

Use of progeny testing in beef cattle: prediction of genetic gain in a Nelore Cattle Breeding Program

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ABSTRACT

Genetic gains predicted for selection, based on both individual performance and progeny testing, were compared to provide information to be used in implementation of progeny testing for a Nelore cattle breeding program. The prediction of genetic gain based on progeny testing was obtained from a formula, derived from methodology of Young and Weiler (*J. Genetics* 57: 329-338, 1960) for two-stage selection, which allows prediction of genetic gain per generation when the individuals under test have been pre-selected on the basis of their own performance. The application of this formula also allowed determination of the number of progeny per tested bull needed to maximize genetic gain, when the total number of tested progeny is limited.

INTRODUCTION

The Nelore Cattle Breeding Program, implemented in 1988 by the Genetics Department of the Faculty of Medicine of Ribeirão Preto, includes 18 breeders from five states of central-southern and northern regions of Brazil. The general breeding goals are improvement of reproductive efficiency, as well as increasing weights and weight gain. One step in the program is the implementation of a progeny test to evaluate sires based on growth traits. However, though it is the most accurate way of evaluating sires (by the definition of breeding value), progeny testing is not always recommended for selection of traits of moderate heritabilities, which can be measured directly on the individual to be selected. Besides the high costs, the increased generation interval may not be compensated

by the greater accuracy of breeding value prediction. According to Van Vleck *et al.* (1987), the use of progeny testing to evaluate the breeding value of animals for traits with heritabilities above 0.4 does not present advantages if the character can be measured in the individual being selected, and if the economic value is not extremely high.

Taking into account that 1) the heritabilities of growth traits being evaluated in the progeny test were estimated for one of the participating herds to be from 0.10 to 0.25 (Lôbo *et al.*, 1993), and 2) the Nelore Project includes elite herds with the capability of contributing improved genetic performance to commercial herds, the option for adopting progeny testing merits further evaluation.

The present study was carried out to compare the genetic gain predicted for yearling weight either using or not using progeny testing. An additional objective was to determine the ideal number of individuals to be tested, considering the availability of animals for selection and the limitation on the total number of tested progeny per year.

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DESCRIPTION OF DATA AND PRESENTATION OF THE PROBLEM

Approximately 14,000 animals belonging to 18 participating herds were recorded by the program since it began; among these 5,322 animals are still alive and in the breeding herds. All animals are registered or controlled by the Brazilian Association of Zebu Cattle Breeders. The distribution of active animals according to their ages and sex is shown in Table I.

Table I - Distribution of active animals in participating herds, by sex and age.

Age (months)	Sex	
	Males	Females
0 - 12	863	812
13 - 24	539	936
25 - 120	172	2000

Every animal in the breeding herds was identified and recorded for birth date, sire, dam, sex, coat color and birth weight. Body weights were recorded monthly until the age of 24 months. After this age, the animals were weighed twice a year.

Females were selected on the basis of an index called Real Fertility (Lôbo, 1994), while male selection was based on yearling weight and scrotal circumference at 18 months. Progeny testing will be applied in the Nelore Program for comparison of sire candidates. The proven sires will be used in all participating herds to increase the genetic gain for these traits. However, it is necessary to determine if the increase in the generation interval using the progeny test will be compensated for sufficiently by an increase in the gain per generation, and whether the costs of the test will be compensated for by an additional gain in response to selection due to progeny testing.

To compare the annual genetic gain obtained by individual selection and progeny testing, it was necessary to clearly define the situation for the application of the test, as well as for utilization of proven animals. This information was not totally available for the herds in the program. Thus, some assumptions representing a situation as close as possible to the real situation were made. The most important assumption made was about the culling of young animals. It was

assumed that about 25% of the animals born in the breeding herds were culled before reaching one year of age, and that the criteria for this early selection were based on traits not related to growth. Another important assumption was that females are not selected for yearling weight.

The character used for comparison was yearling weight. This information, as well as the assumptions used for the achievement of comparisons, is shown in Table II. The heritability of yearling weight (0.17) used in the present work was estimated from data for one of the participating herds (Lôbo *et al.*, 1993).

Table II - Projected conditions for herds participating in progeny testing.

Conditions	Males	Females
Number of proved sires or cows	50	2000
Age at birth of first calf (years)	3	3
Average culling age (years)	6	10 ^a
Replacement sires needed/year	12	250 ^a
Calves weaned/year	750	750
Young animals culled/year	200 ^a	200 ^a
Young animals available for replacement/year	550 ^a	550 ^a
Sires purchased/year	10	-
Animals selected for breeding purposes/year	2	250 ^a

^aAssumptions.

The test will be done on a commercial auxiliary herd that does not participate in the Nelore Program, but only contributes females for the progeny test. Approximately 650 females will be available each year for mating to young bulls for progeny testing.

The use of progeny testing to select individuals for those traits which can be evaluated in the individual characterizes a two-stage selection method. In the first stage, the animals are selected on the basis of their own performance, and in the second stage they are selected on the basis of their progeny averages. The number of individuals to be eliminated during the first stage is important to know, because that selection is important in determining total genetic gain. As the number of selected animals in the first stage increases, the selection intensity decreases, and the selection intensity in the second stage (progeny testing) increases. Furthermore, considering the upper limit of the total number of tested progeny, the progeny groups of each sire in test will be smaller and, consequently, the accuracy of progeny testing will be reduced. Robertson (1957) discussed the problem of progeny group size. However, he did not consider the base

population from which the individuals to be tested came from; consequently, his approach is not adequate for situations where individual performance is taken into account.

TWO-STAGE SELECTION UNDER PROGENY TESTING

Generically the problem can be introduced considering one herd, or a set of herds, with M males available for reproduction per year, from which Mt males are selected for progeny testing on the basis of their own performance. From these, M_s males are selected on the basis of average performance of their progenies. Calculation of expected genetic gain per generation must consider that the capacity of the test (total number of tested progeny) is n progeny per year, and that the number of progeny per tested individual (n_f) is equal to the total progeny tested/year (n) divided by the number of tested males ($n_f = n/Mt$).

This situation characterizes two-stage selection. In the first stage animals which are to be tested are selected, based on the phenotypic value of the individual, and in the second stage (progeny testing), the selection is based on the average phenotypic value of their progenies.

The method described by Young and Weiler (1960) was applied for two-stage selection, in order to obtain a formula to predict genetic gain. This formula allows determination of the optimum number of animals to be progeny tested to maximize gain and a comparison of predicted gain obtained from progeny testing with the predicted gain obtained by individual selection.

An approximate method, utilized by Dickerson and Hazel (1944) and by Ronningen (1970) could be used for the same purpose, without significant loss of accuracy. However, even considering the simplest microcomputers available, the economy of computation time is quite small.

Genetic gain

According to Young and Weiler (1960), when two characters are correlated and selection is done in two stages, first for trait X and later for trait Y, the genetic gain per generation in trait X (ΔG_x) is given by

$$\Delta G_x = \left(\frac{h_x^2 - \rho h_{xy}}{1 - \rho^2} \times E[X] + \frac{h_{xy} - \rho h_x^2}{1 - \rho^2} \times E[Y] \right) \sigma_x, \quad (1)$$

where

$$h_x^2 = \frac{\sigma_{g_x}^2}{\sigma_x^2} = \text{heritability of trait X,}$$

$$\rho = \frac{\sigma_{xy}}{\sigma_x \sigma_y} = \text{phenotypic correlation between X and Y,}$$

$$h_{xy} = \frac{\sigma_{g_{xy}}}{\sigma_x \sigma_y}$$

$E[X]$ = selection differential for trait X (in standard deviation units),

$E[Y]$ = selection differential for trait Y (in standard deviation units),

$\sigma_{g_x}^2$ = genetic variance of trait X,

σ_x^2 = phenotypic variance of trait X,

σ_y^2 = phenotypic variance of trait Y,

σ_{xy} = phenotypic covariance between X and Y, and

$\sigma_{g_{xy}}$ = genetic covariance between X and Y.

For this case, X is the individual phenotypic value for the character and Y is the phenotypic average of n_f progeny of the individual for the same trait. Given that there are no common environmental effects between sire and progeny and between the progeny of the same sire, it follows that

$$\sigma_{xy} = \frac{1}{2} \sigma_{g_x}^2; \quad \sigma_{g_{xy}} = \frac{1}{2} \sigma_{g_x}^2,$$

$$\sigma_y^2 = \frac{1}{n_f} (\sigma_{g_x}^2 + (n_f - 1) \frac{\sigma_{g_x}^2}{4} + \sigma_{e_x}^2),$$

where $\sigma_{e_x}^2$ is the variance of the environmental and non additive genetic effects for the character. Thus, it is possible to obtain

$$\rho = h_x^2 \times \sqrt{\frac{n_f}{4 + (n_f - 1) h_x^2}}, \quad (2)$$

$$h_{xy} = h_x^2 \times \sqrt{\frac{n_f}{4 + (n_f - 1) h_x^2}} = \rho, \quad (3)$$

Substituting (2) and (3) into (1), the genetic gain per generation is given by (4)

$$\Delta G_x = \left(\frac{h_x^2 - \rho^2}{1 - \rho^2} \times E[X] + \frac{\rho (1 - h_x^2)}{1 - \rho^2} \times E[Y] \right) \sigma_x, \quad (4)$$

where

$$E[X] = \frac{z(a) q(A) + \rho z(b) q(B)}{p(a, b; \rho)} ;$$

$$E[Y] = \frac{z(b) q(B) + \rho z(a) q(A)}{p(a, b; \rho)} ;$$

$$A = \frac{b - \rho a}{\sqrt{1 - \rho^2}} ; \quad B = \frac{a - \rho b}{\sqrt{1 - \rho^2}} ;$$

a is the minimum value, in phenotypic standard deviations, below which the animals are culled in the selection on the basis of performance; b is the progeny average value, in standard deviations of the average of the n_f progenies, above which the individuals tested will be considered proven; $z(t)$ is the ordinate of standardized normal curve at any abscissa t ; $q(t)$ is the area of the right-hand tail of the standardized normal curve corresponding to abscissa t ; $p(a, b; \rho)$ is the proportion of one population with values $x > a$ and $y > b$, being the joint distribution normal bivariate of X and Y ; and σ_x is the phenotypic standard deviation of the character.

The value of a may be obtained from the standard univariate normal distribution [$N(0,1)$], and the value of b from the standardized normal bivariate distribution [$N(0,1,0,1,r)$], by solving

$$q(a) = \frac{Mt}{M} ; \quad \text{and} \quad p(a, b, \rho) = \frac{Ms}{M} .$$

The number of proven individuals needed per year (Ms) is usually defined and fixed and so is the proportion of selected individuals [$p(a, b; \rho) = \frac{Ms}{M}$]. The number of individuals selected on the basis of their performance which will be tested (Mt) determines the truncation point in the first stage (a). By transforming X and Y into standard normal variables Z and W , respectively, a may be found in standardized normal curve tables, from the proportion

$$p(z > a) = \frac{Mt}{M} , \quad \text{making} \quad p(z > a) = q(a) ,$$

and if the distribution of X and Y is normal bivariate, the truncation point in the second stage (b), is a function of a and $p(z > a, w > b) = \frac{Ms}{M}$. Using $p(z > a, w > b)$ and a values, b can be found, so that $(p(a, b, \rho) = p(z > a, w > b)$, from the standard bivariate normal distribution.

Efficient numeric algorithms for the normal bivariate curve can be found in the literature (e.g. Donnelly, 1973).

Ideal number of tested males

To compare the genetic gain achieved with and without the use of the progeny test, one must determine the number of males to enter the test each year (Mt), which would be expected to provide maximum genetic gain per year ($\Delta G/L$). As the generation interval does not depend on the number of tested animals, the maximization of genetic gain per generation will also maximize the annual genetic gain. To find the ideal number of males to be tested, the process must be repeated for possible values of (Mt), to find the one which provides the maximum expected genetic gain.

APPLICATION

Conditions of the Nelore Program

The proposed formula (4) was applied to the Nelore Program (Lôbo, 1994), using information presented in Table II. With heritability of 0.17 for yearling weight; 500 controlled progenies per year; 550 males available for first stage selection, and two young proved sires selected per year, expected genetic gains were calculated for combinations of number of sires tested and progeny per tested sire. The results are shown in Table III. The estimated genetic gains per generation result from male selection. Because the calculations do not take into account female selection, genetic gain per generation in the whole population is half that shown in Table III.

The greatest gain per generation is obtained when 13, of a total of 550 available males, are selected to be progeny tested, with about 38 progenies per young sire. However, when from 10 to 20 males are tested, the expected genetic gains are similar. The choice of a smaller number of tested animals is natural due to the costs and consequently, one could test 10 males with 50 progenies per young sire.

For yearling weight with selection applied only to males, with generation intervals of 6.50 years for females, 4.58 years for males not progeny tested and 6.58 years for males submitted to progeny testing, and assuming that purchased males from other herds will have breeding values similar to those animals selected by the program and that the standard deviation for the trait is 30 kg. Then genetic gain with individual selection is expected to be $\Delta G/\text{year} = (0.5100 + 0)/(4.58 + 6.50) = 0.046 \sigma_x/\text{year}$, or $30.0 \times 0.046 = 1.38 \text{ kg/year}$. For progeny testing 13 males per year, the expected gain will be $\Delta G/\text{year} = (0.8535 + 0)/(6.58 + 6.50) = 0.065 \sigma_x/\text{year}$, or 1.96 kg/year . Thus, progeny testing is expected to increase annual genetic gain 41.8%.

Table III - Genetic gain per generation (ΔG), resulting from male selection, expressed in phenotypic standard deviations, according to the number of animals entering the test, under Nelore Program conditions.

No. tested sires	Progeny/Sire	ρ	$E[X]$	$E[Y]$	ΔG
50	10.0	0.229	1.902	2.520	0.7408
40	12.5	0.246	2.000	2.480	0.7725
30	16.6	0.269	2.120	2.426	0.8068
25	20.0	0.287	2.192	2.390	0.8242
20	25.0	0.299	2.277	2.344	0.8403
15	33.3	0.319	2.383	2.278	0.8518
14	35.7	0.323	2.407	2.261	0.8530
13	38.4	0.327	2.433	2.242	0.8535
12	41.6	0.332	2.461	2.220	0.8530
10	50.0	0.342	2.522	2.168	0.8487
8	62.5	0.354	2.596	2.097	0.8367
6	83.3	0.366	2.686	1.990	0.8097
5	100.0	0.373	2.742	1.910	0.7855
4	125.0	0.380	2.808	1.800	0.7474
2	250.0	0.395	3.000	1.185	0.5100

Table IV - Genetic gain per generation (ΔG), due to males, expressed in phenotypic standard deviations, according to the number of animals being tested, without purchase of sires.

No. tested sires	Progeny sire	ρ	$E[X]$	$E[Y]$	ΔG
50	10.00	0.2286	1.8504	1.6546	0.5611
45	11.11	0.2370	1.8963	1.6163	0.5655
40	12.50	0.2463	1.9464	1.5717	0.5686
37	13.51	0.2525	1.9788	1.5409	0.5694
36	13.89	0.2546	1.9900	1.5298	0.5696
35	14.29	0.2568	2.0015	1.5183	0.5694
30	16.67	0.2689	2.0632	1.4517	0.5665
27	18.52	0.2769	2.1042	1.4025	0.5618
24	20.83	0.2858	2.1489	1.3429	0.5536
21	23.81	0.2955	2.1982	1.2679	0.5399
18	27.78	0.3064	2.2532	1.1680	0.5171
15	33.33	0.3185	2.3156	1.0200	0.4768

VARIATIONS IN THE CONDITIONS OF THE PROGRAM

Some projections were made to verify the effect of changes in some of the parameters defined in Table II on genetic gain, with and without progeny testing.

No purchase of sires

The purchase of sires with breeding values similar to those of young sires proven in the test is one of the critical points. Because of the difficulty in obtaining proven animals in the market, an alternative situation, where all the 12 replacement proven sires needed per year were selected in the test, was analyzed. The results for this situation, considering that the other conditions were not changed, are shown in Table IV.

The greatest genetic gain obtained by progeny testing is expected when 36 males are tested (Table IV). But the differences in expected genetic gain are quite small when the number of tested animals ranges from 30 to 50.

With progeny testing of 36 bulls, the resultant gain per generation is 0.5696 standard deviations for males, which represents a genetic gain of 1.31 kg/year

for the population. The genetic gain based on individual selection corresponds to 0.40 standard deviations per generation for males, or 1.08 kg/year for the population. Thus, in this situation expected annual genetic gain with progeny testing is 21.3% greater than that obtained by individual selection.

Variation in the total number of progenies

One of the most probable changes in the Nelore Program is the incorporation of additional auxiliary herds, which would result in an increase in the number of tested progeny. The consequence of a greater total number of tested progeny is an increase in expected genetic gain as well an increase in the ideal number of tested males. Table V shows the maximum expected genetic gain under the conditions of the program, according to the total number of progeny, with and without the purchase of sires.

Since the accuracy of progeny testing as a function of the number of progeny per sire is asymptotic, the expected gain resulting from an increase in the total number of progenies tends to be smaller. However, within some limits, as the number of total progeny increases, the advantages of applying the test increases. Nevertheless, an increase in the number of tested progeny causes an increase in the ideal number of tested males. Although an increase in the total number of progeny does not necessarily result in a significant rise in costs, an increase in the number of animals tested certainly does.

Table V - Maximum expected genetic gain per generation due to males, expressed in standard deviations and per year, in the population, in kilograms (kg) of yearling weight, according to the total number of tested progeny per year.

Progeny	No of tested sires	Progeny/Sire	$\Delta G (\sigma_x)$	$\Delta G/year (kg)$
Purchase of sires				
500	13	38.4	0.8535	1.960
1000	18	55.56	0.9143	2.110
1500	23	65.22	0.9489	2.200
2000	27	74.07	0.9724	2.244
4000	40	100.00	1.0253	2.366
No Purchase of sires				
500	36	13.89	0.5696	1.320
1000	45	22.22	0.6263	1.445
1500	53	28.30	0.6610	1.525
2000	59	33.90	0.6858	1.583
4000	80	50.00	0.7439	1.717

As can be seen from Table V, with purchase of sires the expected genetic gain for 1,000 progenies will be 7.0% superior compared to progeny testing with 500 progenies. With no purchase of sires the use of 1,000 progeny provides a superiority of 9.9%. This difference occurs because the increase in the number of progenies per young sire on test is proportionally greater in the second case.

Differences in heritability

The heritability of a character may vary according to the genetic background of the population and the environmental variance. Thus, it is possible that the heritability will vary among the 18 participating herds.

Differences in heritability result in changes in expected genetic gain. However, the number of tested animals needed to maximize gain is little changed by differences in heritability (Table VI).

As expected, progeny testing is more advantageous for low heritability traits (Table VI). For a heritability of 0.10, the superiority of progeny testing over phenotypic selection, with and without the purchase of sires, corresponds to 57% and 27%, respectively. If the heritability is 0.25, this superiority falls to 30% and 14% respectively. For heritabilities greater than 0.30, the advantage of progeny testing

without the purchase of sires is quite reduced and hardly compensates the costs.

Maternal effects

Although there is no general agreement about the role of maternal effects on yearling weight, in some experiments (Koots *et al.*, 1994) this effect seems to have had importance. Clearly, as the maternal effects increase in importance for the trait, the advantage of progeny testing decreases for a fixed heritability of direct effects. On the other hand, the advantage of progeny testing can increase as the correlation between maternal and direct effects becomes more negative, because the accuracy of phenotypic selection is reduced.

ALTERNATIVE SELECTION SCHEME

Another alternative we examined is the utilization of the 12 best young sires, selected on the basis of their phenotype, in participating herds, at the same time the test is carried out (during two years) in the auxiliary herds. After obtaining the results of the test, the sires not approved in the test would be culled, and the others would be used during two more years. This scheme would allow the use of proven animals without increasing the generation interval.

According to Dickerson and Hazel (1944), the annual genetic gain in the present case is given by,

$$\Delta G/year = \frac{P_p \Delta G_p + P_t \Delta G_t}{P_p L_p + P_t L_t + L_F} \quad (5)$$

where

ΔG_p = genetic superiority of males selected on the basis of their phenotype,

ΔG_t = genetic superiority of males selected by progeny testing,

P_p and P_t = proportion of new generation progeny of sires selected by their phenotype and by progeny testing, respectively,

L_p and L_t = average age of selected animals in phenotype and progeny testing, respectively, by the time their progeny are born,

L_F = generation interval due to females.

The results obtained by the application of this equation, considering equal proportions of new generation progeny of sires selected by phenotype and by progeny test, are presented in Table VII, for several heritability values.

Table VI - Maximum genetic gain per generation due to males, expressed in standard deviations (σ_x) and per year in the population, expressed in kilograms of yearling weight, according to possible heritabilities of the trait, with and without progeny testing.

Heritability	No. tested sires	Progeny/Sire	$\Delta G (\sigma_x)$	$\Delta G/year (kg)$	$\Delta G/year$ without test
Purchase of sires					
0.10	12	41.67	0.5569	1.285	0.816
0.15	13	38.46	0.7722	1.782	1.224
0.20	13	38.46	0.9669	2.231	1.632
0.25	14	35.71	1.1463	2.645	2.039
0.30	14	35.71	1.3135	3.013	2.430
0.35	13	38.46	1.4706	3.373	2.835
0.40	13	38.46	1.6192	3.714	3.240
0.45	13	38.46	1.7600	4.013	3.644
0.50	12	41.67	1.8942	4.345	4.049
No Purchase of sires					
0.10	34	14.71	0.3585	0.822	0.647
0.15	35	14.29	0.5158	1.183	0.970
0.20	35	14.29	0.6628	1.520	1.293
0.25	35	14.29	0.8016	1.838	1.617
0.30	35	14.29	0.9332	2.140	1.940
0.35	34	14.71	1.0588	2.428	2.263
0.40	33	15.15	1.1789	2.703	2.586
0.45	32	15.63	1.2943	2.968	2.910
0.50	31	16.13	1.4055	3.233	3.223

Table VII - Genetic superiority of sires selected by phenotype and by progeny testing and genetic gain in yearling weight per year considering the alternative scheme, with half of the progeny sired by proven sires and the other half by sires in test, according to the heritability of the character, without purchase of sires.

Heritability	No. tested sires	$\Delta G_p (\sigma_x)$	$\Delta G_t (\sigma_x)$	$\Delta G/year (kg)$
0.10	34	0.2389	0.3585	0.8088
0.15	35	0.3583	0.5158	1.1834
0.20	35	0.4778	0.6628	1.5441
0.25	35	0.5972	0.8016	1.8937
0.30	35	0.7166	0.9332	2.2335
0.40	33	0.9555	1.1789	2.8895
0.45	32	1.0750	1.2943	3.2075
0.50	31	1.1944	1.4055	3.5197

This scheme provides genetic gains which are greater than those obtained by the exclusive use of proven sires, when heritability of the selected character is greater than 0.15 (among tested values). Even when the heritability is 0.40, the advantage of this scheme over individual selection is about 12%.

CONCLUSIONS

The method described by Young and Weiler (1960) can be adapted for the prediction of genetic gain in the case of progeny testing, when the character of interest can be used to select the animals to be tested. This method allows estimation of the expected genetic gain and the optimum number of progeny per tested animal to maximize gain for a given total number of tested progeny.

The change in the predicted genetic gain due to differences in the number of tested animals is small for a narrow range around the ideal number.

Predicted genetic gains resulting from progeny testing in the situations foreseen for the Nelore Program were 14% to 57% superior to predicted genetic gain resulting from phenotypic selection. Although no economic evaluation was made, these results indicate that progeny testing is an important alternative for the Nelore Program, especially since the participating herds are considered elite herds and the gain obtained will be multiplied through other commercial herds.

The option for adopting progeny testing depends on accurate estimates of heritability, which

must be obtained from pooled data from all participating herds.

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RESUMO

Com o objetivo de fornecer subsídios à implantação do teste de progênie em um projeto de melhoramento do gado Nelore, foram comparados os ganhos genéticos esperados para a seleção pelo fenótipo e pelo teste de progênie para as condições do Projeto. Este último ganho foi obtido a partir de uma fórmula baseada na metodologia de seleção em dois estágios de Young and Weiler (*J. Genetics* 57: 329-338, 1960), que permite prever o ganho genético por geração de seleção, quando os animais que entram no teste são escolhidos com base em seu próprio desempenho. A aplicação da fórmula permitiu também encontrar o número de progênies por animal testado que maximiza o ganho genético, quando o número total de progênies é limitado.

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