



**Effects of inbreeding and selection on heritability estimates of production traits of Holstein cattle under selection.** Efeitos da endogamia e seleção na estimativa da herdabilidade em características relacionadas a produção em bovinos da raça Holandesa sob seleção.

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## Abstract

Inbreeding and selection are forces that affect heritability, important to selection in livestock species. So, this study aims to relate those forces in a Holstein population under selection for superior milk production. Inbreeding coefficients was calculated considering 3 generations, after the individual inbreeding coefficient was calculated, inbred ( $7.92 \pm 2.72$ ) and non-inbred group ( $0.46 \pm 0.38$ ) were formed. The genetic variance was higher for the inbred group and for the residual variance was lower. As result, those variance changes resulted in higher heritability for all traits analyzed for the inbred group. For the levels of inbreeding observed in this study, the selection for higher productions possibly masked the effects of inbreeding.

**Keywords:** Genetic variance. Genetic diversity. Environmental variance. Dairy cattle. Pedigree.

## Resumo

Endogamia e seleção são forças que afetam a herdabilidade, importante para a seleção de animais de interesse comercial. Com isso, este estudo tem como objetivo de relacionar estes componentes em uma população de bovinos da raça Holandesa sob seleção para superioridade em produção leiteira. O coeficiente de endogamia foi calculado considerando 3 gerações, após o cálculo do coeficiente de endogamia, um grupo de animais endogâmicos ( $7.92 \pm 2.72$ ) e não-endogâmicos ( $0.46 \pm 0.38$ ) foi formado. A variância genética foi maior para o grupo endogâmico enquanto a variância residual foi menor. Como resultado, estas variâncias alteraram a herdabilidade que se mostrou maior para todas as características no grupo endogâmico. Para os níveis de endogamia observados neste estudo, a seleção para superioridade na produção de leite possivelmente mascarou os efeitos de depressão endogâmica.

**Palavras-chave:** Variância genética. Diversidade genética. Variância ambiental. Bovinocultura de leite. Genealogia.

## Introduction

Inbreeding and its implications are a growing concern among Holstein cattle breeders (Weigel and Lin, 2000). Genetic selection programs can identify superior lineages and sires, combined with reproductive technologies can disperse efficiently genes of interest causing an intensive selection for commercial interest traits, mostly for milk yield, fat, and protein content traits (Baes et al., 2019).

However, the selection of genetically superior individuals can increase inbreeding, due to mating between individuals who share one or more common ancestors, leads to a reduction in heterozygous genes leading to greater degrees of homozygosity (Falconer and Mackay, 1985). Higher proportions of homozygosity lead to lower genetic diversity, increases the frequency of deleterious recessive alleles (Weigel and Lin, 2000), reduce the frequency of heterozygotes to express overdominance, and decreases the mean value of a trait, characterizing inbreeding depression (Kristensen and Sørensen, 2005). Also, inbreeding can change the distribution of genetic and environmental variance (López-Fanjul et al., 1989).

Heritability can be used as a method to estimate the genetic and environmental influence on a population. The narrow sense heritability ( $h^2$ ), being a function of genetic and environmental variance (Kristensen et al., 2005). Genetic variance is expected to decrease, and environmental variance is expected to increase in presence of inbreeding, causing inbred populations to be less capable to adapt and being more sensitive to environmental variance (Fowler and Whitlock, 1999; Kristensen et al., 2005). However, the magnitude of genetic variance change is determined by many factors, some of which are difficult to measure or predict (Whitlock and Fowler, 1999). Although, environmental changes, migration and selection can also alter heritability (Visscher et al., 2008).

However, there are few studies that relate the effects of inbreeding on heritability in a population under directional selection. Therefore, the aim of this study was to evaluate the effects of inbreeding and selection on heritability estimates in a population of Holstein cattle from southern Brazil that were under selection.

## Materials and methods

Data for 7340 Holstein cows were provided by GenMate Genética LTDA, including milk productions and pedigree from animals born between 2001 and 2020 were obtained from 7 southern Brazilian herds. All animals were recorded as purebred, containing 4 generations of ancestors. The production traits data recorded for animal are milk yield, fat yield, protein yield, lactose yield and solids yield, based on 305 days production. The INBUPGF90 software was used to estimate the individual inbreeding coefficients based on pedigree using a recursive method (Aguilar and Misztal., 2008). The recursive algorithm assumes that animals are ranked based on birth so that parents precede their progeny, the inbreeding coefficient  $F_x$  is calculated as:

$$F_x = 0.5R_{sd}$$

where  $sd$  corresponds the numerator relationship between the sire ( $s$ ) and the dam ( $d$ ) of the animal  $x$  (Emik and Terril, 1949).

After estimate inbreeding coefficients, animals were ranked in groups of inbred and non-inbred animals (top 10% inbreeding coefficients and bottom 10% inbreeding coefficients, respectively), therefore, in all each group contained 730 animals.

To determine whether the environmental effects were significant, multiple linear regression analyzes were performed for year of milk yield onset, herd and times milked per day effects for each production traits on Graphpad Prism 8 software (Darlington and Hayes, 2016). Linear regression followed the model:

$$y = \beta_0 + \beta_1 * X_1 + \beta_2 * X_2 + \beta_3 * X_3$$

Where, the  $y$  represent the dependent variable or the production trait,  $\beta_0$  the intercept value,  $X_n$  the coefficient of regression, and  $\beta_n$  the independent variable.

Considering only significant environmental effects, genetic values were estimated to obtain the values of genetic and residual variance of each production trait in the AIREMLF90 software, with the methodology of restricted maximum likelihood under the animal model approach (Misztal et al., 2010).

Heritability was estimated for each production trait as following model:

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2}$$

Where,  $h^2$  corresponds the heritability coefficient,  $\sigma_a^2$  additive genetic variance to and  $\sigma_p^2$  to phenotypic variance (sum of additive genetic variance and residual variance).

## Results and discussion

Table 1 shows the descriptive statistics of the inbreeding coefficients and production traits for the Holstein population, The inbreeding coefficient were low with average value of 3.21%. ranging from 0 to 28.13%. Milk yield ranged from 4035.70 kg to 20635.61, with average value from 10325.54, corresponding expected breed variations and average.

Table 1 – Descriptive analysis of inbreeding coefficients and production traits of Holstein cattle.

Trait	N	Mean±SD	Min	Max
<b>Inbreeding</b>	7340	3.21±2.20	0.00	28.13
<b>MY 305</b>	7340	10325.54±2113.72	4035.70	20635.61
<b>FY 305</b>	7340	358.10±84.10	109.96	771.74
<b>PY 305</b>	7340	321.12±66.46	110.91	612.35
<b>LY 305</b>	7340	489.90±108.31	19.16	1007.11
<b>SY 305</b>	7340	1263.87±271.99	46.58	2446.41

Inbreeding = Inbreeding coefficient; MY 305 = Milk yield based on 305 days; FY 305 = Fat yield based on 305 days; PY 305 = Protein yield based on 305 days; LY 305 = Lactose yield based on 305 days; SY 305 = Solid yield based on 305 days; N = Number of observations.

Can be observed in Table 2, that the inbred groups present higher average production yield, as also a higher time milked per day, demonstrating that the inbred group has a small tendency to be in herds where more milkings per day are performed.

Table 2 – Descriptive analysis of inbreeding coefficients and production traits of Holstein cattle inbred and non-inbred groups.

<b>Inbred</b>							
	<b>Year</b>	<b>TMD</b>	<b>MY 305</b>	<b>FY 305</b>	<b>PY 305</b>	<b>LY 305</b>	<b>SY 305</b>
<b>Mean</b>	2014.43	2.77	10591.44	374.15	331.79	504.79	1308.39
<b>Standard deviation</b>	4.42	0.42	2208.78	84.96	70.51	111.78	277.15
<b>Minimum</b>	2001	2	4147.91	144.54	121.49	123.04	309.05
<b>Maximum</b>	2020	3	18679.25	771.74	589.2	900.15	2242.31
<b>Observations</b>	734	734	734	734	734	734	734
<b>Non-inbred</b>							
	<b>Year</b>	<b>TMD</b>	<b>MY 305</b>	<b>FY 305</b>	<b>PY 305</b>	<b>LY 305</b>	<b>SY 305</b>
<b>Mean</b>	2011.28	2.73	9870.31	339.08	313.73	461.41	1198.91
<b>Standard deviation</b>	4.88	0.44	2120.71	87.53	71.19	116.33	301.07
<b>Minimum</b>	2001	2	4325.15	138.71	130.05	37.83	96.31
<b>Maximum</b>	2019	3	17619.87	681.26	604.95	892.96	2273.08
<b>Observations</b>	735	735	735	735	735	735	735

Year = Year of birth; TMD = Times milked per day; MY 305 = Milk yield based on 305 days; FY 305 = Fat yield based on 305 days; PY 305 = Protein yield based on 305 days; LY 305 = Lactose yield based on 305 days; SY 305 = Solid yield based on 305 days.

As can be noted in Table 3 that through the minimum and maximum values it can be assumed that the range of values in the inbred group is greater than the non-inbred group, as can also be observed for standard deviation. The inbreeding values described in this study are compatible with the coefficients found in other studies using similar populations (Sieklicki et al., 2019; Silva et al., 2019).

Table 3 – Descriptive analysis of inbreeding coefficients of Holstein cattle groups.

<b>Group</b>	<b>N</b>	<b>Mean±SD</b>	<b>Min.</b>	<b>Max.</b>
<b>Inbred</b>	734	7.92±2.72	5.71	28.13
<b>Non-inbred</b>	734	0.46±0.38	0.00	1.03

Inbred = top 10% animal group for inbreeding; non-inbred = bottom 10% animal group for inbreeding; N = Number of observations.

The increased level of inbreeding as observed in the inbred group (Table 3) could be due assortative mating (Lynch and Walsh, 1998), fact that can be sustained with the analysis of Table 2.

In table 4, the fixed effects for year, herd and times milked per day were significant for all traits ( $p < 0.0001$ ). The determination coefficients were moderate, ranging from 0.2511 for milk yield, to 0.3537 for solid yield.

Table 5 shows the additive genetic variances, residual variances and heritability for milk yield, fat yield, protein yield, lactose yield and solid traits in the Holstein population studied.

For all production traits analyzed, the genetic variance was higher for the inbred group compared to the non-inbred group, being the same phenomenon observed for heritability (Table 5). Which was not expected, because in the presence of inbreeding the heritability coefficients are lower, this because higher levels of inbreeding lead to higher homozygosity, and in the same proportion

reducing heterozygosity (Kristensen and Sørensen, 2005), however, the behavior of additive genetic variance under inbreeding relies on a large extent in the underlying genetic architecture of the trait (Kristensen and Sørensen, 2005). Classical population genetics theory suggests that genetic variance is reduced under inbreeding (Fowler and Whitlock, 1999).

Table 4 - P value for regression analysis for environmental effects tested for Holstein cattle production traits.

Trait	P value			r <sup>2</sup>
	Year	Herd	TMD	
<b>Milk</b>	<0.0001	<0.0001	<0.0001	0.2511
<b>Fat</b>	<0.0001	<0.0001	<0.0001	0.3275
<b>Protein</b>	<0.0001	<0.0001	<0.0001	0.3030
<b>Lactose</b>	<0.0001	<0.0001	<0.0001	0.3052
<b>Solids</b>	<0.0001	<0.0001	<0.0001	0.3537

Milk = Milk yield based on 305 days; Fat = Fat yield based on 305 days; Protein = Protein yield based on 305 days; Lactose = Lactose yield based on 305 days; Solids = Solids yield based on 305 days; P value = P value for regression analysis; r<sup>2</sup> = Coefficient of determination for the regression model; Year = Effect of year of onset of lactation; Herd = Herd effect; TMD = Times milked per day effect.

Table 5 – Genetic variance, residual variance, and heritability results for Holstein cattle production traits.

Trait	Group Inbred			Group non-Inbred		
	$\alpha^2a$	$\alpha^2res$	$h^2$	$\alpha^2a$	$\alpha^2res$	$h^2$
<b>Milk</b>	1698200	1663900	0.51	1168900	1887700	0.38
<b>Fat</b>	1765.7	3066.9	0.37	1009.8	3573.7	0.22
<b>Protein</b>	1705.5	1473.4	0.54	1137.1	1889.3	0.38
<b>Lactose</b>	4045.8	4040.7	0.50	2514.8	5162.3	0.33
<b>Solids</b>	21649	25712	0.46	13103	34149	0.28

Milk = Milk yield based on 305 days; Fat = Fat yield based on 305 days; Protein = Protein yield based on 305 days; Lactose = Lactose yield based on 305 days; Solids = Solids yield based on 305 days; Inbred = top 10% animal group for inbreeding; Non-inbred = bottom 10% animal group for inbreeding;  $\alpha^2a$  = additive genetic variance;  $\alpha^2res$  = Residual variance;  $h^2$  = Heritability.

Some studies suggest that in some conditions additive genetic variance may increase, because genetic models based on purely additive basis state that inbreeding erodes additive genetic variance, but dominance and epistatic variance can augment additive genetic variance (Buskirk and Willi, 2006).

Different breeding systems are probably one of the major factors that affects genetic variability (Charlesworth, 2015). In the population under study, the inbreeding levels (Table 3) suggest that there is an assortative mating of the animals. The assortative mating changes the additive genetic variance relative to what is expected in a randomly mating population (Lynch and Walsh, 1998). Besides, selection on production traits in livestock species tend to be directional (Kim et al., 2013) and with the positive assortative mating being far more frequently in relation to the negative assortative mating (Kim et al., 2013).

Positive assortative mating increases homozygosity within loci, and consequently inflates the variance of quantitative traits (Kim et al., 2013), this is possibly what was observed in this study (Table 5). Positive assortative mating increases additive genetic variance, while negative assortative mating, known as disassortative mating, decreases additive genetic variance (Lynch and Walsh, 1998). Selection for extreme animals, as is the case of positive assortative mating, may also increase or decrease environmental variance (Lynch and Walsh, 1998), because selection in general is made

for a specific environment, and as result reduces environment sensitivity (Falconer, 1990), fact that can be considered due to the results expressed in the Table 2 and Table 5.

As this increase in genetic additive variance, and consequently heritability, can be substantial in inbred populations compared to outbred populations (Buskirk and Willi, 2006), as shown by Barton and Turelli (2004) simulations that additive genetic variance increases under moderate inbreeding, as we can assume with the population in this study is (Nelson and Lush, 1950; Thompson et al., 2000; Mc Parland et al., 2007).

Moreover, the change in genetic variance occasioned by inbreeding depends on the genetic architecture of the trait, because the new variation emerges from non-additive variance as dominance and epistasis (Buskirk and Willi, 2006). The dominance variance is particularly import for lifetime performance traits as milk yield and is components (Fuerst and Solkner, 1994), showing increasingly levels of additive genetic variance and heritability at higher levels of inbreeding (Buskirk and Willi, 2006). The epistasis can contribute to the increase of additive genetic variance. Being the additive genetic variance responsible for the resemblance between parents and offsprings and contributes to selection response (Goodnight, 1988). And in a non-inbred population, the epistasis will contribute to the resemblance between parents and offsprings (Griffing, 1960). Because the additive genetic variance is set by least square regression of phenotype genotype (Falconer and Mackay, 1985), some parcel of the epistasis variance in an ancestral population will result in additive genetic variance expression after a bottleneck or founder effect (Goodnight, 1988).

For residual variance, which can be interpreted as environmental variance, the opposite was observed, were for all production traits the residual variance was lower for the inbred group in relation to the non-inbred group. Inbred populations often have lower genetic variance and larger environmental variance (Charlesworth, 2015). Hypothesized that the effect of inbreeding on environmental variance could be due stress response, and that this effect is increased even more in fitness related traits than to traits related less to fitness (Kristensen and Sørensen, 2005), causing lower heritability. However, it is reported that the selection can reduce the environmental variance (Merilä et al., 2001; Blasco et al., 2017), this effect may be caused by the fact that the selection for productive traits results in animals more adapted to the inserted environment, at this level of inbreeding.

## **Conclusion**

With the levels of inbreeding observed in this study was possible to assume that it could benefit or that its effects were masked by selection in this population, by increasing heritability and additive genetic variance, consequently improving selection response in subsequent generations. But caution is needed as increased inbreeding depression can be expressed, especially if higher levels of inbreeding is present, as well genetic, and environmental variance can be unpredictable in those circumstances.

## **Conflict of interest**

The authors declare that there is no conflict of interest.

## **Authors' contribution**

Fernando Jean Dijkstra - conceived and designed the analysis, collected the data, performed the analysis, wrote the paper; Rafaela Martins - contributed data and analysis tools, wrote the paper.

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