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Inbreeding depression affecting stayability in Italian Holstein cows

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ABSTRACT

Advances in selection and reproduction methods, particularly the implementation of genomic evaluations alongside assisted reproductive technologies, have substantially enhanced productivity and efficiency, notably within specialized dairy cattle populations. Nevertheless, the widespread use of a limited number of elite sires and dams has also led to increased levels of inbreeding, posing a risk to animal performance in production, reproduction, and functional longevity. The objective of this study was to evaluate the effect of inbreeding on stayability in the Italian Holstein population. Stayability, defined as the ability of cows to remain productive in the herd from one parity to another, was assessed across 5 periods: STAY12, from parity 1 to 2; STAY23, from parity 2 to 3; STAY34, from parity 3 to 4; STAY13, from parity 1 to 3; and STAY14, from parity 1 to 4. Individual inbreeding coefficients were estimated using 3 methods: pedigree information, diagonal elements of the genomic relationship matrix, and the proportion of the total length of runs of homozygosity (ROH) segments relative to the total autosomal genome covered by SNPs. Furthermore, different ROH length classes were evaluated separately to distinguish between the effects of recent and ancient inbreeding. Two datasets were extracted from the breeders' association database with no interference in the herds' usual management: one including both genotyped and nongenotyped individuals and another with only genotyped animals. The first, comprising 828,056 cows, was used to assess pedigree-measured inbreeding depression in the Italian Holstein population. The second, including 48,833 genotyped cows, was used to compare inbreeding measures. The effect of inbreeding was estimated as best linear unbiased estimates on the liability scale within a Bayesian framework. In the stayability analysis, milk yield level relative to contemporary group was included as an additional fixed effect to account for its influence. Estimates were converted to the probability scale, using a cumulative distribution function, and then used to compare models and assess survival probabilities according to varying levels of inbreeding. Increased inbreeding consistently resulted in decreased stayability. The magnitude of inbreeding depression was greater for traits involving cumulative periods, such as STAY13 and STAY14. The expected variation in stayability resulting from a 1-unit increase in the pedigree inbreeding coefficients (F_{PED}), ranged from −0.06% to −0.44%, depending on the model and trait. Models using genomic inbreeding captured larger effects of inbreeding depression. In these cases, the expected variation in stayability ranged from −0.22% to −1.60% per 1-unit increase in F_{PED}. Inbreeding estimated from the sum of ROH segments longer than 2 Mb were associated with reduced stayability, whereas shorter segments were not. This suggests that recent inbreeding contributes to inbreeding depression on this trait, whereas ancient inbreeding does not. It should be noted that part of the observed inbreeding depression may be attributable to voluntary culling related to the production level of cows within their herds. Thus, in a selection index that includes milk yield and penalizes future inbreeding, stayability should preferably be analyzed using a model that incorporates production level as a fixed effect.

Key words: dairy, inbreeding, pedigree, runs of homozygosity

INTRODUCTION

In recent decades, consistent increases in inbreeding levels and concomitant decline in effective population size have been observed within Holstein cattle popula-

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tions across several countries, with Italy, the United States, and Canada showing the most marked trends (Makanjuola et al., 2020b; Ablondi et al., 2022; Lozada-Soto et al., 2022). The increasing use of genomic selection among dairy cattle populations has increased the availability of genomic data, consequently allowing for more precise estimation of individual inbreeding levels, and has provided improved tools for managing co-ancestry through optimized mating strategies (Howard et al., 2017; Wiggans and Carrillo, 2022; Bengtsson et al., 2023). It is important to note that the rate of increase in average inbreeding has accelerated since the widespread adoption of genomic selection around 2010. Significant changes in the Italian population following the introduction of genomic selection have been observed, particularly after 2015, characterized by an accelerated rate of increase in average inbreeding. Ablondi et al. (2022) have found that the overall inbreeding rate accumulation per year before the use of genomic selection was equal to 0.14% and 0.32% based on inbreeding coefficient obtained from the pedigree (**F_{PED}**) and inbreeding coefficient obtained from runs of homozygosity (**F_{ROH}**), respectively, whereas the same rate increased up to 0.47% (based on F_{PED}) and 0.70% (based on F_{ROH}) after the adoption of genomic selection. The increased inbreeding becomes a problem because inbreeding depression tends to occur in purebred populations, as has been the case for dairy cattle (Leroy, 2014).

At the same time, the implementation of genomic selection has significantly enhanced our ability to identify deleterious alleles, enabling more informed and strategic mating decisions at both population and herd levels (Cole et al., 2025). Also, the genomic era has significantly accelerated genetic gains, especially in dairy cattle. In American Holsteins, for example, there were estimates indicating that genomic selection has led to a relative increase in annual gains of 50%–100% for yield traits and from three- to fourfold for lowly heritable traits (García-Ruiz et al., 2016). Genomic data have significantly enhanced the ability to quantify inbreeding depression, allowing for a more accurate evaluation of its negative impacts on economically important traits (Doekes et al., 2021; Ablondi et al., 2023). This improvement is especially relevant for traits such as longevity and stayability, which are heavily influenced by health, fertility, and the overall robustness of dairy cows.

Stayability is a categorical trait that defines the cow's ability to remain alive and productive within the herd over successive time periods. The definition of the trait relies on the presence or absence of the cow in the herd in specific moments, which makes it easy to record. Reproductive performance is a fundamental factor determining productivity and profitability in cattle farm, as it directly controls the number of animals available for production (Silva et al., 2024). This trait plays an important role in the herd's economic sustainability, as premature culling leads to increased replacement costs for the breeders (De Vries, 2006; VanRaden et al., 2021). In fact, one of the main costs in cattle farming is the expense of raising replacement heifers, which can directly impact farm profitability (Callegaro et al., 2024). Therefore, females must remain in the herd long enough to generate sufficient calves to cover rearing costs. De Vries (2020) estimated a period of around 5 years as the optimum productive lifespan of dairy cows. Changes in management practices, such as the use of sexed semen and beef on dairy, can also increase this optimum period.

In a simulation study, Han et al. (2024) demonstrated that extending the productive lifespan of cows in the herd can contribute to reducing greenhouse gas emissions. In that analysis, the number of insemination attempts permitted before culling was modeled as the variable parameter; however, the practical outcome was a longer retention of animals in the herd, comparable to improved stayability. This reduced culling rate lowered the emissions associated with rearing replacement heifers. Other studies have also linked lifespan and selection for longevity to improvement on the carbon footprint of dairy herds (Nguyen et al., 2023; Bell, 2024; Richardson et al., 2025).

Dairy cows can leave the herd prematurely for various reasons, including low productivity, poor fertility, health disorders, or even mortality. If inbreeding impairs the rate of success of cows to remain in the herd, it should certainly be avoided. Despite the economic relevance of stayability, limited research has specifically quantified the effect of inbreeding depression on this trait. A study on Alentejana beef cattle found that increased inbreeding levels were associated with reduced longevity (Carolino and Gama, 2008). In dairy cattle, Thompson et al. (2000) found a decrease in survival associated with increasing levels of inbreeding, and concluded that survival and production represent a major challenge to the genetic programs of the US dairy industry. Also in dairy cattle, Sewalem et al. (2006) found that inbreeding had a statistically significant association with functional longevity in the Canadian population.

Therefore, the main objective of the present study was to investigate the effect of inbreeding depression on the stayability of Italian Holstein dairy cows. Additional objectives were to compare inbreeding measures obtained from pedigree and genomic information, and to determine the effects to be included in the models.

MATERIALS AND METHODS

Phenotypic records, pedigree information, and inbreeding measures were provided by the Italian Holstein, Brown, and Jersey Breeders Association (**ANAFIBJ**, Cremona, Italy).

Pedigree and Inbreeding

The complete pedigree file comprised 9,615,703 animals, including information on sire, dam, and year of birth. Estimates of individual inbreeding (Wright, 1922) were computed following Meuwissen and Luo (1992). The number of equivalent complete generations in the pedigree was traced according to Maignel et al. (1996). Both inbreeding coefficient estimation and the tracing of the number of equivalent generations were conducted using the Endog v 4.8 program (Gutiérrez and Goyache, 2005).

Genotypes and Inbreeding

Using 21 different SNP chips originally, 73,271 cows were genotyped with medium-density (**MD**) chips, each containing 40k to 70k markers, whereas 5,769 cows were genotyped with the GeneSeek Genomic Profiler 100k, 131 with the GeneSeek Genomic Profiler high-density (**HD**) 150k chip, and 655 with the Illumina Infinium BovineHD BeadChip (777,962 markers). The total number of genotyped cows was 79,826. Approximately 80% of these cows had their sires genotyped with HD chips, which was useful for the robustness of the imputation process. Every cow genotyped with MD SNP panels had its genotype imputed to 84,445 SNPs (preselected by ANAFIBJ), whereas those genotyped in HD were downgraded to the 84,445 SNPs. The imputation is part of the routine genomic evaluation procedure of ANAFIBJ, and it is conducted with an improved version of the PedImpute software (Nicolazzi et al., 2013). More detailed information on this imputation process can be found in (Dadousis et al., 2024). Quality control (**QC**) procedures were implemented to ensure data reliability. Individuals with a call rate smaller than 95% or mendelian conflicts larger than 0.01, as well as SNPs with minor allele frequency smaller than 0.02 were removed. After QC, the list of cows with genotypes comprised 79,794 animals.

Genomic inbreeding was estimated using 3 different approaches:

(1) $\mathbf{F_{GRM}}$, obtained from the diagonal of the genomic relationship matrix (**GRM**), following method 1 proposed by VanRaden (2008), with frequencies of alleles fixed to 0.5 and $F_{GRM} = diag(GRM) - 1$.

(2) $\mathbf{F_{ROH\_GENOME}}$, obtained from the proportion between the sum of the length of runs of homozygosity (**ROH**) segments per cow and the total length of the autosomal genome covered by SNPs (2.48 Gbp in this study).

(3) $\mathbf{F_{ROH\_CLASS}}$, obtained from the proportion between the sum of the ROH segments and the total length of the autosomal genome covered by SNPs as described before, but separated into 6 length classes: 1 Mb < ROH ≤ 2 Mb; 2 Mb < ROH ≤ 4 Mb; 4 Mb < ROH ≤ 8 Mb; 8 Mb < ROH ≤ 16 Mb; 16 Mb < ROH ≤ 32 Mb; and 32 Mb < ROH. Shorter segments are associated with more ancient inbreeding, and longer segments are associated with more recent inbreeding (McQuillan et al., 2008; Kirin et al., 2010; Peripolli et al., 2018; Baes et al., 2019).

The ROH segments were previously detected by Ablondi et al. (2022) and Ablondi et al. (2023), using the detectRUNS package in R (Biscarini et al., 2018) and the following parameters:

(a) Minimum of 15 SNPs in a window (–homozyg-window-snp).

(b) Minimum base pair length of 1,000 kb (–homozyg-kb).

(c) Maximum gap of 500 kb between consecutive homozygous SNPs (–homozyg-gap).

(d) Minimum density of 1 SNP per 100 kb (–homozyg-density).

(e) Maximum of 1 missing and 1 heterozygous SNP allowed within the window (–homozyg-window-het).

Before their use as covariates in the models, F_{GRM}, F_{ROH_GENOME}, and F_{ROH_CLASS} were rescaled to have the same average and SD as the F_{PED} estimated for the respective group of animals. This was done by subtracting the mean and dividing by the SD of each covariate, then multiplying by the SD of F_{PED} and adding its mean. The objective was to have a common scale, facilitating later comparisons among inbreeding effects resulting from different inbreeding measures.

Analyzed Traits

In the current research, we investigated stayability as a dairy cow's ability to survive from one point in time to another during its productive life. Dairy cows that successfully survived to the end of the specified period were classified as 1, and the unsuccessful ones were, in turn, classified as 0. In all cases, only cows that had their first calving and initiated their first lactation before 37 mo of age were retained. Censoring was also applied to cows that changed herds or that did not have enough time to recalve and for which, therefore, success or failure could not be called. Phenotypes were defined as 5 binary traits: **STAY12**, **STAY13**, and **STAY14**, representing cows reaching their second, third, and fourth calvings, respectively; additionally, **STAY23** and **STAY34** cap-

Table 1. Number of available records for each trait, after consistency and filtering

	Number of records		Number of animals in the pedigree		Average rate of success (%)	
Trait	Data_g	Data_e	Data_g	Data_e	Data_g	Data_e
STAY12	48,833	828,056	212,263	2,540,592	83.93	78.20
STAY23	23,943	565,696	118,168	1,997,251	74.54	67.41
STAY34	11,904	321,889	67,359	1,412,752	66.58	58.33
STAY13	29,587	750,425	139,674	2,326,945	63.00	51.55
STAY14	20,382	658,307	102,004	1,997,563	42.75	28.81

tured whether cows that completed their second or third calving and initiated subsequent lactations also reached the third or fourth calving, respectively.

Phenotypes, Data Filtering, and Pedigree Pruning

The complete phenotype dataset consisted of 3 files: the first with 7,987,172 records for STAY12, including censored records for STAY13 and STAY14; the second with 5,638,764 records for STAY23; and the third containing 3,488,083 records for STAY34.

From this complete dataset, 2 sets of data were obtained. The first, referred to as **Data_g**, comprised animals born between 2006 and 2020, with phenotypic records of stayability as well as genomic information. The expanded dataset, **Data_e**, included animals born over the most recent 6-year period, regardless of their genotyping status. For STAY12, Data_e included cows born between 2015 and 2020; for STAY13 and STAY23, cows born from 2014 to 2019; for STAY34, cows born from 2013 to 2018; and for STAY14, cows born from 2012 to 2017. These ranges were based on the available information at the time of data collection for the analyses. Phenotypic records were available through 2022, the most recent year with complete data; to avoid censoring bias, information up to the end of this year was included in the analyses. The dataset Data_g was used to compare different inbreeding measurement methods, and Data_e was employed to better represent the studied population. This approach was used to address the potential bias that genotype data might overrepresent elite individuals, as the dataset comprising only genotyped animals may not be randomly selected from the population. Because breeders decide which animals to genotype, their preferences influence this selection process, subsequently affecting the chances of these animals remaining or leaving the herd. For all traits, and both datasets, cows were retained for further analyses when their year at first calving was consistent with their year of birth (less than 36 mo). Also, for each trait, only cows with at least 4 equivalent complete generations of pedigree information were retained. Contemporary groups were defined according to the herd and year of calving.

For Data_e, we included animals from contemporary groups comprising a minimum of 10, a maximum of 712, and an average of 45.1 cows, with each cow being daughter of one of at least 2 different sires within the group. Additionally, sires were required to have at least 3 daughters across 2 different herds.

Pedigree pruning was conducted, retaining only animals with phenotypes and ancestors of the animals with phenotypes. This process resulted in information reaching the base year of 1973 and up to 18 maximum generations for the phenotyped cows. The pedigree depth ranged from 4.0 to 11.53 equivalent complete generations, with average 7.95 ± 1.20. Table 1 shows the number of records after consistency checks and filtering, the number of animals in the pedigree after pruning, and average rates of success, calculated as the number of animals that remained alive divided by the total number of animals with valid observations for each trait in both datasets.

Statistical Analyses

Variance and covariance components and fixed effects were estimated under a Bayesian framework using thrgibbs1f90 software, part of the BLUPF90 programs family (Misztal et al., 2022). A total of 130,000 Markov chain Monte Carlo iterations were conducted in each analysis with a burn-in of 30,000 and a thinning interval of 20 iterations. Convergence was assessed by visual inspection of trace plots. Burn-in was increased in some cases to secure the use of estimates only after full convergence.

The first model (**M1**), included the inbreeding covariate, along with a general intercept, as the only fixed effect, described as follows:

$$\mathbf{y} = \mathbf{1}\beta_0 + \mathbf{F}\boldsymbol{\beta}_1 + \mathbf{Z}_1\mathbf{hy} + \mathbf{Z}_2\mathbf{a} + \mathbf{e},$$

where **y** is a vector of pseudo-observations of stayability (meaning normally distributed continuous values on the underlying scale, derived from the original binary scale of the trait) representing STAY12, STAY23, STAY34, STAY13, and STAY14; **1** is a column vector of ones, and

Table 2. Basic statistics of the inbreeding measures on both datasets, considering the original scales of each measure (F_{PED}, F_{GRM}, or F_{ROH}), before rescaling all to F_{PED} scale

Dataset	Inbreeding measure	Mean	SD	Minimum	Maximum
Data_e	F_{PED}	3.832	1.995	0.000	41.110
Data_g	F_{PED}	5.030	2.093	0.000	29.830
	F_{GRM}	27.533	2.847	1.960	57.070
	F_{ROH_GENOME}	0.166	0.034	0.028	0.493

β_0 represents the intercept; **F** is a matrix of 6 coefficients for each animal in the case where F_{ROH_CLASS} is the inbreeding measure, but it is a vector containing only the inbreeding coefficient of each animal for all other measures (F_{PED}, F_{GRM}, or F_{ROH_GENOME}); β_1 represents the regression coefficient for each measure of inbreeding; $\mathbf{Z_1}$ is the incidence matrix relating records to the herd-year (**hy**) random effects, assumed $\text{hy} \sim N\left(0, \sigma^2_{hy}\mathbf{I}\right)$; $\mathbf{Z_2}$ is the incidence matrix relating records to the additive genetic effects (**a**), assumed $\mathbf{a} \sim N\left(0, \sigma^2_{\mathbf{a}}\mathbf{A}\right)$, with **A** being the additive genetic relationship matrix, obtained from pedigree information constructed while ignoring inbreeding; $\mathbf{e} \sim N(0, \mathbf{I})$ is the vector of residuals, with variance $\left(\sigma^2_e\right)$ fixed at 1.0, as suggested by (Gianola and Foulley, 1983). **I** is an identity matrix of appropriate order.

The second model (**M2**), extended M1 by including a fixed effect of deviation in milk production (**DMY**) per lactation for each cow relative to its contemporary group, categorized into 9 classes. The DMY was calculated in 2 steps: first, each milk record was standardized as the number of standard deviations above or below the mean of its contemporary group, termed standardized production (**SP**). Then, these SP values were classified into 9 DMY categories to account for potential farmer decisions to cull less-productive animals within their herds. These DMY categories were coded as illustrated in Figure 1.

In the dataset, the 9 DMY categories were included as separate columns, with each observation having a 1 in the column corresponding to its category and 0 in the others. One category (category 5) was omitted to serve as the reference group and be absorbed by the intercept. This approach resulted in 8 binary variables for DMY.

M2 was defined as

$$\mathbf{y} = \mathbf{1}\beta_0 + \mathbf{F}\beta_1 + \mathbf{X}\boldsymbol{\beta}_2 + \mathbf{Z}_1\mathbf{hys} + \mathbf{Z}_2\mathbf{a} + \mathbf{e},$$

where **X** is the incidence matrix associating each observation to its respective category of DMY in the lactation corresponding to the beginning of the period (i.e., first lactation for STAY12, STAY13, and STAY14, second lactation for STAY23, and third lactation for STAY34). Only 8 binary columns are included, as the reference category was omitted. $\boldsymbol{\beta}_2$ is the vector of fixed effects corresponding to the included DMY categories, and all other effects are as previously described for M1.

In both cases, the variance-covariance of the random effects was as follows:

$$\begin{bmatrix} \mathbf{hy} \\ \mathbf{a} \\ \mathbf{e} \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma^2_{hy}\mathbf{I} & 0 & 0 \\ 0 & \sigma^2_a\mathbf{A} & 0 \\ 0 & 0 & 1 \end{bmatrix}\right),$$

where σ^2_{hy} is the variance of hy, σ^2_a is the additive genetic variance on the underlying scale; and the residual variance was fixed at 1.

The study applied M1 and M2 models to 5 traits using different inbreeding estimates. For Data_g, 4 estimates (F_{PED}, F_{GRM}, F_{ROH_GENOME}, and F_{ROH_CLASS}) were used, but only F_{PED} was available for Data_e. This resulted in 8 analyses per trait with Data_g and 2 per trait with Data_e.

Best linear unbiased estimates of the intercept and inbreeding slopes were used to estimate stayability across different inbreeding levels on the liability scale. These estimates were then converted to the probability scale using the pnorm function in R 4.3.2 (R Foundation for Statistical Computing, Vienna, Austria), following Hidalgo et al. (2024), who applied similar transformations for GEBV conversions. Predicted values were derived from regression equations based on fixed effects solutions at each iteration, using the formula $P_i = \Phi(p_i)$, where P_i is the stayability probability, Φ is the standard normal cumulative distribution function, and p_i is the stayability on the liability scale. For F_{ROH_CLASS}, the sum of effects across the 6 inbreeding classes was used to estimate expected stayability. This process yielded 5,000 predictions of stayability for each inbreeding level in the population.

Slopes for inbreeding depression were obtained from linear regression of the predicted stayability values on the probability scale against different levels of inbreeding. Extremes were defined as animals below the 10th percentile and those above the 90th percentile regarding inbreeding levels. Differences between the stayability predicted for the extremes were obtained from the mean values predicted for the average inbreeding values of those groups at each analysis, with different

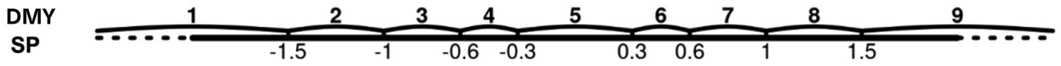

Figure 1. Categorization of DMY (deviation in milk yield) according to SP (standardized production), which is the number of standard deviations of each lactation yield above or below average within its contemporary group.

combinations of model, dataset, method of inbreeding estimation, and trait.

RESULTS

Inbreeding Measures

Table 2 presents summary statistics of inbreeding coefficients in their original scales for both datasets. In Data_g, the correlations were 0.666 between F_{PED} and F_{GRM}, 0.686 between F_{PED} and F_{ROH_GENOME}, and 0.958 between F_{GRM} and F_{ROH_GENOME}. Frequency distributions are shown in Supplemental Figure S1 (see Notes).

The population trend of average inbreeding levels, based on cows in the STAY12 analysis of Data_e, is depicted in Figure 2.

Variance Components

Variance proportions attributable to the random HY effect and additive genetic effect (h^2) are shown in Table 3. Using F_{PED} as the inbreeding measure, results for the 5 traits across both datasets and models are presented. Variance components and proportions derived from genomic inbreeding measures were very similar to those obtained with pedigree inbreeding; therefore, these results are provided in Supplemental Table S1 (see Notes) and are not included in the main text.

Inbreeding Depression in the Italian Population

Figures 3 and 4 display the expected stayability in the Italian Holstein population, estimated with Data_e, and using the pedigree inbreeding measure. The slopes of F_{PED} were significantly negative across all traits, indicating a consistent decline in stayability probabilities with increasing inbreeding levels. Figures 3a, 3b, and 3c show inbreeding depression for STAY12, STAY23, and STAY34, which cover periods of a single calving interval. The depression estimated for the most inbred animals ranged from 3% (STAY34, M2) to 12% (STAY23, M1). Conversely, Figures 4a and 4b illustrate stronger inbreeding depression for STAY13 and STAY14 (~14% for M2 and ~18% for M1), traits spanning longer periods beyond 1 calving interval.

Comparison Between Inbreeding Measures

Figures 5 and 6 show the overall trend in stayability according to inbreeding in Data_g, including both pedigree-based and genomic inbreeding measures (F_{PED}, F_{GRM}, and F_{ROH_GENOME}). Estimates for the slopes were significantly different from zero and negative in every case. Figures 5a, 5b, and 5c represent the inbreeding depression observed for STAY12, STAY23, and STAY34, respectively, whereas Figures 6a and 6b represent the inbreeding depression for STAY13 and STAY14, respectively. The depression estimated for the most inbred animals ranged from 5%, in the case of the effect of F_{PED} on STAY12, to values ~35% to 40% in the cases of the effects of genomic inbreeding on STAY13 and STAY14. Only results from model M1 are shown in Figures 5 and 6, to focus on differences among inbreeding measures rather than between models. Results from model M2, which included milk production level with Data_g, are omitted from the figures but are included in the table

Table 3. Posterior means and SE of the variance proportions estimated for the random effects HY and additive genetic (h^2), obtained on the underlying scale

		M1 model		M2 model	
Trait	Dataset	HY ± SE	h^2 ± SE	HY ± SE	h^2 ± SE
STAY12	Data_g	0.139 ± 0.009	0.077 ± 0.012	0.175 ± 0.010	0.081 ± 0.014
	Data_e	0.118 ± 0.002	0.047 ± 0.002	0.157 ± 0.002	0.050 ± 0.003
STAY23	Data_g	0.155 ± 0.011	0.056 ± 0.011	0.164 ± 0.013	0.060 ± 0.014
	Data_e	0.090 ± 0.002	0.053 ± 0.003	0.124 ± 0.002	0.056 ± 0.004
STAY34	Data_g	0.165 ± 0.015	0.089 ± 0.022	0.191 ± 0.017	0.088 ± 0.021
	Data_e	0.076 ± 0.002	0.059 ± 0.003	0.113 ± 0.002	0.061 ± 0.003
STAY13	Data_g	0.202 ± 0.011	0.108 ± 0.016	0.201 ± 0.011	0.109 ± 0.012
	Data_e	0.134 ± 0.002	0.071 ± 0.003	0.143 ± 0.002	0.071 ± 0.003
STAY14	Data_g	0.265 ± 0.015	0.133 ± 0.020	0.261 ± 0.016	0.125 ± 0.018
	Data_e	0.120 ± 0.002	0.115 ± 0.005	0.123 ± 0.002	0.110 ± 0.005

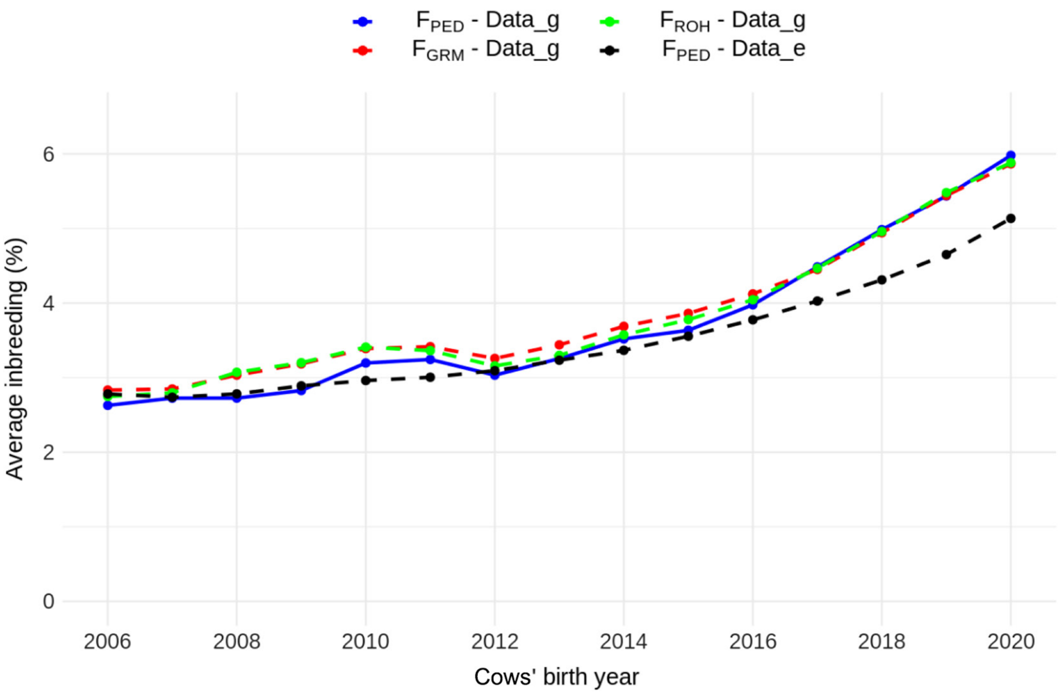

Figure 2. Trends of average inbreeding according to birth year for the Italian Holstein cows. Pedigree-based (F_{PED}) and genomic inbreeding measures (F_{GRM} and F_{ROH}) were used in the dataset of genotyped cows (Data_g), and pedigree-based inbreeding (F_{PED}) was used for the expanded dataset (Data_e).

described in the next paragraph, because they reveal inbreeding effects that lead to the same conclusions already apparent from Data_e.

Values and SD for the estimated slopes of the regressions of inbreeding on each of the 5 stayability traits are presented in Table 4. These values are in the probability scale and allow comparison between datasets, between models, and among inbreeding measures. Each slope indicates the expected percentage change in the probability of cows remaining in the herd, according to an increase of 1 unit in the inbreeding coefficient. Every value was significantly different from zero, indicating that inbreeding depression was significant in every case. The pedigree inbreeding scale was considered for all inbreeding measures.

Figures 7 and 8 illustrate the probability of success for STAY12, from the analyses using F_{ROH_CLASS}, with the M1 model and with the M2 model, respectively. Differences between the 2 different models, without or with the DMY effect, can be observed by comparison between Figures 7 and 8. The slopes are in the original scale of the ROH inbreeding, representing the expected change in the probability of cows staying in the herd, according to an increase of 1.00 (100%) in the ROH proportion in the genome. In the case of STAY12, illustrated in Figures 7 and 8, the depression estimated for the most inbred animals was ~11% for M1 and ~7% for M2.

Supplemental Figures S2, S3, S4, S5, S6, S7, S8, and S9 (see Notes) illustrate the results from the analyses using F_{ROH_CLASS} (both models) for STAY23, STAY34, STAY13, and STAY14.

Assessing the Impacts of Realized Inbreeding

Table 5 compares predicted stayability between the 10% least inbred and 10% most inbred animals, using both datasets (Data_g and Data_e), different inbreeding measures (F_{PED}, F_{GRM}, F_{ROH_GENOME}, F_{ROH_CLASS}), and models (M1 and M2). For F_{ROH_CLASS}, the sum of all 6 classes was used. The differences in predicted stayability were substantial, reaching ~10% for STAY13 and STAY14.

Table 6 shows the expected differences in STAY12 between extremes of inbreeding levels for each of the 6 classes separately. Additional results for STAY23, STAY34, STAY13, and STAY14 are provided in Supplemental Table S2 (see Notes).

Inbreeding, Genetic, and Phenotypic Trends

In the dataset used for the STAY12 analysis, the average F_{PED} by year of birth increased from 3.56% for cows born in 2015 to 5.00% for those born in 2020. Over the same period, predicted breeding values for these cows

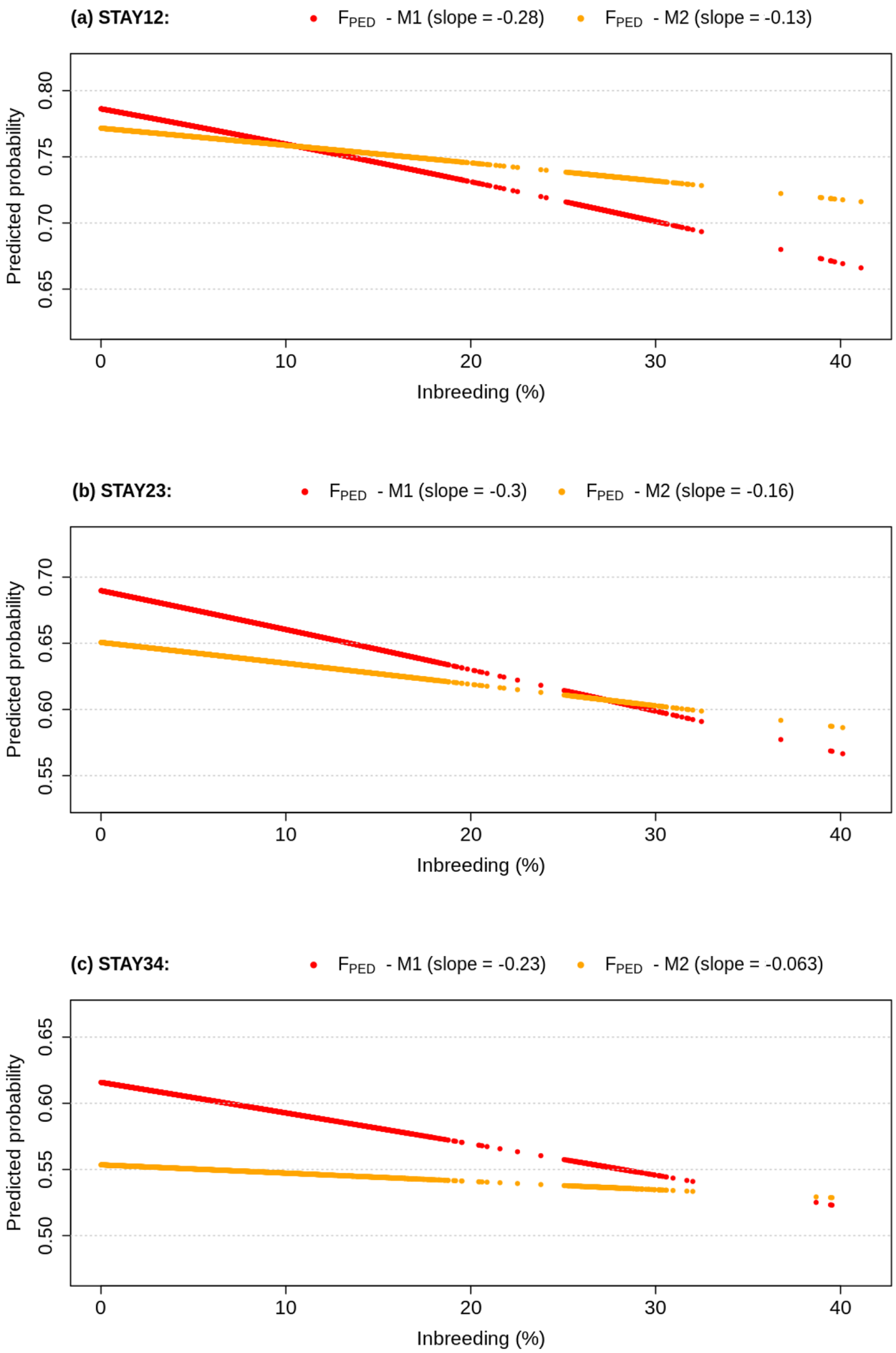

Figure 3. Probability of survival predicted for the Italian Holstein population, according to the inbreeding estimated from pedigree (F_{PED}) on (a) STAY12, (b) STAY23, and (c) STAY34.

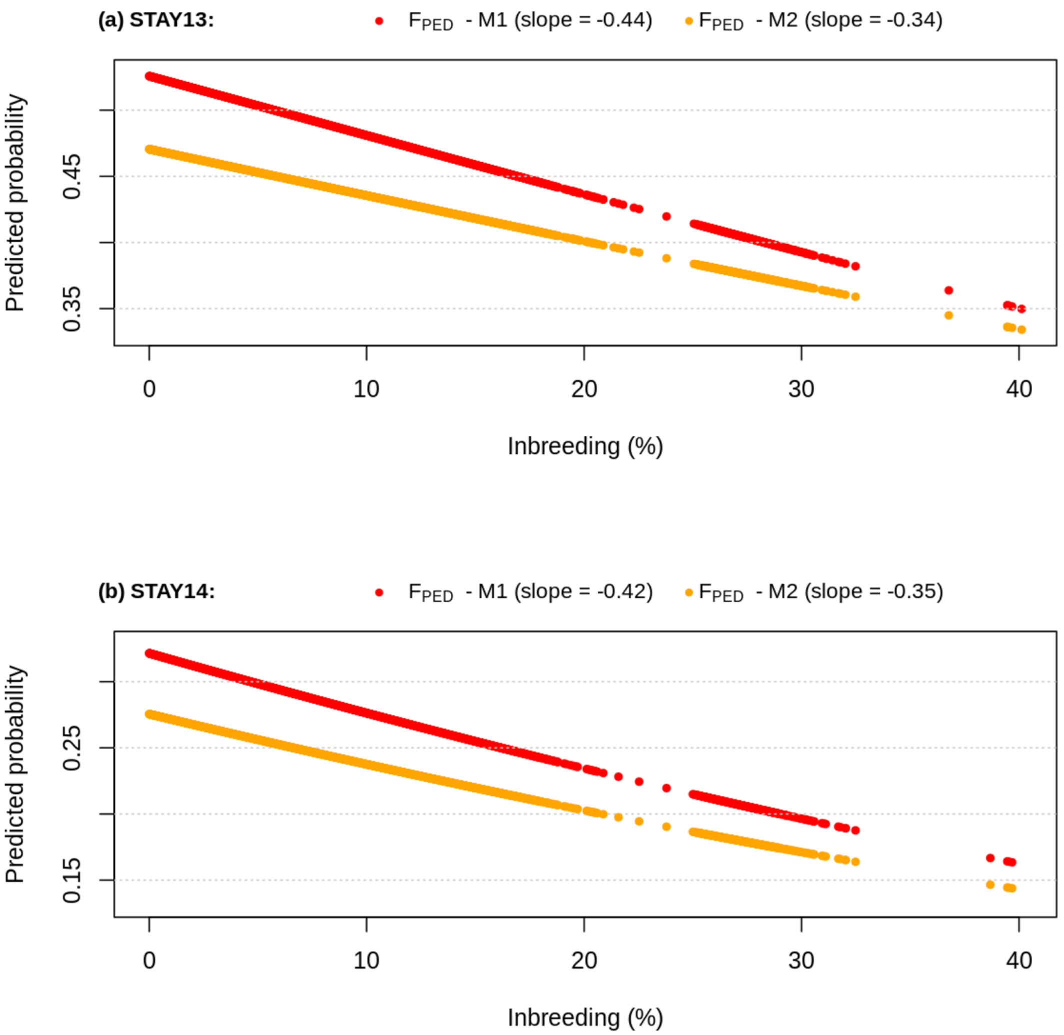

Figure 4. Probability of survival predicted for the Italian Holstein population, according to the inbreeding estimated from pedigree (F_{PED}) on (a) STAY13 and (b) STAY14.

increased by 3.6%, whereas their realized phenotypes increased by only 0.9%. Figure 9 displays the average estimated breeding values by year of birth, alongside the average survival rates of these cows for STAY12. Such trends were similar for STAY23 and STAY34 in the population, and are presented in supplemental Figures S10 and S11 (see Notes).

DISCUSSION

This study examined inbreeding depression on stayability, focusing on the type of inbreeding measure and the statistical models used. The genotyped cow dataset Data_g enabled comparison among different inbreeding measures, whereas Data_e was used to estimate the effect of inbreeding on the stayability of Italian Holstein cows. Results indicated that cows with milk production below the average of their contemporary groups had lower stayability, and incorporating a fixed effect for this factor also altered the prediction of inbreeding depression.

Comparison Between Datasets

Because breeders selected which animals to genotype and not all breeders participated, Data_g comprised a subset of herds and animals. As shown in the Results section, this led to consistently higher success rates in stayability for Data_g compared with Data_e. Specifically, for traits covering a single calving interval, success rates in Data_g were 5.73% higher for STAY12, 7.13% higher for STAY23, and 8.25% higher for STAY34. For traits involving longer periods, the differences between datasets were even more pronounced, with success rates in Data_g being 11.45% and 13.94% higher than those

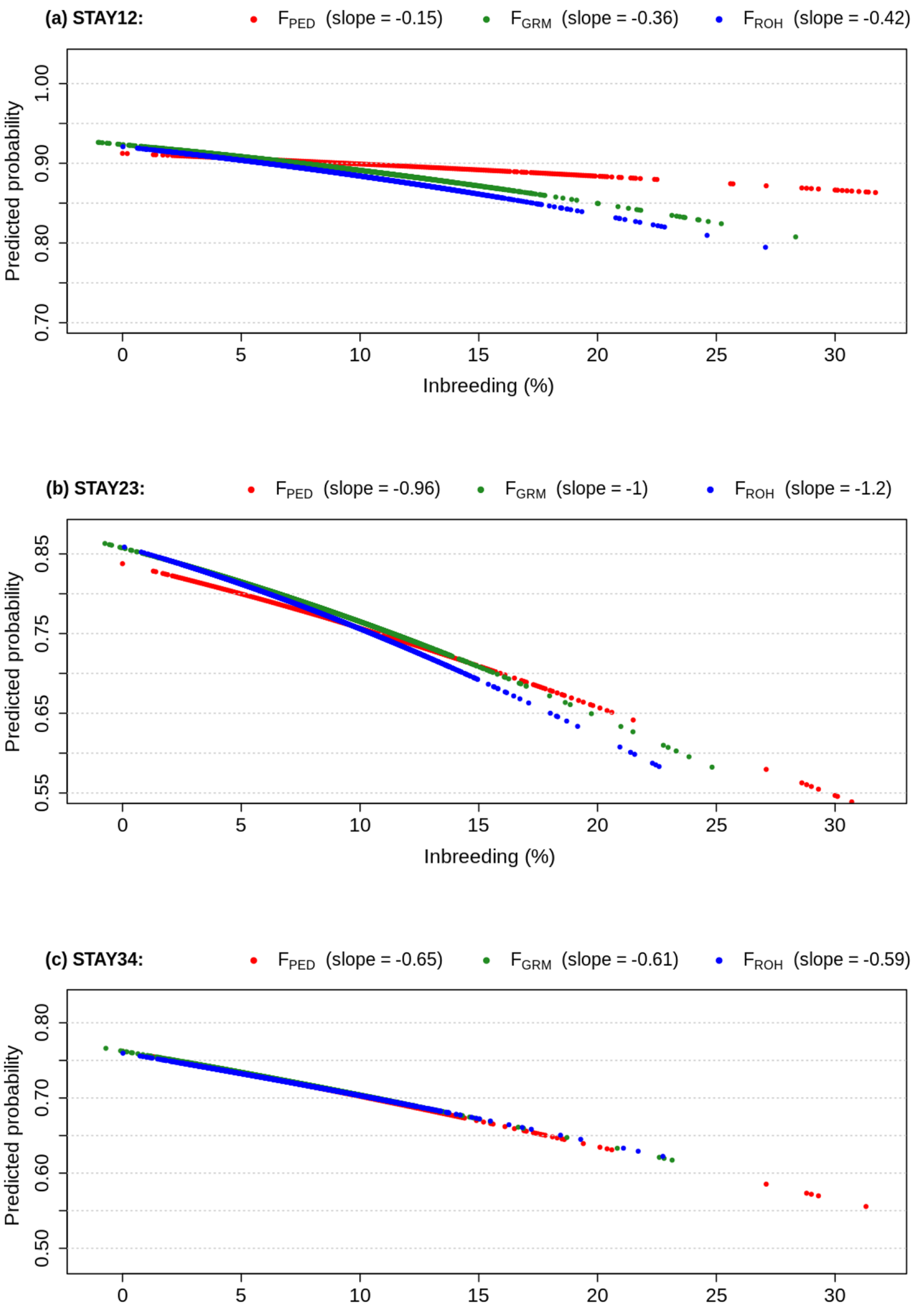

Figure 5. Probability of survival predicted for the Italian Holstein population, using the datafiles of genotyped cows (Data_g), according to the inbreeding estimated from either pedigree or genotypes, using the M1 model and expressed on the pedigree inbreeding scale on (a) STAY12, (b) STAY23, and (c) STAY34.

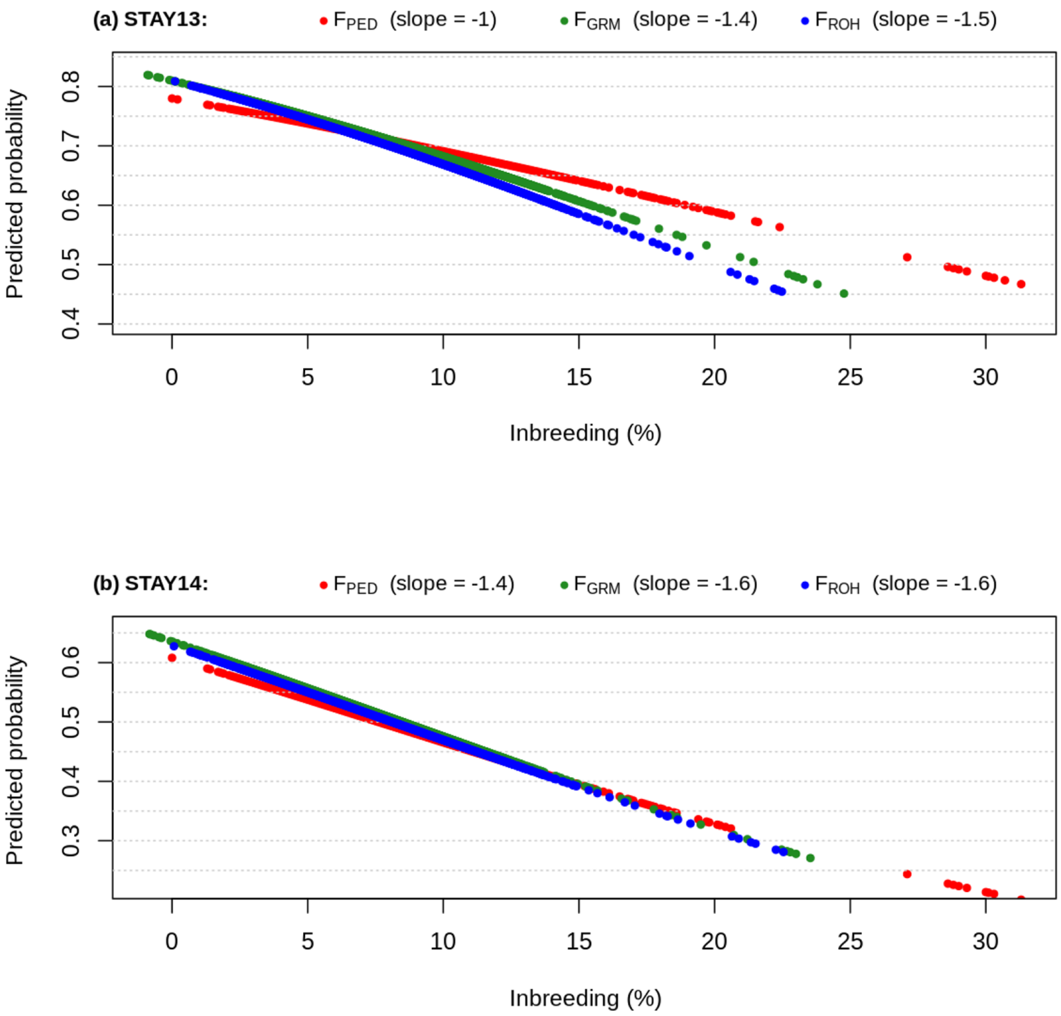

Figure 6. Probability of survival predicted for the Italian Holstein population, using the datafiles of genotyped cows (Data_g), according to the inbreeding estimated from either pedigree or genotypes, using the M1 model and expressed on the pedigree inbreeding scale on (a) STAY13 and (b) STAY14.

in Data_e, for STAY13 and STAY14, respectively. These differences support our earlier assumption that breeders prioritized genotyping animals of their preference, which were naturally more likely to be retained in their herds.

Variance proportions also differed between datasets, possibly because only a selected group of herds were included in Data_g. Heritability coefficients were higher in Data_g for all traits except for STAY23. In contrast, Data_e included a larger number of herds and animals, more indicative of the Italian Holstein population. Also, in our results, Data_g presented higher average inbreeding than Data_e. These differences in variance proportions and inbreeding levels highlight the importance of using Data_e to better understand the expected outcomes of selection practices in the Italian population. Meanwhile, results from the genotyped cow dataset proved useful for comparing the effectiveness of various inbreeding measures in capturing inbreeding depression.

Inbreeding depression slopes obtained with the M2 model were generally ~70% of the values obtained with the M1 model in the case of Data_g, and 47% in the case of Data_e, where animals were not previously selected. A plausible biological explanation is that milk yield played a larger role in determining culling decisions in the overall population than in the genotyped subset, as less productive animals were likely excluded from genotyping lists.

Comparison Between Models

Variance Components and Heritability Estimates. As a general observation, heritability estimates for stayability ranged from low to moderate values (0.047 to 0.133).

Table 4. Estimates of regression slopes (± SD) of inbreeding on STAY12, STAY23, STAY34, STAY13 or STAY14, obtained using both models and different methods of inbreeding measure[1]

			Slope ± SD (%)	
Trait	Dataset	Method of inbreeding measure	M1 model	M2 model
STAY12	Data_g	F_{GRM}	−0.3650 ± 0.0008	−0.2179 ± 0.0003
		F_{ROH_GENOME}	−0.4189 ± 0.0009	−0.2783 ± 0.0003
		F_{PED}	−0.1529 ± 0.0007	−0.1256 ± 0.0004
	Data_e	F_{PED}	−0.2847 ± 0.0002	−0.1330 ± 0.0000
STAY23	Data_g	F_{GRM}	−1.0285 ± 0.0022	−0.7711 ± 0.0008
		F_{ROH_GENOME}	−1.1564 ± 0.0023	−0.9675 ± 0.0011
		F_{PED}	−0.9638 ± 0.0054	−0.7688 ± 0.0024
	Data_e	F_{PED}	−0.3035 ± 0.0001	−0.1594 ± 0.0000
STAY34	Data_g	F_{GRM}	−0.6070 ± 0.0006	−0.3065 ± 0.0001
		F_{ROH_GENOME}	−0.5867 ± 0.0005	−0.3449 ± 0.0001
		F_{PED}	−0.6530 ± 0.0020	−0.5665 ± 0.0006
	Data_e	F_{PED}	−0.2335 ± 0.0000	−0.0627 ± 0.0000
STAY13	Data_g	F_{GRM}	−1.3934 ± 0.0022	−1.3701 ± 0.0014
		F_{ROH_GENOME}	−1.5459 ± 0.0022	−1.5329 ± 0.0013
		F_{PED}	−0.9981 ± 0.0032	−1.0047 ± 0.0018
	Data_e	F_{PED}	−0.4441 ± 0.0001	−0.3445 ± 0.0001
STAY14	Data_g	F_{GRM}	−1.6070 ± 0.0008	−1.5682 ± 0.0013
		F_{ROH_GENOME}	−1.5950 ± 0.0007	−1.5453 ± 0.0011
		F_{PED}	−1.3507 ± 0.0055	−1.3051 ± 0.0074
	Data_e	F_{PED}	−0.4173 ± 0.0003	−0.3480 ± 0.0003

[1] Estimates are on the probability scale and refer to 1-unit change in the inbreeding coefficients.

This information suggests that genetic selection for those traits is possible but would achieve slow progress. Longer-term stayability traits showed increased values of heritability, namely STAY13 and STAY14 in our study. Regarding the comparison between models, the proportion of variance explained by the HY effect was bigger in the M2 model, where the dairy cows' production level relative to their contemporary groups was included as a fixed effect. This was true in the cases of STAY12, STAY23, and STAY34, where the involved periods of survival were shorter, and consequently the DMY considered was from the immediately preceding lactation. Those results indicate better adjustment of the M2 model compared with the M1 model. No significant differences in heritability estimates were observed between the M1 and M2 models. Similarly, Hardie et al. (2021) reported heritability coefficients between 0.07 and 0.15 in a selected population of organic Holsteins in the United States, which closely aligns with our findings.

Inbreeding Depression Slopes. For STAY12, STAY23, and STAY34, the effects of inbreeding depression were smaller for the M2 model compared with the M1 model. However, this trend was not observed for STAY13 and STAY14, in which accounting for production level did not significantly affect expected inbreeding depression. Slope values from the M2 model for STAY12, STAY23, and STAY34 were consistently lower, ranging from 27% to 53% of M1 estimates, indicating that the inbreeding depression detected with M1 may partly reflect voluntary culling practices targeting lower-producing cows within herds. Statistical expectations support this, as cows with DMY levels 1 to 4, representing the poorest milk yields within their groups, had significantly lower probabilities of remaining in the herd. Including production level in analyzing STAY13 and STAY14 had minimal influence on inbreeding effects, likely because the production measure was only from the first lactation, exerting a less pronounced influence on traits spanning multiple lactations. Because inbreeding can reduce milk production (Ablondi et al., 2023), incorporating the DMY effect in models (M2) provides an adjustment for milk yield, making inbreeding depression estimates less confounded. Consequently, inbreeding depression appears higher in the M1 model because it partly captures the influence of inbreeding on milk production. Correcting stayability breeding values for milk yield effects prevents double-counting of inbreeding effects within selection indexes that include milk yield, thereby enabling selection to improve stayability independently of milk production. Such an approach (the use of model M2) may represent an appropriate strategy for dairy breeding programs aiming to improve stayability.

Comparison Between Extremes. Our results comparing predictions for extreme inbreeding levels clearly showed that part of the inbreeding depression observed with the M1 model was related to animals' production levels within their herds, supporting the earlier slope analyses. The differences between the inbred extremes were notably smaller with the M2 model, which captured 48%, 54%, 27%, 78%, and 84% of the inbreed-

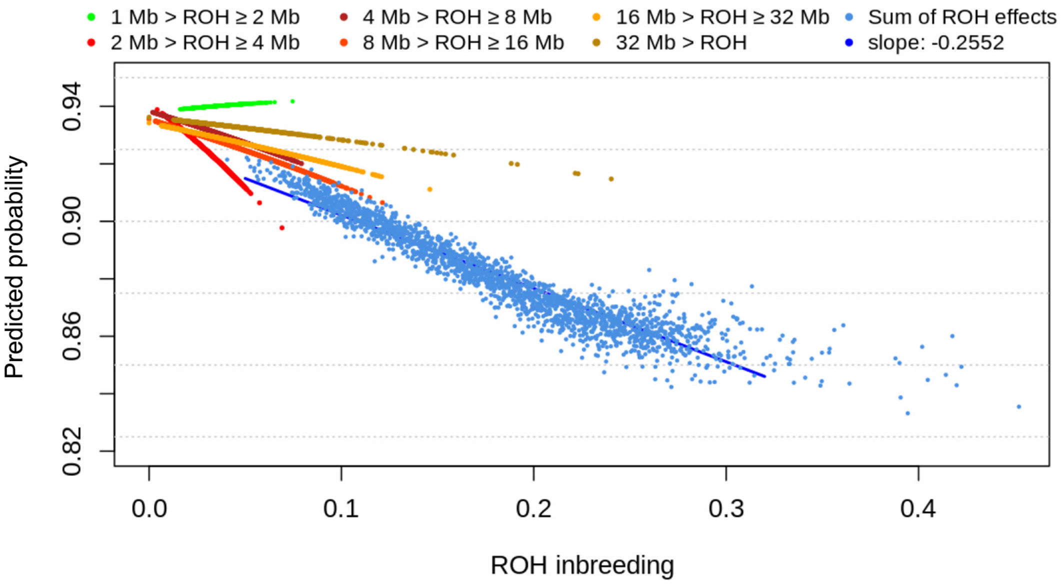

Figure 7. Probability of survival on STAY12 predicted for the Italian Holstein population, using Data_g, according to the level of inbreeding estimated from ROH separated into classes. Lines of different colors illustrate the effects of inbreeding estimated from ROH segments of different sizes: green, red, dark red, light red, orange and brown, from the shorter to the longer segments. Blue dots represent the sum of the estimated effects of the 6 classes, and the blue line represents the linear regression of these points (M1 model).

ing depression detected by M1 for STAY12, STAY23, STAY34, STAY13, and STAY14, respectively, when using Data_e. Because the production level considered was from the lactation before the period evaluated, the effect of inbreeding depression linked to productivity was more prominent in short-term stayability traits such as STAY12, STAY23, and STAY34.

Inbreeding Depression and Inbreeding Measures

Previous studies on the Italian Holstein population by Ablondi et al. (2023) examined inbreeding depression for traits such as milk yield, fat yield, and protein yield, and reported significant effects. They found a correlation of 0.65 between genomic and pedigree inbreeding, similar to the value observed in the present study.

In our analyses, for all 5 traits considered, an increase in inbreeding consistently resulted in a decrease in stayability. All estimated slopes were negative, indicating that higher inbreeding levels were associated with reduced stayability success. We observed a consistent trend of inbreeding-induced depression in the Italian Holstein cows' stayability. For context, McParland et al. (2007) estimated a 0.3% decrease in the chances of survival from the first to the second calving per 1-unit increase in the inbreeding coefficients of Irish Holsteins. Similarly, Doekes et al. (2021), in a meta-analysis of 154 livestock studies, reported an average inbreeding depression of ~0.302% per 1-unit increase in F_{PED} within the category of reproduction and survival traits.

In our study, when expressed as a percentage of the trait mean, the estimated inbreeding depression resulting from a 1-unit increase in the inbreeding coefficients ranged from −0.094% (STAY34 on Data_e, M2 model, F_{PED}) to −3.759% (STAY14 on Data_g, M1 model, F_{GRM}). These results align with findings in the literature, but we detected slightly larger effects for certain traits, especially those representing cumulative stayability periods such as STAY13 and STAY14. McParland et al. (2007) previously found that inbreeding depression in longevity becomes more pronounced as animals age, likely due to the accumulation of deleterious alleles affecting survival and reproduction.

Comparison Between Pedigree and Genomic Measures. The objective was to demonstrate the ability of different inbreeding measures to capture the effects of inbreeding depression on stayability.

For STAY12, the most negative inbreeding slope was observed using the M1 model with F_{ROH_GENOME} as the inbreeding measure, indicating an estimated 0.42% decline in stayability per 1-unit increase in the inbreeding coefficient. In both models, slopes derived from genomic inbreeding measures were notably more negative than those from pedigree inbreeding.

Regarding STAY23, the largest inbreeding depression slopes in our study were among the traits analyzed between 2 consecutive calvings, with F_{ROH_GENOME} producing the most negative value, an expected decrease of 1.16% per 1-unit increase in the inbreeding coefficient in the M1 model. The slope from F_{GRM} was slightly more negative than that from F_{PED} for STAY23, aligning

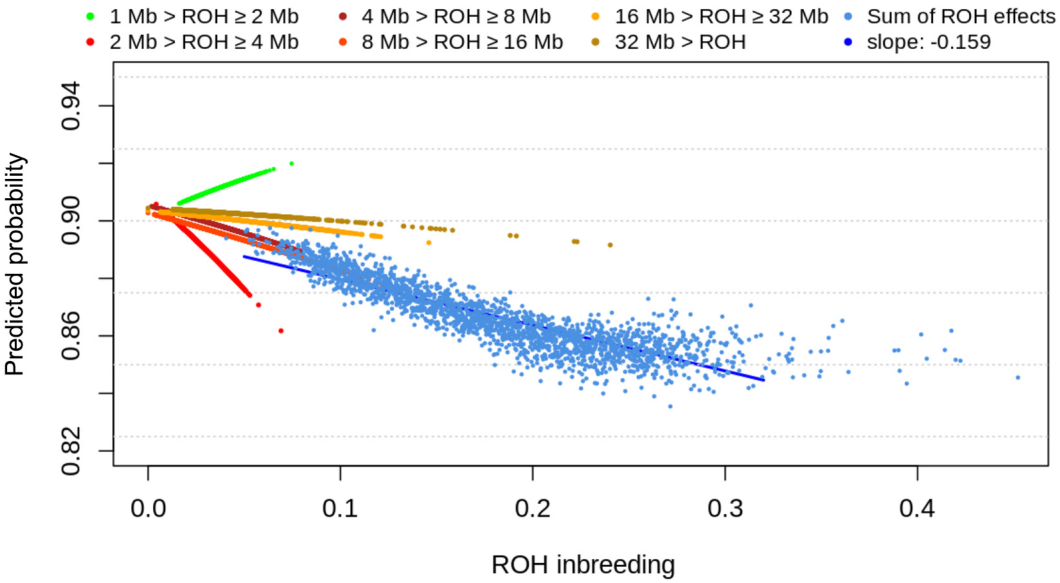

Figure 8. Probability of survival on STAY12 predicted for the Italian Holstein population, using Data_g, according to the level of inbreeding estimated from ROH separated into classes. Lines of different colors illustrate the effects of inbreeding estimated from ROH segments of different sizes: green, red, dark red, light red, orange and brown, from the shorter to the longer segments. Blue dots represent the sum of the estimated effects of the 6 classes, and the blue line represents the linear regression of these points (M2 model).

with prior research indicating that F_{ROH} most effectively captures inbreeding depression across traits (Keller et al., 2011; Wang, 2016).

The absolute slope values were smaller for STAY34 compared with STAY23, suggesting a reduced influence of inbreeding on stayability between the third and fourth calving. One explanation is that animals assessed for this trait were mainly those successful in prior stayability traits, likely having experienced early losses due to inbreeding depression already leading to earlier culling. No significant differences among inbreeding measures were observed for STAY34.

Both STAY13 and STAY14 involve longer evaluation periods—from the first to the third calving and from the first to the fourth calving, respectively. The use of genomic measures resulted in more pronounced inbreeding effects for STAY13, but no difference was observed among inbreeding measures for STAY14.

The comparison of predicted stayability between the 10% most and least inbred cows supported the slope analyses, providing a clearer picture of inbreeding depression at the population level by considering the actual distribution of inbreeding levels. Consistent with earlier findings, models incorporating genomic inbreeding captured larger effects. Notably, the differences in inbreeding depression were more substantial when using F_{ROH_GENOME} or F_{ROH_CLASS} compared with F_{GRM}, except for traits evaluated after the third calving (STAY14 and STAY34), where differences between the 2 genomic measures were not significant.

In modern dairy breeding programs, which largely rely on genomic selection, the availability of genomic information enables the use of genomic inbreeding measures as a powerful tool to prevent future inbreeding depression on the population (Clark et al., 2013; Makanjuola et al., 2020b).

Segment Sizes for F_{ROH} Inbreeding. Short ROH segments (<2 Mb) were associated with increased stayability in STAY12, suggesting these segments, likely resulting from ancient inbreeding, are linked to the purging of deleterious alleles rather than causing inbreeding depression. These results are consistent with previous findings from Makanjuola et al. (2020a), who suggested that ancestral inbreeding could have had favorable effects, as well as with the study of Tenhunen et al. (2025), which reported a positive effect of short ROH segments on survival.

Conversely, intermediate-sized to longer ROH segments (2–32 Mb), associated with more recent inbreeding, had significant effects on estimates based on F_{ROH_CLASS}, especially for STAY12, STAY23, and STAY13, with the largest effects observed for classes from 2 to 16 Mb. In a previous study on the American Holstein breed, Lozada-Soto et al. (2024) similarly found detrimental effects of recent inbreeding, in that case on reproductive diseases. They found the same pattern of older inbreeding not negatively influencing performance. Although this pattern was less clear for STAY34 and STAY14, likely due to smaller sample sizes, larger effects generally persisted in these classes. The analysis of the sums of ROH segments and their regressions for STAY12 revealed similar

Table 5. Performance advantage of the 10% least inbred compared with the 10% most inbred dairy cows on the expected stayability, using different inbreeding measures and models

Trait	Dataset	Inbreeding measure	M1 model, difference ± SD (%)	M2 model, difference ± SD (%)
STAY12	Data_g	F_{PED}	2.362 ± 0.017	1.443 ± 0.032
		F_{GRM}	2.774 ± 0.014	1.879 ± 0.021
		F_{ROH_GENOME}	2.377 ± 0.016	1.102 ± 0.028
		F_{ROH_CLASS}	0.931 ± 0.018	0.779 ± 0.033
	Data_e	F_{PED}	1.879 ± 0.012	0.908 ± 0.013
STAY23	Data_g	F_{PED}	6.250 ± 0.029	4.776 ± 0.034
		F_{GRM}	7.197 ± 0.029	6.133 ± 0.035
		F_{ROH_GENOME}	9.078 ± 0.026	7.408 ± 0.032
		F_{ROH_CLASS}	5.431 ± 0.040	4.552 ± 0.036
	Data_e	F_{PED}	1.940 ± 0.007	1.039 ± 0.019
STAY34	Data_g	F_{PED}	3.551 ± 0.052	1.808 ± 0.052
		F_{GRM}	3.573 ± 0.053	2.116 ± 0.053
		F_{ROH_GENOME}	3.465 ± 0.049	0.992 ± 0.059
		F_{ROH_CLASS}	3.654 ± 0.091	3.283 ± 0.055
	Data_e	F_{PED}	1.453 ± 0.013	0.395 ± 0.022
STAY13	Data_g	F_{PED}	8.592 ± 0.040	8.541 ± 0.060
		F_{GRM}	9.763 ± 0.041	9.786 ± 0.060
		F_{ROH_GENOME}	9.999 ± 0.056	9.677 ± 0.045
		F_{ROH_CLASS}	5.770 ± 0.043	5.996 ± 0.063
	Data_e	F_{PED}	3.007 ± 0.018	2.353 ± 0.017
STAY14	Data_g	F_{PED}	9.659 ± 0.075	9.494 ± 0.056
		F_{GRM}	9.924 ± 0.075	9.681 ± 0.056
		F_{ROH_GENOME}	9.440 ± 0.081	8.962 ± 0.059
		F_{ROH_CLASS}	8.480 ± 0.078	8.445 ± 0.057
	Data_e	F_{PED}	2.857 ± 0.013	2.399 ± 0.015

trends for models M1 and M2, consistent with the other genomic inbreeding measures for this trait.

Overall, genomic measures, particularly the proportions of ROH segments longer than 2 Mb, proved more effective in capturing inbreeding depression. Incorporating this approach could benefit dairy breeding programs by helping to optimize selection strategies that balance achieving genetic progress while minimizing the risks of inbreeding depression.

Genetic and Inbreeding Trends

In the Italian Holstein population, inbreeding levels increased over time among cows with stayability records born between 2006 and 2020, with a sharper rise after 2015 coinciding with the increased use of genomic selection. For cows born after 2015, their genetic values for STAY12 tended to improve at an average rate of ~0.6% per year. Notably, phenotypic values for the same animals did not follow this trend. Similar genetic gains of ~0.6% annually were observed for STAY23 and STAY34 based on recent phenotypic data. Meanwhile, the average inbreeding coefficient increased by ~0.3% per year over the same period. According to our predicted effects, this inbreeding increase could have caused a depression of ~0.3% to 1.2% per trait, potentially offsetting the estimated 3% genetic gain over 6 years, being a possible explanation for the lack of phenotypic improvement in these traits, as exemplified for STAY12. Although we could estimate inbreeding depression and compare measures across the population, doing so within a single dataset was not feasible; as a suggestion for future research, incorporating a randomly sampled set of genotyped animals could provide a more comprehensive view of inbreeding's impact at the population level.

CONCLUSIONS

Based on pedigree inbreeding (F_{PED}), average losses in stayability ranged from 1.5% to 3% when comparing the 10% most inbred Italian Holstein cows with the 10% least inbred. In this context, extremely inbred cows (F_{PED} ~40%) showed predicted losses exceeding 15% in their probabilities of survival in the herd from first to fourth

Table 6. Performance advantage of the 10% least inbred compared with the 10% most inbred dairy cows on the expected STAY12 using different classes of ROH and both models

ROH class (Mb)	M1 model, difference ± SD (%)	M2 model, difference ± SD (%)
1 > ROH ≥ 2	−0.087 ± 0.013	−0.406 ± 0.027
2 > ROH ≥ 4	1.221 ± 0.016	1.332 ± 0.033
4 > ROH ≥ 8	0.802 ± 0.015	0.702 ± 0.032
8 > ROH ≥ 16	1.201 ± 0.016	1.043 ± 0.033
16 > ROH ≥ 32	0.852 ± 0.015	0.419 ± 0.031
32 > ROH	0.264 ± 0.015	0.148 ± 0.030

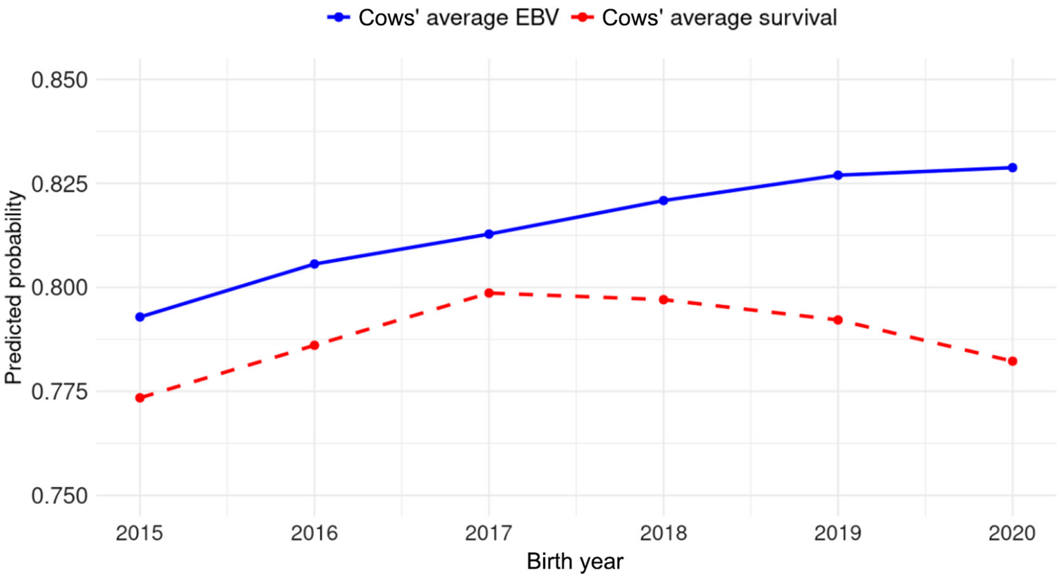

Figure 9. Genetic and phenotypic trends for STAY12 in the Italian Holstein population.

calving, highlighting the marked influence of inbreeding across different stages of the cows' productive life. The model including production level as a fixed effect provided a good option to account for inbreeding on stayability, especially if the predicted breeding values are to be used in a selection index where milk yield is also included. Genomic measures of inbreeding were more effective in capturing the inbreeding depression; among them, F_{GRM} consistently performed well, and F_{ROH} was generally the most informative measure. We found that ROH segments shorter than 2 Mb were not related to inbreeding depression on stayability, whereas longer segments were clearly associated with substantial depression effects. Overall, inbreeding depression offsets part of the improved performance that the Italian Holstein population could be experiencing from its genetic evolution on stayability traits.

NOTES

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Nonstandard abbreviations used: ANAFIBJ = Italian Holstein, Brown, and Jersey Breeders Association; Data_e = expanded dataset; Data_g = dataset of genotyped cows; DMY = deviation in milk yield; F_{GRM} = inbreeding coefficient obtained from the diagonal of the genomic relationship matrix; F_{PED} = inbreeding coefficient obtained from the pedigree; F_{ROH} = inbreeding coefficient obtained from runs of homozygosity; F_{ROH_CLASS} = inbreeding coefficient obtained from the proportion between the sum of the ROH segments as divided into 6 different classes, according to the sizes of segments; F_{ROH_GENOME} = inbreeding coefficient obtained from the proportion between the sum of the ROH segments and the complete genome of the animals; GRM = genomic relationship matrix; HD = high-density; HY = herd-year; M1, M2 = models 1 and 2, respectively; MD = medium-density; QC = quality control; ROH = runs of homozygosity; SP = standardized production; STAY12 = ability of the cow to stay alive from calving 1 to 2; STAY13 = ability of the cow to stay alive from calving 1 to 3; STAY14 = ability of the cow to stay alive from calving 1 to 4; STAY23 = ability of the cow to stay alive from calving 2 to 3; STAY34 = ability of the cow to stay alive from calving 3 to 4.

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