent levels.

When n > 2, it is recommended simplifying the objective of the selection from 3 to 2 characters when k = 2 and the multiple correlation is greater than 0.35.

With k = 2, the transition from 4 to 3 characters is recommended even with a correlation of 0.3.

Keywords: multiple traits, genetic progress, indirect selection

INTRODUCTION

The depression of the genetic progress for a trait selected together with other traits has been noticed ass soon as the selection by multiple traits was theorised (Hazel et al.). The first classical papers of the literature stated that when selecting $\boldsymbol{n}$ traits from the same generation by independent levels, when the correlation between them is null, only $\boldsymbol{1/\sqrt{n}}$ is obtained for each trait from

what would have been obtained if selection would have been done just for that specific trait.

Sandu (1980) proposed a more general solution, which also took into account the size of the correlation between the traits, with the additional specification that the simple correlation must be replaced by a multiple correlation if $n>2$.

On that occasion, the author didn't do any comment on the annual effect if the modifications associated to the generation interval are involved. The consideration of such effects raises the question whether simplifying the goal of selection by replacing the selection by independent levels by the indirect selection of the traits known later, would be a better solution to maximize the genetic progress. Maximization concerns not just the late traits, but also the traits known earlier, because for them too the generation interval increases, as well as the global genetic progress cumulated for all traits.

The purpose of the paper was to fill in these shortcomings and to study the conjectures in which the indirect selection can be recommended as sufficient.

MATERIAL AND METHODS

We can reach this purpose by modelling.

The goal of selection consists of a number of traits $j = 1,...,n$.

Using the selection for just one traits, the genetic progress by generation would be $R_j = i.h^2_j$, and the annual progress would be $\Delta G_j = i.h^2_j / T_j$ (i = intensity of selection, T = generation interval). The measure unit is the phenotypic standard deviation.

When selection by independent levels is done for all n traits of the goal of selection, $t = T_{j/n} / T_j$ ratio has the value of 1 for the last trait from the increasing succession of the ages at which they can be checked and is higher than 1 for any preceding trait, increasing with the earliness of the trait.

The effect of the selection for a trait selected together with the other ones has been determined by (1980) as a fraction $f = \sqrt{n^{r-1}}$ of R_j (r = multiple correlation between the traits included in selection).

Therefore, $R_{j/n} = f.R_j$, and $\Delta G_{j/n} = f.R_j / T_{j/n}$.

For a given trait, the ratio of the annual response obtained using the selection by independent levels and the response expected by selection just for the specific trait is:

$$\Delta G_{j/n} / \Delta G_j = [f.h^2_j.i / T_{j/n}] / [h^2_j.i / T_j] = f / t.$$

In order to maximize the genetic progress, a partial solution, resuming to the selection by independent levels, is to maximize this f/t ratio. For the traits before the last one, the annual effect will also be diminished because the generation interval increases, besides the decrease of the generation effect due to the selection by several traits. The last trait has $t = 1$ and is decreased proportionally with f.

The only way to compensate the decrease of the effect of doing selection by multiple traits by decreasing the generation interval is to simplify the goals of selection by eliminating the traits that are known later (***j***), for which we will only use the correlated effect of the selection by previous traits (***x***).

Such proposal must be substantiated using a comparison of the correlated response of selection (R_c) with the response of selection for multiple traits.

It is known that $R_{cjx} = h_x.h_j.\ r_{xj}.i$, where r_{xj} is the genetic correlation between the traits.

Therefore $R_{cjx} / R_j = h_x.h_j.\ r_{xj}.i / h_j.h_j.i = r_{xj}.h_x / h_j$.

The ratio becomes:

$R_{cjx} / R_{j/n} = R_j.r_{xj}.h_x / h_j.\ / f.R_j = r_{xj}.h_x / f.h_j$.

Shifting to the annual effects of the selection creates a new ratio (***m***) which bears the following changes:

$m = \Delta G_{cjx} / \Delta G_{j/n} = [r_{xj}.h_x / T_x] / [f.h_j / T_{j/n}] = r_{xj}.h_x.\ T_{j/n} / f.h_j.T_x$.

Ratio r_{xj} / f plays now an essential role in the maximization of ***m***.

In order to make a graphical representation of the values of ***m***, ratio r_{xj} / f will be regarded as a single variable (***c***), because ***f*** depends on ***r*** for a given number of traits (***n***) and it will be represented on the x series. The y series will display the values of ***m*** that we seek, and we will have as many curves as values of $k = h_x.\ T_{j/n} / h_j.T_x$ are considered. Equation $m = c.k$ will we exemplified for $k = 4$, $k = 2$, $k = 1.5$ and $k = 1$.

RESULTS AND DISCUSSION

Figure 1 shows the values of ***f*** which show the decrease of the effect of selection by independent levels, compared to the selection by a single trait.

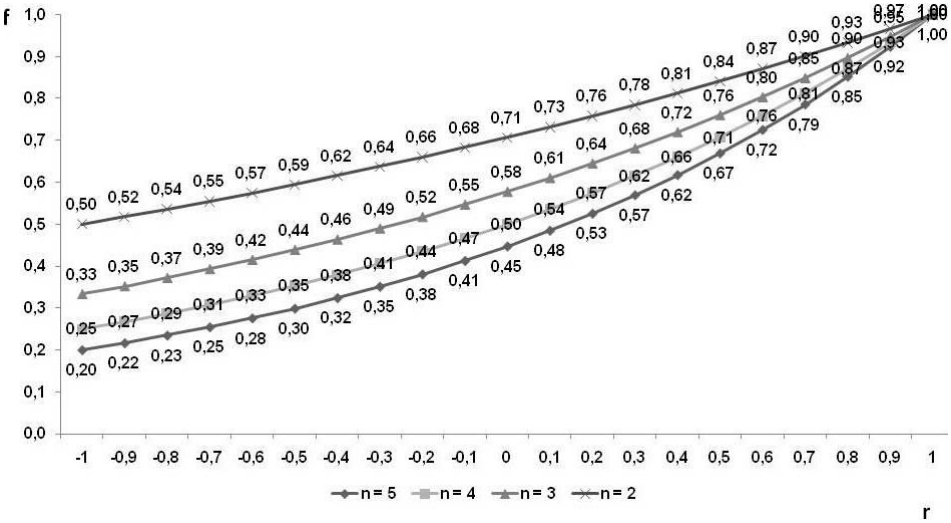

Figure 1. Decrease of selection effect for a trait by selection by independent levels together with other **n** traits ($f = \sqrt{n^{r-1}}$)

The solution to the problem stated in the purpose of this paper requires two additional statements. The first one refers to the removal of the particular cases $r = +1$, because the n traits would behave as a single trait, and $r = 0$ because there would be no correlated effect of the selection (Falconer, 1969). The second refers to the sign of the correlations. Function of the direction in which man wants to change the traits, sometimes a negative correlation is favourable. Therefore, the sign of the favourable correlation will be overlooked and only the actual value will be taken into consideration.

Variant 1 refers to a trait which is known before the other ones. In this case, besides $f<1$ we will also have $t>1$, which shows that if ratio f/t is minimised, this is the most unfavourable situation for a precedent trait As the first trait is concerned ($j=1$), the exclusion of the other traits would yield a maximal gain, equal to $(1 - f/t)\Delta G_1$.

Variant 2 takes into consideration what happens in the succeeding traits. It remains to be seen if giving up selection beyond a trait which precedes other traits, yields a gain for the overall objective of selection. Theoretically, the gain exists if the relative reduction of the generation interval is larger than the relative reduction of the generation effect by shifting to indirect selection for the subsequent traits no longer included in the objective of selection. This is shown by the evolution of the values of m.

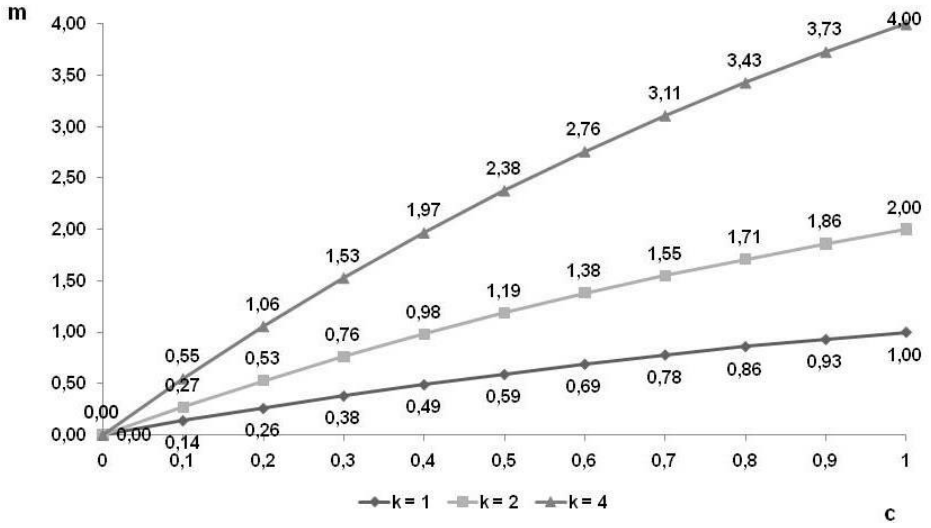

Figure 2. Ratio of the correlated effect of selection with the effect of the direct selection by independent levels (m) in the case $n = 2$

Putting the condition that the heritability of the trait used for direct selection must be two times higher than the heritability of the traits used for indirect selection, and that the generation interval through the moment of

selection by the removed trait must be two times larger than that obtained by direct selection by the precedent trait, it results that the highest value of variable k may be $k = 4$.

We also studied the situation for $k = 2$, which is possible if trait heritability is identical, but the generation interval would be just half if indirect selection is used, and vice versa, if the heritability of the trait used for direct selection is two times higher than the heritability of the removed trait, but the traits would be measured at the same age, so there would be no change in the generation interval.

Value $k = 1$ would presume the same heritability and the same generation intervals. Other combinations of values might certainly lead to the same results.

Case A. Figure 2 shows the graphical expression of the results obtained with these hypotheses for $n = 2$. It can be noticed that for $k = 1$ by indirect selection we might eventually obtain the effect of selection by independent levels, with the hypothetical condition $r = 1$. For any other value of the correlation, no matter how large, the selection by independent levels of both traits is the only recommendable one

For $k = 2$, we might obtain by indirect selection by the first trait more than we would obtain by selection by independent levels on both traits, with condition $r>0.4$. With a correlation which tends towards 1, we may even get a two-fold higher estimated annual effect of the selection. A reasonable correlation of 0.5 allows a surplus of 20% if half of the generation interval is used, or if heritability is doubled by indirect selection by the precedent trait. If very small correlations are used, the effect of indirect selection on a single trait might decrease to about ¼f that produced by the selection by independent levels on both traits.

For $k = 4$, the indirect selection is preferred as soon as the correlation exceeds the value of 0.2, and the result is more than double compared to the selection by independent levels if the value of the correlation is around 0.5. Even for very small correlations ($r = 0.1$), no more than half of the estimated effect by independent levels would be used by shifting to a more simple indirect selection.

In an imaginary example, if we would find a precedent trait (x) correlated 0.6 ($f=0.87$) with the succeeding one (y), but which would reduce the generation interval from 4 to 3 years, with $h^2_x = 0.5$, compared to $h^2y = 0.3$, then we would obtain $k=1.75$ and $m= 1.20$, which means 20% gain of the annual genetic progress for trait y by replacing the selection by independent levels for traits x and y with the direct selection just for x and indirect for y. The global effect of selection would be even higher because it would increase by $(1 – f/t)\Delta G_x = 0.35\ \Delta G_x$ and the direct effect for trait x, making selection just on it. If the value of the correlation decreases to 0.5, the gain narrows to 4%.

Case B. For $n>2$, the results from Fig. 1 suggest that the advantages of simplifying selection would increase with the increase of n. The decrease of f with the increase of n allows maximising ratio r_{xj} / f on the background of

decreasing ***r*** when it becomes multiple correlation of the removed trait with the remaining ***n – 1*** traits which were kept for direct selection.

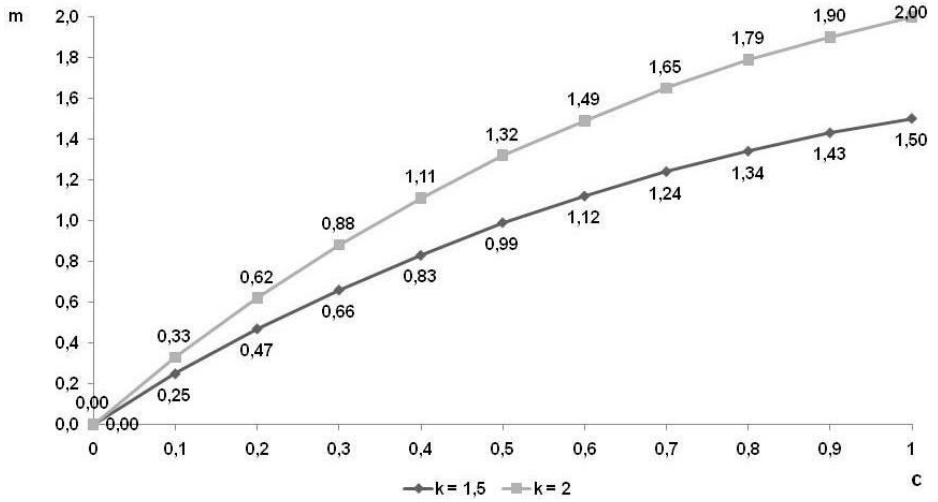

Figure 3. Ratio of the correlated effect of selection with the effect of the direct selection by independent levels (***m***) in the case ***n = 3***

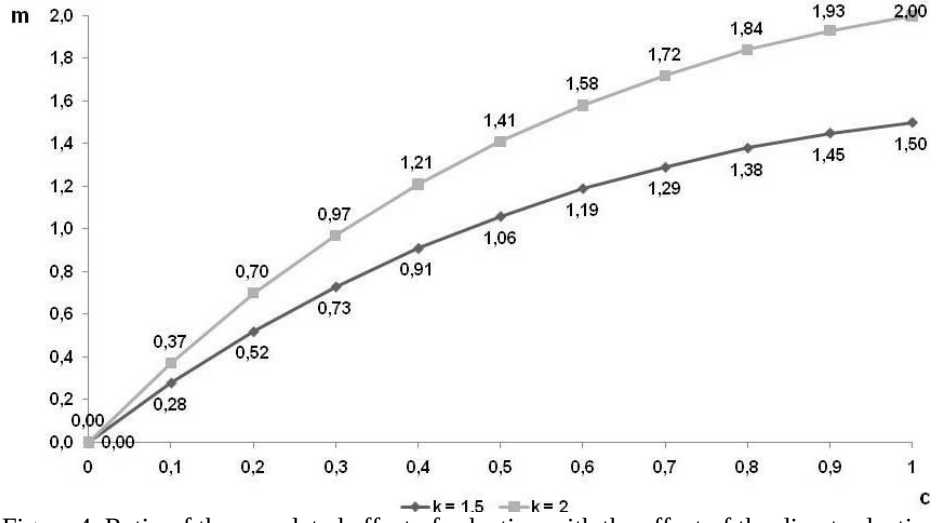

Figure 4. Ratio of the correlated effect of selection with the effect of the direct selection by independent levels (***m***) in the case ***n = 4***

Even with a smaller ***f***, ratio ***f/t*** can also be maximized because the generation interval might also decrease further in this case by shifting the latest traits to indirect selection.

Exceeding ***k = 2*** seems however extremely optimistic, because the heritability within an aggregated genotype of the ***n – 1*** traits is expected to be

rather small and hard to increase by changing the combination of traits which remained for direct selection.

Figure 3 shows that at $k = 2$ for $n = 3$ we may recommend simplifying the objective to $n = 2$ by removing the last trait starting from a multiple correlation of 0.35. If $k = 1.5$, the critical value of the correlation will be slightly higher than 0.5.

Figure 4 suggests that for $k = 2$ and $n = 4$ a multiple correlation higher than 0.3 would recommend simplifying the objective to $n = 3$. For $k = 1.5$ the multiple correlation should be higher than 0.45 for the same recommendation.

CONCLUSIONS

1. The modelling confirms that in certain conjectures, in order to maximize the annual genetic progress estimated for a trait, it is advisable to replace the selection by independent levels with the indirect selection.

2. The decision depends on the ratio of heritability, on the ratio of the generation intervals and on the ratio of the correlation to the decrease of the effect of selection by selecting a trait by independent levels from a group of n traits, compared to the effect expected by the exclusive selection for that particular trait (f).

3. The results of exemplified modelling gives minimal values of the correlation (between 0.2 and 0.5), recommending in various conjectures described by parameter k, the replacement of one selection method by the other.

4. The advantages are greater when a more complex objective of selection (larger number of traits) is simplified, because in this case the value of f decreased more and ratio r/f on which the maximization of the correlated effect of the indirect selection depends, can be maximized even with smaller values of the correlation.

5. Because the maximization of the annual genetic progress demands the maximization of f/t ration, it is extremely important to narrow the generation interval by removing from the objective of selection, the traits that are known later.

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