The Effect of Dams of Sire Path Management on Genetic and Economic Parameters in a Simulated Genomic Selection Program

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ABSTRACT

A deterministic model based on the gene flow method, considering the features of Iranian Holstein cattle population, was implemented in this study to evaluate the effect of altering the number of age-classes in the dams of future sire (DS) path and the number of dams required for breeding a young bull (YB), to be evaluated as future sire, on genetic gain and resultant economic efficiency of a genomic selection program for milk production as a selection goal. Based on the simulation, changing the number of age-classes from 10 to 1 resulted in higher replacement rate of DS path (from 0.22 to 1) and shorter generation interval. Consequently, the economic efficiency of the program increased up to a maximum point and then a descending trend was observed. The maximum economic efficiency (25.68) was obtained when 7 age-classes in DS path was assumed. By chaining the number of dams required for breeding a YB from 7 to 1, the genetic gain in selection goal increased from 0.0232 to 0.0264 kg per dairy cattle and therefore, the economic efficiency rose from 25.42 to 28.52. The results revealed that a decrease in generation interval does not necessarily result in maximum economic efficiency and there is an optimum level for generation interval. Less number of required dams per YB could result in higher economic efficiency and therefore should be considered as an effective management strategy to improve the economic efficiency of a genomic selection program for milk production.

KEY WORDS economic, efficiency, genetic, genomic selection, Holstein.

INTRODUCTION

Genetic improvement of farm animals has been a prime concern over the years for researchers. Several reproductive and selection technologies have been employed to achieve this. Nowadays, advances in genetic analysis and mapping technologies have enabled the implementation of genomic selection (GS) in cattle’s. Genomic selection (GS) based on medium SNP density (~50,000; 50K) is now routinely implemented in several large cattle breeds (Hozé et al. 2014). Genomic selection provides higher accuracy in prediction of breeding values for animals without records or progeny information or for traits where selection on phenotypic records is difficult and shortens generation interval by using more young superior animals to increase the number of selection cycles per unit of time (Meeuwissen et al. 2001). The availability of genomic estimated breeding values (GEBV) allows for possible modifications to existing dairy cattle breeding programs. One of the most important developments resulting from the introduction of genomic testing for dairy cattle is the application of reasonably priced low-density SNP technology in the selection of females. Genotyping females can increase the genetic gain through shorter generation interval and better reliability of breeding values
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(Mc Hugh et al. 2011). On the other hand, Joezy-Shekalgorabi et al. (2010a) demonstrated the remarkable role of the dams of future sires (DS) path on the rate of genetic gain due to its high selection intensity.

Because of genome testing capability in early evaluation of cows, this technique can be combined with assisted reproductive technologies in order to detect and increase number of younger elite cows (Calus et al. 2015). Ponsart et al. (2014) has demonstrated the effectiveness of this strategy in reducing the number of dams required for breeding a young bull (YB) and the age of selecting superior individuals. In the context of GS, the potential advantages of combining intensive embryo production with genotyping are even higher. Gene flow study through a population via gene flow methods can be used to determine the time at which genes are expressed. By knowing the value of gene expression and the number of animals involved, the economic value of the expression can be calculated. Discounting future profits and costs then allows cost-benefit analysis of a breeding program (Hill, 1974).

Therefore, this study was aimed to evaluate the effect of altering the number of age-classes in the dams of future sire (DS) path and the number of dams required for breeding a young bull on genetic and economical outputs of Iranian Holstein. The final purpose was to define the optimal level of these factors in the maximum economic efficiency view point.

MATERIALS AND METHODS

Simulation method

In the current study a deterministic model based on gene flow method (Hill, 1974) was used to estimate the genetic gain and economic efficiency (EE) of the simulated program. The parameters of population structure, production, reproduction and cost reflected dairy cattle production system in Iran. Breeding and productive parameters of Iranian Holstein cattle are summarized in Table 1. Milk production was considered as the selection objective.

Due to higher number of age-classes in breeding population of Iranian Holstein cattle, it takes a long time to reach the equilibrium phase of genetic growth (Joezy-Shekalgorabi et al. 2010b), therefore, in this study the time horizon of 70 years was chosen for genetic and economic evaluations (Joezy-Shekalgorabi et al. 2010a).

Characterization of genomic selection program

Selection paths were consisted of sire of future sires (SS), sire of future dams (SD), dams of future sires (DS) and dams of future dams (DD). Elite cows were preselected among a population of 502400 Holstein cattle at the age of 15 months based on pedigree and body condition score. The number of preselected elite cows for being genotyped was calculated as the product of replacement rate of DS path and the number of available cows in DS path.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Required number of YB’s</td>
<td>109</td>
</tr>
<tr>
<td>Daughters per YB</td>
<td>100</td>
</tr>
<tr>
<td>The number of productive cows</td>
<td>502400</td>
</tr>
<tr>
<td>Percentage of herdbook population</td>
<td>33</td>
</tr>
<tr>
<td>Test capacity (%)</td>
<td>20</td>
</tr>
<tr>
<td>Insemination number per pregnancy</td>
<td>2.22</td>
</tr>
<tr>
<td>Required number of dams per YB</td>
<td>6.07</td>
</tr>
<tr>
<td>Milk productions heritability</td>
<td>0.29</td>
</tr>
<tr>
<td>Genetic standard deviation of milk production (kg)</td>
<td>477</td>
</tr>
<tr>
<td>Discount rate of costs</td>
<td>0.06</td>
</tr>
<tr>
<td>Discount rate of returns</td>
<td>0.08</td>
</tr>
<tr>
<td>Economic value of milk production (US $)</td>
<td>0.23</td>
</tr>
<tr>
<td>Genome length (Morgan)</td>
<td>30</td>
</tr>
<tr>
<td>The number of independent genomic segments</td>
<td>516</td>
</tr>
</tbody>
</table>

After genomic evaluations, the required numbers of DS individuals were selected for producing 109 YB’s (the available and required numbers of individuals in different paths were calculated based on Table 2 formulas). The available YB’s produced by DS were genetically evaluated at the age of 1 year, and among them 16 YB’s were selected for being used as sire for the next generation for a period of 4 years.

Genetic superiority in different paths was calculated as the product of accuracy and the selection intensity of the related path and the genetic standard deviation of goal trait. In all paths except DD, selection was based on the genomic information. According to Erbe et al. (2013), accuracy of genomic evaluations in SS, SD and DS paths were calculated as:

\[ \gamma = \frac{\gamma_p R^2}{\sqrt{\gamma_p R^2 + \gamma_d}} \]

(Equation 1)

Where:

- \( R^2 \): reliability of breeding values in the sire’s population and was calculated by \( (n/(4-h^2/h^2)+n) \).
- \( n \): number of daughters per progeny tested bulls.
- \( Me \): number of independent genome segments.

In all paths, except DD, selection based on genomic information was implemented. Accuracy of DD path was calculated as the square root of heritability. \( Ne \) was calculated based theory which emphasizes that the inbreeding in the nucleus controls inbreeding rate in the whole population. Therefore, based on Falconer and Mackay (1996) formula, \( Ne \) was calculated by the use of the number of tested YB’s and required number of DS path.
According to the estimated effective number of Holstein population in Iran (62.49), the calculated Me was equal to 440.07.

The selection intensity was calculated as outlined by Falconer and Mackay (1996) using the required number to available number of individuals in DS path.

According to Hill (1974), a transition-matrix (P-matrix) was designed in order to trace the flow of genetic superiority resulting from a selection strategy to the whole population. Reproductive contribution of different age-classes in each path was inserted in the reproductive rows of P-matrix. The replacement rate (rds) of each path was calculated as the contribution of individuals of the first age-class (one year old). Reproductive contribution of individuals in different age-classes of selection paths according to Joezy-Shekalgorabi et al. (2010a) are represented in Table 3.

Table 3: Reproductive contribution of individuals in different age-classes of selection paths according to Joezy-Shekalgorabi et al. (2010a)

<table>
<thead>
<tr>
<th>Selection path</th>
<th>Contribution of different age-classes in selection paths</th>
</tr>
</thead>
<tbody>
<tr>
<td>SS and SD</td>
<td>(25.25, 25.25)</td>
</tr>
<tr>
<td>DS</td>
<td>[25.5; 24.5; 20; 14; 10; 6; 0; 0; 0; 0; 0]</td>
</tr>
<tr>
<td>DD</td>
<td>[32.16, 24.74, 17.23, 11.37, 6.95, 3.86, 2.05, 0.97, 0.42, 0.17, 0.06, 0.02]</td>
</tr>
</tbody>
</table>


Economic model

Required costs for implementing the genomic selection program were consistent of quarantine, proofing, and after proof costs, which were integrated together as the total cost. Quarantine costs included cost of testing for disease, feeding and maintenance through a 6 months period. After-proof costs were consisted of feeding and maintenance costs through a 4 years period. Genotyping cost in the training set was calculated by the following formula:

\[
G_{\text{cost}} = (NYB 	imes r_{DS} 	imes NDS + (NP/2)) \times G_{\text{notype}} = c
\] (Equation 1)

Where:

Gcost: total genotyping cost.

rds: replacement rate in DS path.

NYB: number of YBs.

NDS: number of individuals available in DS path.

NP: number of individuals in the base population.

2: time interval for haplotype effects recalculation.

Gnotype - c: genotyping cost per dairy cattle.

Finally, the proofing cost was estimated as follows:

\[
\text{proof} = NYB \times (C_{\text{YB}}) + G_{\text{scost}} + (NP/2) \times \text{Recor} - c
\] (Equation 2)

Where:

Recor - c: proofing cost.

C_{\text{YB}}: purchasing cost per YB.

Record - c: total cost of recording the daughters of base population (7 times recording).

Returns were divided into two parts: 1) returns from the genetic gain and 2) returns from selling the omitted sires or the young unproved bulls. Genetic gain in different selection paths and different age-classes were calculated using gene flow theory (Hill, 1974). All the returns and costs were discounted to their present value according to Hill (1974). Economic efficiency (EE=ratio of discounted returns to discounted costs) was the final goal of comparing different selection strategies. The optimum level of evaluated parameters was assumed to be the value which leads to the maximum EE.

Evaluated strategies

This study was divided into two parts. In the first part, the number of age-classes in DS path (NCDS) decreased from 10 to 1 where by omitting each age-class, the contribution of individuals of that class was uniformly transmitted to the remaining classes. The decreasing scheme of age-classes in DS path is shown in Table 4. In the second part of the study, the number of dams required for breeding a YB (RYBD) decreased from 7 to 1. According to Table 2, RYBD was utilized in calculating the required number of individuals in DS path and subsequently the selection intensity of this path. Therefore, the effect of varying selection intensity resulting from RYBD reduction on EE was studied. In order to obtain a better understanding of the results, the final results of continuous selection were divided by the total number of productive dairy cattle in Iranian Holstein cattle population and were represented as the cumulative genetic gain per dairy cattle (CGG), cumulative discounted costs per dairy cattle (CDC) and cumulative discounted benefit per dairy cattle (CDB). Finally, the optimal levels in maximum EE and maximum CDB were examined to determine whether there is difference in the optimum value in order to reach maximum EE and Maximum CDB. CDB...
was estimated as dividing cumulative discounted returns per dairy cattle by CDC.

### RESULTS AND DISCUSSION

#### Decreasing the number of age-classes

In this study, except for DS, the contribution of age-classes in the three paths of SS, SD and DD were considered constant. The changing trends of generation interval in DS path (LDS), replacement rate in DS path (rrds), CGG, CDC (US$) and CDB (US$) resulting from decrease in the number of age-classes in DS path through 10 steps are represented in Table 5. According to Table 5, LDS decreased from 4.75 to 2.13 years as a result of decrease in the number of age-classes from 10 to 1. In case of the change of individuals’ contribution pattern in each age-class, compared to what was addressed in this study, the generation interval will also change. For example, considering the constant number on age-classes in DS path, it is possible to change the individuals’ distribution pattern in different age-classes. As can been seen from Table 6, reduction in the number of age-classes increased the contribution of residual age-classes especially for the first age-class. Since in this study, the replacement rate was calculated as the percent of individuals’ contribution in the first age-class, hence, with the reduction of age-class number from 10 to 1, rrds increased from 0.22 to 1. According to the formula for estimating the required numbers in DS path in Table 2, any increase in rrds leads to an increase in the required number of individuals in DS path (nDS;); and therefore, the selection intensity decreased from 3.05 to 2.57.

Interaction between simultaneous variation of selection intensity and generation interval resulted in 0.0031 kg increase in CGG (Table 5), and therefore, CGG increased from 0.0224 to 0.0255 kg as the result of decrease in the number of age-classes (equal to 13.84 percent increase). This assures that the effect of decrease in LDS (55.16 percent decrease) on the genetic gain is more effective than selection intensity (15.74 percent decrease).

According to equation 2, the number of individuals being genotyped in DS path was calculated as the multiplication of available number of individuals in DS path (nDS; according to Table 2) in rrds. Therefore, with decrease in the NCDS and hence, increase of rrds, it was necessary to genotype more individuals in order to replace the available individuals in DS path. This resulted in $126.37 increase in CDC (equal to 88.41 percent increase). Since In this study, the calculation on maintaining and feeding costs of individuals in DS and DD paths was dispensed and merely the costs related to the selection program were considered, they did not affect the results of the evaluation.

Maximum EE (calculated as the ratio of revenue to the costs of selection program) was considered as an index for determining the optimal level of NCDS. For this reason, EE was calculated per level of NCDS and the level with maximum EE was introduced as optimal. The effect of varying the number of age-classes on EE of the selection program is represented in Figure 1. The trend of EE was different from CGG. EE of the program increased up to a maximum point and then a descending trend was observed by increasing NCDS. Maximum EE value (25.68) was obtained in DS path by assuming 7 NCDS. In the case of maximum EE (assuming 7 age-classes), CGG value was 9.41 percent lower than maximum achievable CGG (by assuming 1 age-class). Decrease of EE due to decrease in NCDS to less than 7 age-classes is a consequence of faster increase in the costs (due to rrds increase) compared to revenues from genetic gain. What is interesting about the results of Table 5 is that unlike the trend of EE (Figure 2), CDB increased from $3507.65 to $3940.73 due to more increase of NCDS.

#### Decrease of RYBD

RYBD is one of the necessary constituents in calculating nDS (Table 2). So, a reduction in RYBD, decreased the nDS and as a result the selection intensity increased.

In the second part of this study (Table 6), with a reduction in RYBD from 7 to 1, the number of required individuals in DS path decreased and the selection intensity increased from 2.97 to 3.52. This 0.63 increase in selection intensity resulted in 0.0032 kg increase in CGG and its value changed from 0.0232 kg to 0.0264 kg which is in agreement with Ponsart et al. (2014) report who pointed out that entering genomic information of reproduction and health traits will decrease RYBD. Hence, it was assumed that genomic information were used for decreasing RYBD, and therefore, the costs regarding this strategy were included in genotyping selection candidates and the costs of the selection program during 7 phases of RYBD decrease remained constant.

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**Table 4**

<table>
<thead>
<tr>
<th>Analysis steps</th>
<th>Contribution of individuals in different age-classes in DS path</th>
</tr>
</thead>
<tbody>
<tr>
<td>The 1st step</td>
<td>[22; 20.5; 18; 12.5; 9; 8; 4; 3; 2; 1]</td>
</tr>
<tr>
<td>The 2nd step</td>
<td>[22.5; 21; 18; 12.5; 9; 8; 4; 3; 2]</td>
</tr>
<tr>
<td>The 3rd step</td>
<td>[23; 22; 18; 13; 9; 8; 4; 3]</td>
</tr>
<tr>
<td>The 4th step</td>
<td>[24; 23; 19; 14; 9; 8; 3]</td>
</tr>
<tr>
<td>The 5th step</td>
<td>[25.5; 24.5; 20; 14; 10; 6]</td>
</tr>
<tr>
<td>The 6th step</td>
<td>[26.5; 26; 21.5; 15; 11]</td>
</tr>
<tr>
<td>The 7th step</td>
<td>[29; 28.5; 24.5; 18]</td>
</tr>
<tr>
<td>The 8th step</td>
<td>[35; 34.5; 30.5]</td>
</tr>
<tr>
<td>The 9th step</td>
<td>[51; 49]</td>
</tr>
<tr>
<td>The 10th step</td>
<td>[100]</td>
</tr>
</tbody>
</table>

All these values were estimated after 70 years since the breeding program starting.

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Considering this fact that the increase in revenues due to genetic gain (data not presented) and the selection program's costs being constant, the trend of changes in CDB was ascending and increased by $461.35 (12.71 percent). The trend for the profit was similar to EE (EE increased from 25.42 to 28.52%). Hence, maximum EE resulted in maximum profit. This strategy is desirable for both consumers and producers and simultaneously increases competitiveness in the world market (Dickerson, 1978).

The aim of this article was to examine the genetic and economic aspects of prioritizing young cows to contribute in breeding as a DS and decrease of required dams for breeding a YB entering the genomic selection program. Utilization of a deterministic model allowed for the change of parameters in a specific range in order to specify the optimal values of parameters which result in maximum EE. Genetic superiorities transmission resulting from selection program in a 70 years period from age-classes of different paths to the whole population was examined using gene flow method and the genetic gain resulting from this gene flow was calculated as the cumulative genetic gain (continuous selection) per dairy cattle. Considering the costs and revenues of the selection program, EE was calculated as the final aim of evaluating the selection strategies. In the first strategy, examination of the effect of prioritizing young cows to contribute in breeding as DS was performed with decrease of the NCDS and increase in the contribution of residual age-classes.

Decrease of age-classes from 10 to 1 resulted in 2.62 years decrease in the generation interval and the generation interval reached to 2.13 years. The age of the first calving in Iran situation was assumed 2.13 years and in this way it is equal to the least generation interval possible. In most resources addressing genomic selection program, mean generation interval of DS path is assume 2 to 2.5 years (e.g. Schaeffer, 2006; König and Swalve, 2009; König et al. 2009; Thomasen et al. 2014). According to Table 5, the value of generation interval in DS path in the current condition of Iranian Holstein population (in case of performing progeny test program) is 4.05 years (6 age-classes in DS path) which could decrease to 2.13 years in case of performing genomic selection program and assuming 1 age-class in DS path.

Shorter generation interval directly results in more replacement rate in each path (Calus et al. 2015). Therefore, decrease of LDS and increase of contribution of lower age-classes increased the rrds to 0.78. Increase of rrds raised the number of required individuals in DS path, whereby, selection intensity in this path decreased. Nevertheless, decrease in the selection intensity could not decrease the positive effects of decrease in LDS on genetic gain and CGG increased 13.84 percent. The same as these results, there are many resources demonstrating the positive effect of decrease in generation interval on genetic gain (e.g. Jonas and Koning, 2015; Schaeffer, 2006; König and Swalve, 2009; König et al. 2009; Thomasen et al. 2014) and consider it as
an advantage of genomic selection program. Nevertheless, the analysis of selection program without considering the relationship between generation interval and replacement rate was performed in these investigations and the genetic gain was calculated considering a specific value of generation interval and replacement rate. While, it is the relationship between generation interval and the replacement rate that is more effective on genetic and economic results of the genomic selection program than decrease of generation interval (Hjorto et al. 2015; Calus et al. 2015).

Calus et al. 2015 emphasized on important role of replacement rate on economic factors and claim that the maximum economic efficiency of the genomic selection program is possible only by minimum rrds.

They concluded that extra costs for genotyping the replaced individuals are compensated only through extra revenues resulted from elite heifers for replacement. In order to decrease the replacement rate which results in decrease of breeding costs or increase of selection intensity of substitutes, the generation interval should improve. In their results the negative effect of replacement rate on genomic selection program was more than the positive effect of decrease in generation interval. The difference in the methods of estimating the generation interval, required numbers in dams’ path and input parameters resulted in different optimal level of generation interval and the replacement rate in dams’ path compared with the current study. Also they ignored the effect of individuals’ contribution in different age-classes in DS path. Calus et al. 2015 emphasized that the factors such as economic value, and genotyping costs, and the number of required individuals in the selection program is effective on the relationship of replacement rate and generation interval and determination of optimal level of replacement rate. In this study the amount of CGG and EE in Iran’s current situation were estimated 0.0234 kg and 25.60, respectively (considering the contribution of age-classes in Iron’s condition). The amount of CGG in Iran’s current situation was estimated 1.28% percent lower than the amount of CGG in the case of maximum EE. On the other hand, EE in Iran’s current situation is 3.13% lower than maximum EE approachable considering 7 age-classes. Therefore, increasing NCDS from 6 to 7, it is possible to reach maximum EE of genomic selection program.

What differentiates this study from similar studies is considering the pattern of individuals’ distribution in age-classes in selection program’s analysis, which was dispensed in the other performed studies and affects the results of optimization. That’s the reason why it is more emphasized on positive role of genomic information in decreasing the generation interval without addressing the optimal level of parameters like replacement rate, generation interval and selection intensity (caused by change in replacement rate) in the other resources (König and Swalve, 2009; König et al. 2009; Thomasen et al. 2014; Meuwissen et al. 2001).

Unlike EE, with decrease of NCDS, the profit was kept in its increasing trend. In this condition, maximum EE would not be obtained if the breeders try to increase the profit of the selection program. Generally, maximization of EE allows for the presence and stability in competitive market. As Dickerson (1978) mentioned earlier, EE is a criterion which decreases the difference between value and the cost and is dependent of the production system size.
In a competitive market the only breeding objective is EE defined as the ratio of production revenue divided by production costs. In industrial terms especially in consumers’ point of view, EE is of special importance. Both breeding organizations and their consumers and manufacturers prefer to maximize their net profit and are not that much interested in efficiency except that maximum EE is obtained through maximum profit.

Reducing RYBD in the breeding program

RYBD was calculated according to percent of premature births, twinning’s, abortions, stillbirths, calf mortalities through first 3 months after birth, fertility rate of cows (being 39 percent in Iran’s current situation) and sex ratio of calves. In Iran’s current situation, through implementing progeny test program, heifers are not used in breeding of YB’s. Utilization of genomic information allows for the selection and improvement of reproduction and health traits with low heritability (Ponsart et al. 2014; Jonas and Koning, 2015). Also, applying genomic selection program makes it possible to select and improve reproductive and health traits (Ponsart et al. 2014) with low heritability which leads to fewer elite productive dams to produce specific number of bulls in DS path through leads to decrease of RYBD in a breeding program. In addition, Widely used ‘intensive’ embryo-based reproductive techniques can also be used to increase the number of YB’s from limited number of dams by repeating the number of flushes in multiple ovulation embryo transfer (MOET) and ovum pick-up (OPU) combined with IVF schemes (Humblot, 2011).

Imposing such a management strategy requires the analysis of the effect of change in RYBD on economic and genetic factors. According to the results of the second section, and assuming genetic information in the management of DS path, improvement of RYBD results in 13.79 percent increase in genetic gain. With such an increase in CGG and the revenues resulting from the selection program, EE increased by 12.20 percent. The changes trend of CGG and EE was regular and ascending.

RYBD value in Iran’s current situation is 6.07 and considering this value, the selection intensity of DS path was 3.02 and the resulting CGG was estimated 0.02345 kg. CDB and EE resulting from this value of RYBD were estimated $3656.20 and $25.60. According to the results of the second section it is possible to improve the values of CGG, CDB and EE to 0.0003 kg, $433.59 and 2.92 units.

In case of utilizing the other breeding technologies for improving this factor such as sexed semen, more costs are imposed on the selection program and the results would be different from the outputs of the current research. Utilization of technologies such as sexed semen would have two simultaneous effects in the selection program. First it could increase the selection space by increasing the required number of individuals and second, decrease the required number of dams for breeding a YB. Calus et al. 2015 also mentions the positive effect of sorted sperm on increase of genetic gain and the EE of selection program. Including new technologies for decrease of RYBD needs more precise considerations to evaluate their effect on EE of a selection program.

CONCLUSION

Reducing the required number of young bull dams will increase the rate of economic efficiency along with genetic gain in a genomic selection program. Using expensive reproductive technologies would affect the efficiency of reducing the required number of young bull dams. Decreasing the number of age-classes in the DS path did not necessarily leads to a higher economic efficiency. In this respect, the structure of individuals’ distribution in age-classes is a more effective parameter than reducing the age-class numbers. Along with reducing the number of age classes, a reduction in the replacement rate of the first age class is necessary to increase the economic efficiency.

REFERENCES


