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ESTIMATION OF VARIANCE COMPONENTS AND HERITABILITY FOR STAYABILITY IN HOLSTEIN AND BROWN SWISS CATTLE

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ABSTRACT

Stayability (STAY) reflects the ability of a cow to avoid both voluntary and involuntary culling. The present study aimed to estimate variance components and heritability for STAY in Holstein and Brown Swiss cattle. Genealogical and productive data from 340 cows were used. The data were provided by Las Margaritas experimental farm, belonging to the National Institute of Forestry, Agricultural and Livestock Research of Mexico. STAY was defined as a cow's probability of achieving a specific lactation. STAY traits analyzed were the probabilities that a cow had one (STAY1), two (STAY2), three (STAY3), four (STAY4), and five (STAY5) lactations, given that it had a first calving. Variance components and heritability were estimated with the ASREML statistical software. An animal threshold model was fitted. It included the fixed effect of the contemporary group and the covariate percentage of Holstein genes, heterozygosity, and recombination loss. The direct additive genetic effect was included as a random effect. Heritability values of 0.33 ± 0.33, 0.23 ± 0.11, 0.27 ± 0.09,

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0.24 ± 0.09 and 0.29 ± 0.09 were obtained for STAY1, STAY2, STAY3, STAY4 and STAY5, respectively. The heritability values obtained were in the range of low to moderate, which suggests that the traits could be taken into account in future genetic selection programs.

Keywords: Dairy cattle, genetic parameters, stayability, Mexico.

INTRODUCTION

In cattle, longevity is a measure of the time a cow remains in the herd (Shabalina et al., 2020) and is associated with increased average milk yield of the herd and decreased production costs of replacement females (Schuster et al., 2020). Longevity is a complex trait that depends on both intrinsic characteristics of the animal itself (milk production, health, fertility) and extrinsic factors (milk price, cost, and availability of replacements) (Schuster et al., 2020); therefore, it reflects the cow's ability to avoid voluntary and involuntary culling (Abdelharith et al., 2019). However, traits that measure the productive performance of an animal during its life can only be estimated after its death (Shabalina et al., 2020). An early indicator of longevity is stayability.

Stayability (STAY) is defined as the probability of surviving to a specific age, given the opportunity for the animal to reach that age (Hudson and Van Vleck, 1981). STAY has an important economic impact on livestock production systems because it combines cow reproductive efficiency and longevity (Ramos et al., 2020). Furthermore, it reflects the potential of a female cow to have a long productive life in the herd (Shabalina et al., 2020). Its inclusion in genetic improvement programs has been shown to lead to an increase in net income per cow per year, and a reduction in involuntary culling rates (Imbayarwo-Chikosi et al., 2015).

The amount of variation associated with a trait is measured and expressed as the phenotypic variance (σ^2_P). The σ^2_P is divided into a genetic component (σ^2_G) and an environmental component (σ^2_E). In turn, σ^2_G is decomposed into direct and maternal additive (σ^2_{Ad} and σ^2_{Am}) and non-additive (dominance and epistasis) genetic effects (Hill et al., 2008). Of all the components, σ^2_A is the most important for two reasons: first, it contributes to the similarity of related individuals; second, it represents the fraction of genetic variance that is transmitted from parents to offspring (Thompson, 2012). Heritability (h^2) refers to the fraction of phenotypic variation that is due to additive genetic differences between animals (Spangler, 2022). The estimated value of h^2 for a specific trait in a given population allows determining which genetic improvement method is the most appropriate for a given population: direct selection or crossing (Getabalew et al., 2019).

Several authors have estimated h^2 for different definitions of stayability, both in beef and dairy cattle (Rocha et al., 2018; Shabalina et al., 2020; Silva et al., 2021; Stefani et al., 2018). According to the literature, these values are usually low to moderate (0.02–0.28), suggesting a marked influence from the environment. Furthermore, h^2 depends largely on how the trait is analyzed and the starting point from which it begins to be measured. Farmers also play an important role, since they decide when a cow should be eliminated from the herd (Clasen et al., 2017). In Mexico, studies on STAY have focused mainly on beef cattle (Baeza-Rodríguez et al., 2017; Leano et al., 2017; Ríos-Utrera et al., 2015) due to the importance of functional traits in herd profitability. However, there is scarce information regarding estimates of genetic parameters for longevity characteristics in dairy cattle. It is necessary to delve deeper into the subject in order to understand the genetic architecture of this complex trait and, in the future, develop genetic improvement programs that contribute to increasing the permanence of dairy cattle in the herd. Therefore, the present study aimed to estimate the variance components and heritability for STAY in Holstein and Brown Swiss cattle.

MATERIALS AND METHODS

The study used information obtained from the Las Margaritas experimental farm, located in the state of Puebla, Mexico (Lat. 19°, 20'N and Long. 97°, 20'W, at 500 m altitude). The climate is semi-warm humid subtropical, with an average annual temperature of 20.8 °C, and an average annual rainfall of 3,000 mm (Calderón-Robles et al., 2011). The productive and pedigree records of 340 cows born between January 1996 and May 2011 were used (Table 1). Three seasons were formed based on calvings: (1) dry, (2) rainy, and (3) cold. Cows born in the same year and season were grouped into contemporary groups to reduce environmental variation. Contemporary groups with fewer than three cows were not taken into account for the analyses.

Reproductive management of animals

Heifers weighing approximately 350 kg were

Table 1. Total number of cows and lactations by breed.

Breed	Total animals	Total lactations
Holstein-Brown Swiss crosses	46	142
Brown Swiss-Holstein crosses	76	220
Holstein	103	287
Brown Swiss	115	308
Total	340	957

integrated into the reproductive flock. Palpations of the internal genitalia were performed every two weeks to check physiological and anatomical status and to identify possible uterine problems on time. Detection of estrus was carried out from 06:00 to 07:00 and from 17:00 to 18:00 hours, with the help of a bull with a deviated penis. Females in estrus were inseminated conventionally: if detected in heat in the morning, they were inseminated in the afternoon; and if detected in heat in the afternoon, they were inseminated the following morning. Estrus repeater heifers were allowed the opportunity to receive two artificial insemination (AI) services and two natural mating services upon detection of heat. If they did not become pregnant with these opportunities, they were discarded from the herd. The pregnancy diagnosis was made 40 days after the last insemination.

Feeding

The cows were kept in rotational grazing. The diet consisted mainly of forage such as Japanese cane (*Saccharum sinense*) or sugar cane (*Saccharum officinarum*), corn silage (*Zea mays*), sorghum (*Sorghum bicolor*), and hay grasses from the African Star (*Cynodon plectostachyus*), Pangola (*Digitaria decumbens*), among other plant species. During the dry season, the cows individually received between 20 and 30 kg of cutting forage per day, added with a mixture of molasses (97%) and urea (3%) at a rate of 2 to 3 kg per animal per day. During milking, lactating cows received 3.5 kg of commercial concentrated feed (16% crude protein and 70% digestible nutrients). Dry cows received 2 kg of the same type of feed per day.

Statistical analysis

Stayability was defined as the probability of a cow of achieving a specific lactation. The lactation records of each cow were used to assign the binary observations. Stayability traits analyzed were the probabilities that a female cow had one (STAY1), two (STAY2), three (STAY3), four (STAY4), and five (STAY5) lactations, given that it had a first calving. Binary observations, with zero indicating failure and one indicating success, were assigned to cows old enough to have had the required number of lactations.

Variance components and heritability were estimated with the ASREML statistical software (Butler et al., 2017). The following animal threshold model was fitted:

$$\eta = \mathrm{Xb} + \mathrm{Za} + \mathrm{e}$$

Where η is the linear predictor that follows a Bernoulli distribution, b is the px1 vector that includes the fixed effect of the contemporary group and the covariate percentage of Holstein genes, heterozygosity, and recombination loss, a is the qx1 vector that includes the direct additive genetic effect as a random effect. X and Z are design matrices that associate the elements of b and a, respectively, to the elements of y: the vector of observations, or its conditional expectation:

$$\mathrm{E}\langle \mathrm{y_i} | \eta_\mathrm{i} \rangle = \mathrm{h}(\eta_\mathrm{i}) = \mathrm{p_i}$$

Each STAY trait was analyzed independently with an univariate model.

h describes how the mean response E(y_i) is linked η_i . In this case, the link function modeled was the logit pi function:

$$E(\mathrm{y_i} | \mathrm{p_i}) = \mathrm{p_i} = \ln\left(\frac{(\mathrm{X_i b} + \mathrm{Z_i a})}{1 - (\mathrm{X_i b} + \mathrm{Z_i a})}\right)$$

Where p_i denotes the probability of success for cow i, with success defined as, for example, a cow that had one, two, three, four or five lactations, given that it had a first calving. The Bernoulli distribution for persistence to a specific lactation, where y=0, denotes lactation failure (either the first, second, third, fourth, or fifth lactation), given that the cow had a first calving, and y=1 denotes achieved lactation (one or more), given that the cow had a first calving, it is:

$$\mathrm{Prob}\ (\mathrm{y_i} | \mathrm{p_i}) = (\mathrm{p_i})^{\mathrm{y_i}} (1 - \mathrm{p_i})^{1 - \mathrm{y_1}}$$

It was assumed that the random effects of the model follow a multivariate normal distribution, with means equal to zero and with the following (co)variance structure:

$$\begin{pmatrix} a \\ e \end{pmatrix} \Big| \sigma_a^2 \quad \sigma_e^2 \Big) \sim N\left[0, \begin{pmatrix} A\sigma_a^2 & 0 \\ 0 & I_n\sigma_e^2 \end{pmatrix}\right]$$

Where A is the additive genetic relationship matrix among the animals that make up the pedigree, σ^2_a is the direct additive genetic variance, σ^2_e is the residual variance, and I_n is an identity matrix of size equal to the number of records. Furthermore, the direct additive genetic and residual effects were assumed to be independent. The percentage of Holstein genes (PG), heterozygosity (HET), and recombination loss (RL) were estimated for each animal as follows:

$$PG = \frac{Sire_i + Dam_i}{2}$$

$$HET = \big(Sire_i * (1 - Dam_i)\big) + \big(Dam_i * (1 - Sire_i)\big)$$

$$RL = \big(Sire_i * (1 - Sire_i)\big) + \big(Dam_i * (1 - Dam_i)\big)$$

Where Sire and Dam represent the percentage of Holstein genes from the sire and dam, respectively. Heritability was estimated using the following formula:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2}$$

The variance of the logit link function was used, which implied a correction of the residual variance by the factor $\square^2/3 \approx 3.29$ (Shabalina et al., 2020). Least squares means were transformed to the observable scale with the inverse of the link function, while the standard errors were transformed with the Delta method (Bishop et al., 1975).

RESULTS AND DISCUSSION

Table 2 presents the variance components and heritability (h^2) for each measure of stayability analyzed. The h^2 values were in the range of 0.23 ± 0.11 to 0.33 ± 0.33, which is higher as compared to what is published in the literature.

Valencia-Posadas et al. (2004) estimated h^2 for permanence ability at 48 months of age of 47 609 Holstein cows in Mexico. These authors used a univariate animal model that assumed a normal distribution of the data and reported an h^2 value of 0.03 ± 0.01. This result differs notably from what was found for STAY2, STAY3, STAY4 and STAY5 in the present study, which may be due to sample size and environmental differences between populations. The database used to carry out these analyses corresponds to a single herd. The sample size is small because those were the only animal records available at the Las Margaritas experimental farm. Due to the limited number of animals, the standard error of heritability is large in STAY1. Valencia-Posadas et al. (2004) concluded that direct selection to improve longevity might be possible. However, low h^2 values suggest that little genetic gain would be obtained; in particular, when animals are selected without progeny information. An alternative to increase the precision of the estimates could be indirect selection through correlated characteristics of early expression, such as reproductive and conformation traits (Rocha et al., 2018).

Numerous studies have indicated that stayability has moderate to high correlations with several traits: age at first calving (-0.63), milk yield at 305 days (0.46), leg set (0.69), udder depth (0.52), and days in milk (> 78) (Buzanskas et al., 2010; Rocha et al., 2018; Valencia-Posadas et al., 2004). These correlations could imply that selecting for higher milk yield and desirable type traits can indirectly enhance stayability. Heavier dairy heifers tend to remain in the herd for their first, second, and third calvings more often than

Table 2. Variance components and heritability for measures of stayability (STAY) from the first to fifth lactation.

STAY	Additive genetic variance	Residual variance	h^2 (standard error)
STAY1	1.63	3.29	0.33 (0.33)
STAY2	0.99	3.29	0.23 (0.11)
STAY3	1.20	3.29	0.27 (0.09)
STAY4	1.03	3.29	0.24 (0.09)
STAY5	1.36	3.29	0.29 (0.09)

lighter heifers, suggesting a positive relationship between body weight and stayability (Handcock et al., 2020). Additionally, selecting sexually precocious cows could lead to improved stayability, since females who begin their reproductive lives earlier are likely to produce more calves over their lifetime (Buzanskas et al., 2010).

The results obtained in the present study agree with those of Ahlman et al. (2011) and Irano et al. (2014) for Holstein cows. The authors estimated variance components and heritability for STAY until the third lactation and reported h^2 of 0.08 ± 0.01, 0.20 ± 0.01 and 0.28 ± 0.07, respectively. Comparable to our results, an increase in the magnitude of h^2 was also observed as the lactation number progressed. It has been proven that h^2 for categorical data depends on the frequency of animals present in each class. The high number of cows discarded in the later stages of lactation could explain this slight increase (Shabalina et al., 2020).

The low h^2 (0.01 – 0.28) associated with STAY suggests that environment plays an important role (Schuster et al., 2020). Buzanskas et al. (2010) propose that STAY is a trait highly influenced by climatic, nutritional, and management conditions to which the animals are exposed over the years. In turn, environmental stressors can inhibit or promote the expression of certain genes via epigenetics and affect cow performance (Schuster et al., 2020). This shows that longevity does not depend only on the additive effect of the animal's genes, but also on the role of environment on phenotype.

Rocha et al. (2018), in a study with Brazilian Holstein cattle, estimated genetic parameters for permanence ability at different ages. To do this, they defined two characteristics: the probability of a female cow remaining in the herd from birth until 48 and 54 months of age; and the probability of remaining until 36 and 48 months after first calving. The authors used a threshold animal model and a Bayesian approach for data analysis and reported h^2 values in the range of 0.05 ± 0.01 to 0.26 ± 0.08, which partially coincides with what is reported in this study. The h^2 obtained suggests the existence of additive genetic variation; anyway, direct selection for this trait would not imply rapid genetic progress. However, this does not mean that STAY should not be taken into account in genetic improvement programs.

Valente et al. (2017) suggest that genetic improvement of STAY, through selection, could imply an increase in generation interval and consequently, a reduction in the annual genetic gain for this trait. Furthermore, to achieve a selection accuracy of approximately 0.70, phenotypes of 127 progenies per sire are needed. The lower the value of h^2, the greater the required number of record progenies to achieve a high precision value (Berry et al., 2019). An alternative to improve STAY is the implementation of crossbreeding to exploit hybrid vigor. As a rule, the lower the heritability for a given trait, the greater the effect of heterosis on that trait (Getabalew et al., 2019).

Heritability results obtained in this study are higher than those published by Shabalina et al. (2020) for German Holstein cattle. The authors reported h^2 values ranging from 0.01 ± 0.002 to 0.06 ± 0.007 when STAY was defined as the probability of surviving a specific stage of lactation. Haagen et al. (2021) used a threshold animal model and estimated h^2 values of 0.085 ± 0.020 for STAY until the first year of age. Hardie et al. (2021), in a study with American Holstein cows, reported h^2 of 0.10 ± 0.01 to 0.07 ± 0.03 for STAY from birth to fifth calving. It should be taken into account that differences in the genetic composition of each population, the definition of the trait, the statistical models used as well as the frequency of dead or discarded cows from the herd are factors that can contribute to the variation observed in h^2 between the different studies (Zhang et al., 2022).

It is important to note that h^2 is commonly reported as a universal measure of the analyzed characteristic (Robette et al., 2022); this is incorrect since h^2 is inherent to each population and depends on the moment in which it is measured. The degree of genetic variation in a population depends on factors such as allele frequencies and the mechanism of action of the genes. These factors can change as a result of migration, selection, inbreeding, and/or genetic drift (Berry et al., 2019). Furthermore, heritability can vary over time, as a consequence of environmental changes. Two groups of animals with the same genetic composition can have, for a given trait, different heritability values if the environment in which they live and the management or feeding conditions are different (Robette et al., 2022).

CONCLUSIONS

The variance components and heritability were estimated for the five measures of stayability analyzed. The heritability values obtained were in the range of low to moderate, which suggests that the traits could be taken into account in future genetic selection programs.

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Conflict of interest

The authors declare that there are no conflicts of interest in this study and agree to the publication of the manuscript.

Author contributions

All authors contributed to the conception and design of the study. Material preparation and data collection were carried out by René Carlos Calderón-Robles, Angel Ríos-Utrera, Guillermo Martínez-Velázquez, Moisés Montaño-Bermúdez and Vicente Elizer Vega-Murillo. Analyses were performed by Anel Ledesma-Rodríguez, Vicente Eliezer Vega-Murillo and Juan José Baeza-Rodríguez . The first draft of the manuscript was written by Anel Ledesma-Rodríguez and all authors reviewed and commented on subsequent versions of the manuscript. All authors read and approved the final manuscript.

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