Distributional characterizations and testing for differences of relatedness and inbreeding of a subpopulation of American Hereford bulls

M. A. Simmons[†], P. K. Riggs[†], S. Sanders[‡], A. D. Herring[†,], J. O. Sanders[†], and D. G. Riley[†,1,]

[†]Department of Animal Science, Texas A&M University, College Station, TX 77843; and [‡]American Hereford Association, Kansas City, MO 64153

ABSTRACT: Beta distributions are characterized by two determining parameters and a parameter space from 0 to 1, and may be useful for examining population genetic parameters such as the relationship or inbreeding coefficients. Often subpopulations exist within breeds that are congregated around particular lineages of cattle or ancestors that breeders value. These subpopulations are more related to each other than to the majority of other animals; they may have higher inbreeding as well. Value may be added to these subpopulations because of their relatedness with important or renowned ancestors. The objectives of this work were to compare the relatedness and inbreeding of a group of 26 modern bulls from a subpopulation of the American Hereford breed relative to 1) 30 males with the most descendants present in the pedigree, 2) 15 renowned American Hereford bulls considered important individuals in the breed's history, and 3) 19 prominent subpopulation male ancestors. Conformance of the mean relationship coefficients of the bulls with the three groups and the mean inbreeding coefficient with all pedigree animals to beta distributions was assessed by 1) visually determining the parameters of the beta distributions based on the entire pedigree, 2) testing the mean relationship coefficient or inbreeding coefficient of the group of subpopulation bulls for its positional inclusion in those distributions, and 3) bootstrap sampling methodology. The mean relationship coefficients of the 26 Trask bulls with the 30 bulls with the most descendants, the 15 renowned ancestors, and the 19 Trask male ancestors were 0.15, 0.132, and 0.208, respectively. Testing of these means in beta distributions indicated that the group of 26 Trask bulls were no more related to the three groups of bulls than all of the animals in the pedigree ($0.06 < P < 0.25$). Bootstrap sampling indicated that the 26 bulls were more related to the three groups of male ancestors than the remainder of the animals in the pedigree ($P < 0.0001$). The mean inbreeding coefficient of the 26 bulls (0.13) did not differ from the overall inbreeding coefficient (0.056) when tested using a beta distribution; however, bootstrap sampling indicated otherwise ($P < 0.0001$). Results may indicate the inadequacy of visually parameterizing a beta distribution. Quantification of pedigree relatedness of a group of animals to key ancestors, especially with no DNA available, may add value to that group and individuals.

Key words: beta distribution, Hereford, inbreeding, relatedness

Transl. Anim. Sci. 2021.5:1-10
doi: 10.1093/tas/txab008

[1]Corresponding author: david-riley@tamu.edu
Received July 16, 2020.
Accepted January 21, 2021.

INTRODUCTION

A genetic population such as a breed or race of livestock likely is comprised of subpopulations due to the selection that is independently conducted by different animal breeders. These subpopulations can become more similar within and more distinct to those external due to relatedness and inbreeding. The distinctiveness of subpopulations can be substantial enough to affect heterosis in crosses of animals from different groups within the same breed (MacNeil et al., 1989). The influence of ancestors that are renowned because of their popularity, economic influence, or wide usage in earlier time likely varies among those subpopulations. Unselected cattle populations or lines within a breed are valuable for overall improvement strategies. They serve a conservation role and present the ability to genetically return performance traits back to a more intermediate value with relative ease. Mr Neil Trask of South Carolina was an important American Hereford breeder in the 20th century (Trask, 1958). His implementation of breeding strategies represented more of the "art" side of animal breeding rather than the science side. His efforts resulted in a unique, competent subpopulation of Hereford cattle that were developed and excel in pasture conditions for production on forage, especially in the Southeastern United States. Particularly, this line of cattle was selected for fertility with minimal feed supplementation. They conformed to this breeder's preference in terms of correct structure and deep rib and body; these cattle were never selected to be smaller when small frame cattle were popular in the United States (mid-20th century), nor larger when those cattle became popular in the 1970s and 1980s. Although his cattle were sold after his death, they have been maintained by a group of Hereford breeders and offer a unique opportunity to assess quantitatively the subpopulation as a part of the overall Hereford breed. This project is a study of the ancestry of the Trask line of cattle and is intended to measure the genetic relationships between a sample (n = 26) of the Trask bulls and their ancestors. The objectives of this work were to assess the genetic influence of prominent ancestors on Trask bred bulls in recent/current herds, evaluate the relationships among the Trask bulls, and compare the level of inbreeding of a group of 26 modern bulls relative to 1) 30 males with the most descendants present in the American Hereford Association pedigree, 2) 15 renowned American Hereford bulls considered key individuals in the breed's history by the American Hereford Association and Hereford breeders, and 3) 19 prominent subpopulation male ancestors as identified by cattlemen within the line. An additional objective was to compare the average inbreeding coefficient of the Trask bulls to the average of all the cattle in their pedigrees.

MATERIALS AND METHODS

Pedigree information for a sample group of 26 recently or currently living bulls (Table 1) of Trask breeding (Trask Bulls 26) was obtained from the American Hereford Association (AHA). The pedigree included 42,718 individuals, and included ancestors registered in the middle 19th century. There were 1,034 sires and 28,662 dams with averages of 2.8 and 1.3 progeny, respectively, in the pedigree.

Table 1. Hereford bulls from Neil Trask lines of breeding (Trask Bulls 26)

Animal name	AHA[a] registration	Animal name	AHA registration
NT Plato Rupert 167	23453801	Plato Rupert MOH 172	42650292
BTF 511 6007	23905741	BTF 9245 4108 ET	42656366
NT Plato Rupert 123	24046601	BTF 252 4168 ET	42656370
BTF 61 0178	42186827	Edisto 136 Battle Rupert T352	42860368
DPH BTF E132 M636 ET	42373311	Edisto 167 Plato Rupert U347 ET	42904180
BTF6104 M171	42453113	Edisto 810 Excel Plato U336 ET	42904253
DPH BTF 123 M179	42505661	HCC 178 P001	42935103
BTF 4 3100 ET	42586465	PPH Domino Plato Rupert 2	42965967
BTF 4 3119 ET	42586488	HPH 6007 Plato Real P-17	43011115
BTF E132 3120 ET	42586489	BTF HCC 834 M636 5095	43142302
BTF E132 4064	42586515	BTF M035 M179 5003	43142667
BTF E132 4087	42586554	HPH 6007 Plato Vic P-5	43182206
BTF DPH E132 4091	42590228	BTF 167 5100 ET	43275810

[a]AHA: American Hereford Association.

The additive genetic covariance between two animals (a_{xy}; x and y indicate animals), sometimes referred to as the additive or numerator relationship, is two times the probability of these individuals having genes identical by descent. This implies that the two genes stem from the duplication of a gene within a third individual from a preceding generation (Van Vleck, 1993; Falconer and Mackay, 1996). The additive genetic covariance matrix is an important component of the mixed model equations to predict genetic merit (Henderson, 1963). This symmetric, square matrix contains additive genetic covariance values for each pair of animals in a pedigree on off-diagonal elements. The diagonal elements of the additive genetic covariance matrix are the additive covariances of each individual animal with itself ($a_{xx} = 1 + F_x$). The R Project for Statistical Computing environment was used to calculate the additive genetic covariance for all pairs of animals in the pedigree (R Core Team, 2017) using the R package "kinship2" (Therneau and Sinnwell, 2015). This package was used to generate a matrix of kinship coefficients for the animals. The kinship coefficient is the probability that two single genes, drawn at random from two individuals, are identical by descent (Lynch and Walsh, 1998). The additive genetic covariance matrix ($\mathbf{A_{xy}}$) is equal to two times the kinship coefficient matrix $\mathbf{\Theta_{xy}}$.

This matrix was constructed using the Texas A&M Institute for Genome Sciences and Society computer cluster. Inbreeding coefficients (F_x) were calculated as $a_{xx} - 1$ (Van Vleck, 1993) for the 42,718 animals in the pedigree.

Three distinct groups of Hereford ancestors were identified. The supplied pedigree information was used to identify the 30 individuals with the most offspring present (average 80.33 progeny) in the pedigree (Most Progeny 30; Table 2). The second group included 19 individuals that were considered by breeders of Hereford Trask cattle to have significant influence (average 11.9 progeny) in Mr Trask's breeding program (Key Trask 19; Table 3). Fifteen influential Hereford bulls were identified by Hereford breeders and AHA personnel as representative of famous or renowned individuals in AHA history (Key AHA 15; Table 4); they included both polled and horned bulls with historical significance and averaged 45.9 progeny in this pedigree.

The additive genetic covariance a_{xy} has a parameter space of 0 to 2 (Falconer and Mackay, 1996). Wright's coefficient of relationship (R_{xy}; Wright, 1922) was calculated for all pairs of animals in the pedigree using the a_{xy} values and the diagonal elements from the additive genetic covariance matrix. The coefficient standardizes relationship within a pedigree, and has a parameter space from 0 to 1. It is defined as the probable proportion of one individual's genes that are identical by descent to genes of a second individual (Bourdon, 2000), and is estimated as:

$$R_{xy} = \frac{a_{xy}}{\sqrt{(1 + F_x)(1 + F_y)}}$$

in which a_{xy} is the additive covariance value, and F_x and F_y are the respective inbreeding coefficients of animals x and y (Van Vleck, 1993; Falconer and Mackay, 1996; Bourdon, 2000). Inbreeding coefficients also have a parameter space from 0 to 1.

The beta (β) distribution is a bivariate distribution with a parameter space of 0 to 1 (Bouguila

Table 2. Hereford bulls classified as animals with the most progeny in the pedigree (Most Progeny 30)

Animal name	AHA[a] registration	Animal name	AHA registration
Sir Thomas	20	Domino	264259
The Grove 3rd	2490	Beau Mischief	268371
Lord Wilton	4057	Repeater	289598
Anxiety 3	4466	Beau Picture	308177
Garfield	7015	Polled Plato	353393
Anxiety 4	9904	Beau Blanchard	362904
Don Carlos	33734	Bright Stanway	366600
Beau Brummel	51817	Beau Aster	412145
Lamplighter	51834	Beau Randolph	418893
Beau Donald	58996	Prince Domino	499611
Militant	71755	Superior Mischief	590259
Beau Dandy	145564	Onward Domino	812380
Beau Modest	160589	Dandy Domino 2	1090962
Beau President	171349	Advance Mischief	1323063
Perfection Fairfax	179767	Advance Domino	1381854

[a]AHA: American Hereford Association.

Table 3. Hereford bulls classified as important ancestors in Neil Trask lines of cattle (Key Trask 19)

Animal name	AHA[a] registration	Animal name	AHA registration
Hazford Seminole	1815001	Victor Plato 35	7314476
M P Domino 3	1967033	Plato Woodford 34	7363063
Plato Domino 1	2350712	Rupert Gem	7809132
Plato Domino 43	3080818	NT Rupert	9446404
Battle Domino 18	3320225	FF Battle R948	11213062
Pure Plato Domino	3775927	Hartland Rupert 48	12199616
Plato Hazford	4279424	Hartland Rupert 66	13219124
Palmetto Woodford	5249256	Hazford Bocaldo	14628869
Double Domino 5	5745343	NT Mischief Mixer	20015879
Plato Mischief	6285578		

[a]AHA: American Hereford Association.

Table 4. Hereford bulls classified as renowned with substantial influence on the breed (Key AHA 15)

Animal name	AHA[a] registration	Animal name	AHA registration
North Pole	8946	Hazford Rupert 25	1209734
Anxiety 4th	9904	Mossy Plato	1341320
Prince Rupert	79539	Mossy Plato 26	1719194
Polled Admiral 2d	230299	Victor Domino	2060000
Polled Plato	353393	Victor Domino 14	2220966
Beau Aster	412145	Hazford Rupert 81	2348825
Prince Domino	499611	TR Zato Heir	5380000
Woodford	500000		

[a]AHA: American Hereford Association.

et al., 2006; Olkin and Trikalinos, 2014). Two parameters, $\boldsymbol{\alpha}$ and $\boldsymbol{\beta}$ completely characterize this distribution. The first two moments of the β distribution are:

$$\mu = \frac{\alpha}{\alpha + \beta}$$

$$\sigma^2 = \frac{\alpha\beta}{(\alpha+\beta)^2(\alpha+\beta+1)}$$

and α and β can be expressed as functions of moments and each other:

$$\alpha = \left(\frac{1-\mu}{\sigma^2} - \frac{1}{\mu}\right)\mu^2$$

$$\beta = \alpha\left(\frac{1}{\mu} - 1\right)$$

(Farnum and Stanton, 1987).

The tested null hypotheses were:

1. The average R_{xy} of the 26 Trask bulls with the Most Progeny 30 ancestors is similar to the average R_{xy} of the Most Progeny 30 ancestors with the entire pedigree.
2. The average R_{xy} of the 26 Trask bulls with the Key Trask 19 ancestors is similar to the average R_{xy} of the Key Trask 19 ancestors with the entire pedigree.
3. The average R_{xy} of the 26 Trask bulls with the Key AHA 15 ancestors is similar to the average relationship of the key breed ancestors with the R_{xy} pedigree.
4. The average F_x for the sample of (n = 26) Trask bulls (descendants) is similar to the average F_x of the entire pedigree.

Distributions of the R_{xy} values for pairs of each of the three ancestor groups and the group of Trask descendants with the remainder of the animals in the pedigree were visualized using plotting functions in the R statistical software computing environment. The algebraic relationships (shown above) of α and β parameters with each other and the distribution mean (μ) were used to construct a grid of values for each parameter that preserved those relationships. Parameter values were successively altered in attempts to identify β distributions that matched (by plotting) the actual distributions of the R_{xy} values in three distinct efforts: R_{xy} of Most Progeny 30 bulls with the entire pedigree; R_{xy} of Key AHA 15 bulls with the entire pedigree; and R_{xy} of Key Trask 19 ancestors with the entire pedigree. This process was 1) to change one of the two

parameters, and 2) visually compare the β distribution with the actual using random sampling techniques and plotting functions in the R computing environment. After the closest approximations to the actual distributions had paired β distributions (visually determined), those β distributions were queried with the R_{xy} mean as an ordinate for the 26 Trask descendants with each of the three ancestor groups. This ordinate was used to identify a probability (P) value that the R_{xy} mean was a part of that distribution using probability functions using the R computing environment (once for each ancestor group).

Grids of parameter values were used to generate α and β values that satisfied the above algebraic relationships of the parameters and the β distribution mean. Iterative parameter updating, visualization through plotting, and comparison to the plotted distribution of F_x values for the entire pedigree was conducted as described for R_{xy}. Once the actual distribution was best (visually determined) simulated with a β distribution, that β distribution was used to assess the fourth hypothesis above.

Hypotheses for each comparison of R_{xy} and the F_x were additionally tested with bootstrap methodology (Hesterberg, 2014). For each hypothesis test, 100,000 bootstrap samples were generated in the R software environment; each consisted of 26 rows (animals) and the number of columns in the respective data file for each of the three comparisons (Most Progeny 30, Key Trask 19, and Key AHA 15). As such, they were a sequence of random draws from the actual set of values. Means of each of those draws represented the ultimate sampled value; those constituted the empirical distribution that the R_{xy} and F_x means were tested against. Bootstrapped distributions were visualized as plots, and respective empirical P values for each hypothesis test were calculated using our written scripts in the R computer programming language.

RESULTS

The average R_{xy} for the Trask Bulls 26 with the Most Progeny 30, Key AHA 15, and Key Trask 19 groups of bulls were 0.15, 0.132, and 0.208, respectively. On average, the animals within each of the three ancestor groups appeared to be more related to the sample of Trask Bulls 26 than with the rest of the cattle in the pedigree. Average R_{xy} estimates for the entire pedigree with the Most Progeny 30, Key AHA 15, and Key Trask 19 groups of bulls were 0.104, 0.074, and 0.072, respectively. It was not surprising that the Key Trask 19 ancestors had the closest relationship with the Trask Bulls 26, followed by that with the Most Progeny 30 ancestors, and then with the Key AHA ancestors.

R_{xy} Hypothesis Testing

Most Progeny 30 ancestors. The best approximation of the actual distribution of R_{xy} values of the Trask Bulls 26 with the Most Progeny 30 ancestors was distributed as β with parameters $\alpha = 0.6493$ and $\beta = 5.6188$. This was not an excellent match as can be seen in Fig. 1. The distribution of actual values had a higher peak than the plotted β function and deviated slightly at that peak and much from about 0.08 to 0.32. Although the remainder of the parameter space (0.51 to 1.0) is not shown, both curves asymptotically approached 0 at approximately the same rate and magnitude through that interval. The mean R_{xy} of the Trask Bulls 26 with the Most Progeny 30 ancestors (0.15) appeared to fit appropriately into this distribution (P = 0.246), and based on this would be failure to reject the corresponding null hypothesis.

However, the observed mean R_{xy} (μ = 0.15) for the Trask Bulls 26 with the Most Progeny 30 ancestors was located in the far-right tail of the distribution of the bootstrapped samples (Fig. 2). The mean of the R_{xy} bootstrap sample (μ = 0.104) was very close (as it should be if sampled appropriately) to the mean R_{xy} of the Most Progeny 30 ancestors with the Trask pedigree (μ = 0.104). Using this empirical distribution, the null hypothesis would be rejected (P = 0.005) in favor of an observed difference.

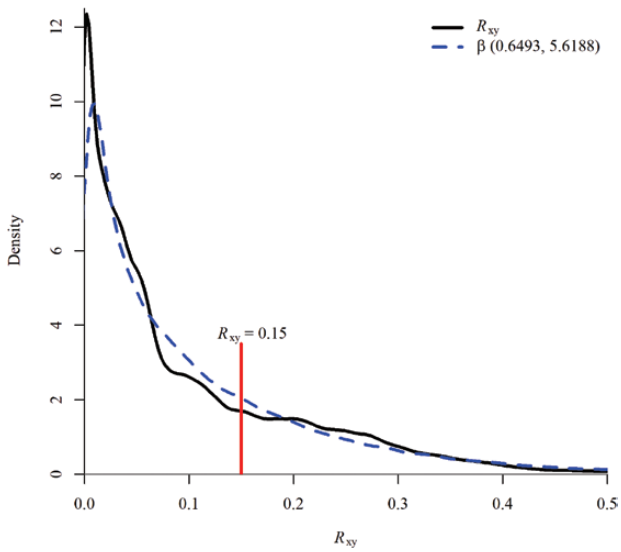

Figure 1. R_{xy} for Trask 26 with Most Progeny 30 sires: actual and β densities.

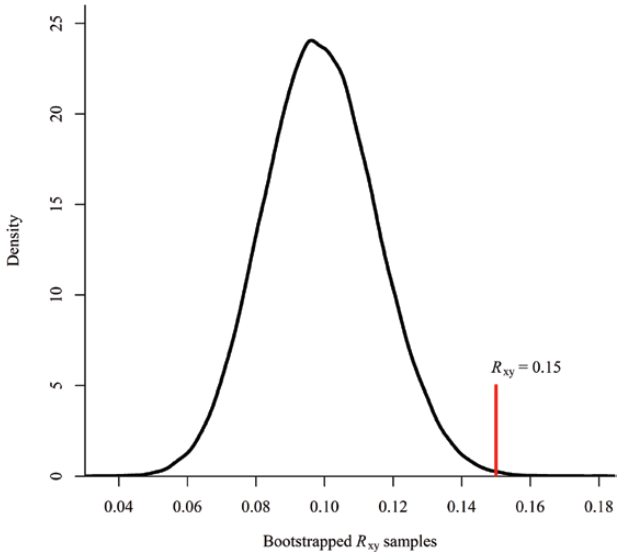

Figure 2. R_{xy} for Trask 26 with Most Progeny 30 sires: bootstrap R_{xy} sample density and mean R_{xy} value.

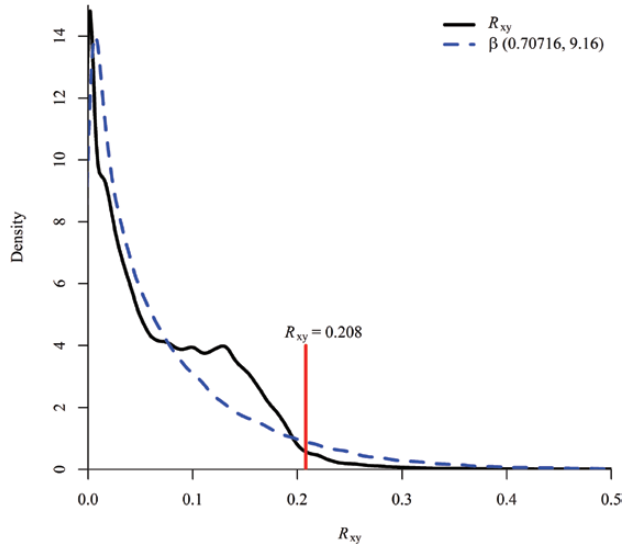

Figure 3. R_{xy} for Trask 26 with Key Trask 19 sires: actual and β densities.

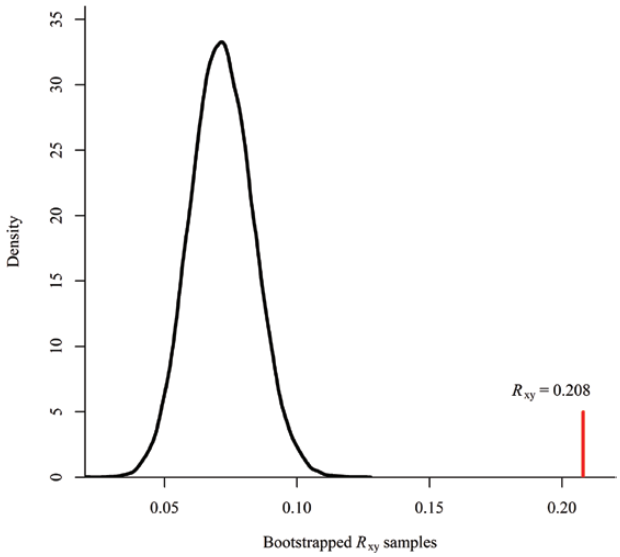

Figure 4. R_{xy} for Trask 26 with Key Trask 19 sires: bootstrap R_{xy} sample density and mean R_{xy} value.

That is, the Trask Bulls 26 were more closely related with the Most Progeny 30 ancestors than the remainder of the animals in the pedigree.

Key Trask 19 ancestors. The peak of the best β distribution curve and the initial decline were reasonably similar to the actual R_{xy} distribution. However, there was substantial mismatch of the actual distribution with the modeled β distribution ($\alpha = 0.70716$, $\beta = 9.16$) from parameter space 0.08 to 0.35 (Fig. 3). The mean R_{xy} of the Trask Bulls 26 with the Key Trask 19 herd ancestors ($R_{xy} = 0.208$) was in the tail of this estimated β distribution ($P = 0.069$). However, strict adherence to statistical inference again would direct a failure to reject the null hypothesis and suggest that the Trask Bulls 26 were no more related to the Key Trask 19 ancestors than the remainder of the pedigree ($R_{xy} = 0.072$).

The observed mean R_{xy} ($\mu = 0.208$) for the Trask Bulls 26 with the Key Trask 19 ancestors was positioned in the far tail of the distribution for the bootstrapped values (Fig. 4). The empirical P-value ($P < 0.0001$) strongly promotes the rejection of the null hypothesis. We conclude that the mean R_{xy} of the ($n = 26$) Trask Bulls 26 differed substantially from the overall mean R_{xy} (0.072) of the Trask pedigree with the Key Trask 19 ancestors. This seems more reasonable than the failure to reject the null hypothesis mandated by testing against the β distribution as parameterized.

Key AHA 15 ancestors. Although not identical, the curves representing the actual R_{xy} distribution (Trask Bulls 26 with Key AHA 15 ancestors) and the $\beta(\alpha = 0.564,\ \beta = 7.081)$ distribution were the most similar of all comparisons (Fig. 5). The distribution of the actual R_{xy} values had a slightly shorter peak and marginally diverged from about 0.06 R_{xy} to 0.36 R_{xy} on the x-axis. The mean R_{xy} of the Trask Bulls 26 with the Key AHA 15 did not differ ($P = 0.19$) from the mean R_{xy} (0.074) of the entire pedigree with this famous group.

The observed mean R_{xy} ($\mu = 0.132$) for the Trask Bulls 26 with the Key AHA 15 ancestors is in the far right tail of the bootstrapped R_{xy} distribution (Fig. 6). The empirical P-value ($P < 0.0001$) authorized the rejection of the null hypothesis; the mean R_{xy} of the ($n = 26$) Trask Bulls 26 with the Key AHA 15 differed from the overall mean R_{xy} of the pedigree with this group. That is, this set of bulls appeared to be more closely related to these prominent ancestors in the Hereford breed.

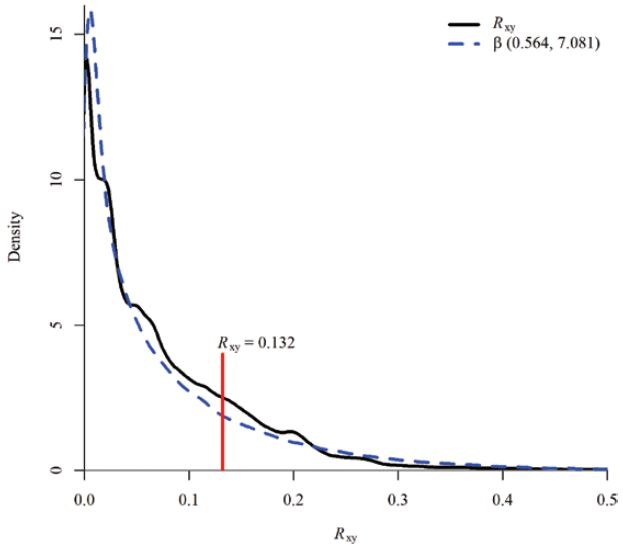

Figure 5. R_{xy} for Trask 26 with Key AHA 15 sires: actual and β densities.

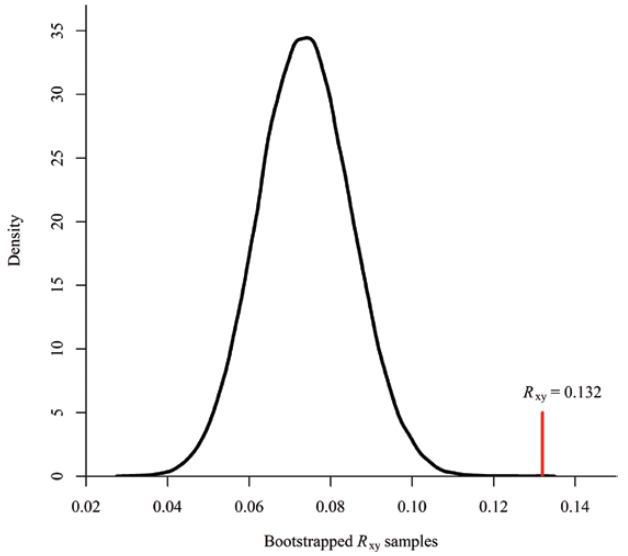

Figure 6. R_{xy} for Trask 26 with Key AHA 15 sires: bootstrap R_{xy} sample density and mean R_{xy} value.

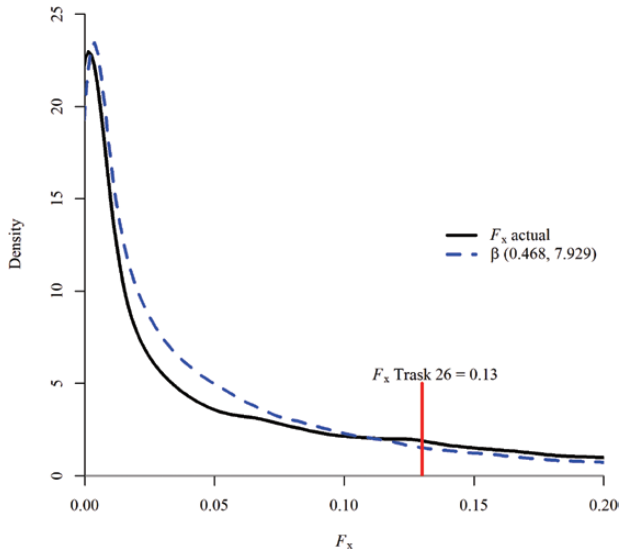

Figure 7. F_x values for all animals in pedigree and the Trask bulls 26.

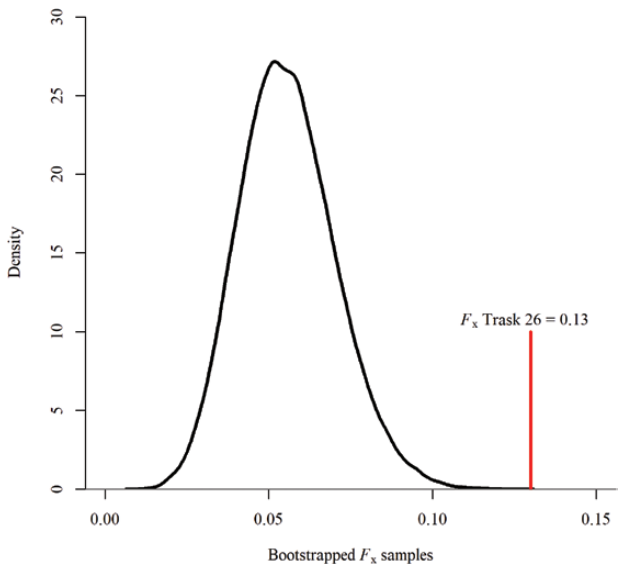

Figure 8. F_x: bootstrap samples and mean Trask 26 value.

F_x Hypothesis Testing

The mean F_x values for the entire pedigree and the Trask Bull 26 group were 0.056 and 0.13, respectively. A $\beta(\alpha = 0.468,\ \beta = 7.929)$ distribution and the actual F_x distribution of the entire pedigree matched reasonably well (Fig. 7). The estimated β distribution appears to be shifted slightly up and right relative to the actual distribution of inbreeding coefficients. The mean F_x of the Trask Bulls 26 did not differ from the overall F_x mean ($P = 0.105$).

The plotted bootstrap samples are shown in Fig. 8, and the observed mean F_x ($\mu = 0.13$) of the Trask bulls sample is solidly positioned in the rejection region ($P < 0.0001$); this test indicates that the mean of this group of 26 bulls is different from the average in the pedigree.

DISCUSSION

Pedigree information has been used often to describe demographics of various livestock populations (e.g., Dang et al., 2011; Pienaar et al., 2015; Ramírez-Valverde et al., 2018), as well as to establish a basis for conservation efforts for small breeds and populations (Goyache et al., 2003; Fernández et al., 2007; Barros et al., 2011; Cortes et al., 2014). These efforts frequently include assessment of rate of inbreeding, effective population size, relative ancestor contributions, and some quantification of

correspondence of performance with some of these metrics. More recently, extension of these concepts in a genomic context has been substantial, particularly with estimation of genomic relationships (VanRaden, 2008; Hayes et al., 2009; Legarra et al., 2009). Genomic relatedness based upon shared markers such as single nucleotide polymorphisms or haplotypes (Nani et al., 2020) consists of these steps: 1) construction of a matrix of individuals and the marker loci with values assigned to genotypes at each marker, 2) adjustment of that matrix with centered minor allele frequencies, and 3) division of that squared matrix by the sum of marker heterozygosities across all loci (VanRaden, 2008). The use of genomic information may enhance the ability to genetically connect (for analysis purposes) herds that had few documented pedigree ties (Yu et al., 2017).

Estimates of inbreeding coefficients (0.056 and 0.13 for the overall pedigree and the Trask 26 bulls, respectively) appeared to be reasonable for such populations. Very few inbreeding coefficients for livestock populations have been reported. Contiguous homozygosity ("runs of homozygosity") of single nucleotide polymorphism markers has been considered as a genomic counterpart to the pedigree-based inbreeding coefficient (e.g., Gomez-Raya et al., 2015a; Sumreddee et al., 2019), and that value was almost twice as high (0.09) as pedigree values (0.048) in U.S. populations of Wagyu (Scraggs et al., 2014). This could be because pedigree relationships are based on expectations. Other than those, mean inbreeding coefficients for livestock reported are consistently low, generally less than 0.01 in many different breeds of cattle around the world (Peixoto et al., 2010; Dang et al., 2011; Oliveira et al., 2012; Santana Junior et al., 2012; Steyn et al., 2012; Barbosa et al., 2013; Worede et al., 2013; Pavlik et al., 2014; Pienaar et al., 2015; Bernardes et al., 2016). Domínguez-Viveros et al. (2012) presented tabular summaries as distributions of inbreeding coefficients and additive relatedness within equine and taurine populations involved in Mexican bullfighting. Otherwise, there has apparently been no effort to characterize the distributions of relatedness or inbreeding based on pedigree; although Huisman et al. (2016) graphically depicted inbreeding coefficients in a pedigree and genomic context and asserted that the distribution of their genomic inbreeding coefficient was "more convenient statistically" than the traditional inbreeding coefficient based on pedigree relatedness. Gomez-Raya et al. (2015a, 2015b) fitted an exponential distribution to runs of homozygosity lengths as a "normalized" genomic inbreeding coefficient.

Mean estimates of Wright's relationship coefficient from the present study for the Trask 26 bulls with the different ancestor groups (range from 0.15 to 0.208) were higher than reported estimates from other cattle populations. Mean relatedness ranged from less than 0.02 in Gir (Oliveira et al., 2012), Brown Swiss (Worede et al., 2013), and Nellore (Barbosa et al., 2013) to a high of 0.065 in Brangus cattle in Mexico (Ramírez-Valverde et al., 2018). Leesburg et al. (2013) reported an average relationship coefficient of 0.24 for Line 1 Hereford (MacNeil, 2009) in the United States with South African Hereford cattle. Leesburg et al. (2014) reported from 0.048 to 0.086 relatedness of Line 1 animals to all Hereford cattle born in the years from 1980 to 2008. Domínguez Viveros et al. (2010; 2012) reported a higher range (0.024 to 0.13) for different ranches of fighting bulls.

There may be various reasons for these conflicting results for the tests conducted using β distributions and bootstrap methodology. First, it should be noted that the P-values from testing within the β distributions were of magnitudes ($0.06 < P < 0.25$) that would at least arouse suspicion of differences. The β distributions were approximations only from a visual perspective; our methodology for arriving at the final parameterization was primitive. It could be that these traits could be better characterized with another distribution; we believe this is the first effort to consider either with such a distribution. In general, resampling methods like the bootstrap are more reliable, because they are better at accounting for the variation that occurs among samples drawn from a given population (Hesterberg, 2014). In other words, resampling produces more uniform and/or repeatable results. Bootstrap resampling procedures were proposed as a way to test inbreeding coefficients at single loci (Dongen and van Backeljau, 1995).

It seemed reasonable to consider that groups of ancestors with substantial documented influence like the Most Progeny 30 or with the prominence and reputation of the Key AHA 15 would be fairly strongly related to most of the animals in the breed. The conclusion that this group of evaluated bulls (Trask Bulls 26) is more related to both of those than the remainder of the pedigree is of historical interest and in some cases, could be considered attributes that distinguish or add value to the group. It should be recognized that the remainder of the animals in the pedigree do not constitute the entire

AHA pedigree, but are themselves connected to the evaluated bulls.

The Trask Bulls 26 group was much more related to the Key Trask 19 ancestors; this fact also casts doubt on the parameterization of the R_{xy} values with a $\beta(\alpha = 0.70716, \beta = 9.16)$ distribution (Fig. 3) and the failure to reject the corresponding null hypothesis when testing in that context.

Conclusion that an inbreeding coefficient is higher in a highly selected subgroup than in the overall pedigree is not a surprise either. It is likely that F_x is underestimated for the earliest ancestors in the pedigree; we believe that if their pedigrees were included the overall mean F_x would increase.

CONCLUSION

Results provide a distributional assessment on the genetic influence of the Trask pedigree ancestors on the Trask bred bulls in recent/current herds. Testing against β distributions constructed by visual approximation appeared to be less than effective. Bootstrapping appeared to be a useful resampling method for values. These results may be foundational for non-genomic characterization of subpopulation distinctiveness in the development of mating strategies, especially for crossing between lines. Results may serve as a way to quantify prominent ancestor influence in groups, especially as DNA is likely unavailable from those animals. Assessment of genomic parameters that characterize relatedness, inbreeding, or runs of homozygosity may be enhanced by refinement of distributional assumptions of those parameters.

Conflict of interest statement. None declared.

LITERATURE CITED

Barbosa, A. C. B., C. H. M. Malhado, P. L. S. Carneiro, L. M. Muniz, D. P. Ambrosini, J. A. Carrillo, and R. Martins Filho. 2013. Population structure of Nellore cattle in northeastern Brazil. Rev. Bras. Zootec. 42:639–644.

Barros, E. A., M. N. Ribeiro, M. J. O. Almeida, and A. M. Araújo. 2011. Estrutura populacional e variabilidade genética da raça caprina Marota. Arch. Zootec. 60:543–552.

Bernardes, P. A., D. A. Grossi, R. P. Savegnago, M. E. Buzanskas, S. B. Ramos, E. P. Romanzini, D. G. F. Guidolin, L. A. F. Bezerra, R. B. Lobo, and D. P. Munari. 2016. Population structure of Tabapua beef cattle using pedigree analysis. Livest. Sci. 187:96–101.

Bouguila, N., D. Ziou, and E. Monga. 2006. Practical Bayesian estimation of a finite beta mixture through Gibbs sampling and its applications. Springer Science and Business Media, LLC. Stat. Comput. 16:215–225. doi:10.1007/s11222-006-8451-7

Bourdon, R. M. 2000. Understanding animal breeding. 2nd ed. Upper Saddle River, NJ, USA: Prentice Hall.

Cortes, O., N. Sevane, J.A. Baro, and J. Canon. 2014. Pedigree analysis of a highly fragmented population, the Lidia cattle breed. Livest. Sci. 167:1–8.

Dang, C. G., J. J. Lee, and N. S. Kim. 2011. Estimation of inbreeding coefficients and effective population size in breeding bulls of Hanwoo (Korean cattle). J. Anim. Sci. Tech. 53:297–302.

Domínguez Viveros, J., F. A. Rodríguez Almeida, R. Nuñez Domínguez, R. Ramírez Valverde, J. A. Ortega Gutiérrez, and A. Ruíz Flores. 2010. Análisis del pedigrí y efectos de la consanguinidad en el comportamiento del ganado de lidia mexicano. Arch. Zootec. 59:225.

Domínguez-Viveros, J., F. A. Rodríguez-Almeida, J. A. Ortega-Gutiérrez, and E. Santellano-Estrada. 2012. Análisis de la información genealógica y estimación de parámetros de poblaciones en bovinos de lidia y equinos de pura raza Española de México. Rev. Cient. Fac. Cienc. Vet., Univ. del Zulia. 22:443–450.

Dongen, S., and T. van Backeljau. 1995. One- and two-sample tests for single-locus inbreeding coefficients using the bootstrap. Heredity 74:129–135.

Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics. 4th ed. Essex, England: Longman Group Ltd.

Farnum, N. R., and L. W. Stanton. 1987. Some results concerning the estimation of beta distribution parameters in PERT. J. Opl. Res. Soc. 38:287–290.

Fernández, M., J. R. Justo, C. J. Rivero, S. Adán, D. Rois, and J. Lama. 2007. Analisis de la información genealógica en las razas bovinas Morenas Gallegas. Arch. Zootec. 56(Suppl.1):607–615.

Gomez-Raya, L., C. Rodríguez, C. Barragán, and L. Silió. 2015a. Genomic inbreeding coefficients based on the distribution of the length of runs of homozygosity in a closed line of Iberian pigs. Genet. Sel. Evol. 47:81. doi:10.1186/s12711-015-0153-1

Gomez-Raya, L., C. Rodríguez, C. Barragán, and L. Silio. 2015b. Normalización de coeficientes de consanguinidad basados en regiones de homocigosidad. Asoc. Interprof. Des. Agrario XVI Jornadas sobre Produccion Animal, Zaragoza, España. Tomo II: 570–572.

Goyache, F., J. P. Gutierrez, I. Fernandez, E. Gomes, I. Alvarez, J. Díez, and L. J. Royo. 2003. Using pedigree information to monitor genetic variability of endangered population: the Xalda sheep breed of Asturias as an example. J. Anim. Breed. Genet. 120:95–105.

Hayes, B. J., P. M. Visscher, and M. E. Goddard. 2009. Increased accuracy of artificial selection by using the realized relationship matrix. Genet. Res. (Camb). 91:47–60. doi:10.1017/S0016672308009981

Henderson, C. R. 1963. Selection index and expected genetic advance. In: Hanson, W. D., and H. F. Robinson, editors. Statistical genetics and plant breeding. Washington, DC: NAS-NRC Publication No. 982; p. 141–163.

Hesterberg, T. C. 2014. What teachers should know about the bootstrap: resampling in the undergraduate statistics curriculum. Am. Stat. 69:371–386. doi:10.1080/00031305.2015.1089789

Huisman, J., L. E. B. Kruuk, P. A. Ellis, T. Clutton-Brock, and J. M. Pemberton. 2016. Inbreeding depression in a wild mammal population. Proc. Nat. Acad. Sci. U.S.A. 113:3585–3590. doi:10.1073/pnas.1518046113

Leesburg, V. L. R., M. D. MacNeil, E. van Marle-Köster, O. Mapholi, and F. W. C. Neser. 2013. Impact of Line 1 germplasm on South African Hereford cattle. S. Afric. J. Anim. Sci. 43:153–158.

Leesburg, V. L., M. D. MacNeil, and F. W. Neser. 2014. Influence of Miles City Line 1 on the United States Hereford population. J. Anim. Sci. 92:2387–2394. doi:10.2527/jas.2013-6890

Legarra, A., I. Aguilar, and I. Misztal. 2009. A relationship matrix including full pedigree and genomic information. J. Dairy Sci. 92:4656–4663. doi:10.3168/jds.2009-2061

Lynch, M., and B. Walsh. 1998. Resemblance between relatives. In: Genetics and analysis of quantitative traits. Sunderland, MA, USA: Sinauer Associates, Inc.; p. 131–175.

MacNeil, M. D. 2009. Research contributions from seventy-five years of breeding Line 1 Hereford cattle at Miles City, Montana. J. Anim. Sci. 87:2489–2501.

MacNeil, M. D., D. D. Dearborn, L. V. Cundiff, C. A. Dinkel, and K. E. Gregory. 1989. Effects of inbreeding and heterosis in Hereford females on fertility, calf survival and preweaning growth. J. Anim. Sci. 67:895–901. doi:10.2527/jas1989.674895x

Nani, J. P., L. R. Bacheller, J. B. Cole, and P. M. VanRaden. 2020. Discovering ancestors and connecting relatives in large genomic databases. J. Dairy Sci. 103:1729–1734. doi:10.3168/jds.2019-17580

Oliveira, A. P. de, C. H. M. Malhado, P. L. S. Carneiro, R. Martins Filho, E. S. Silveira, L. de A. Souza, L. M. S. Muniz, and D. M. M. R. Azevedo. 2012. Pedigree analysis on the population of Gir cattle in Northeast Brazil. Rev. Bras. Zootec. 41:1153–1157.

Olkin, I., and T. A. Trikalinos. 2014. Constructions for a bivariate beta distribution. Stat. Prob. Lett. 96:54–60.

Pavlik, I., J. Sölkner, O. Kadlečík, R. Kasarda, G. Mészáros, C. Fuerst, and B. Fuerst-Waltl. 2014. Joint genealogical analysis as a tool for diversity evaluation in Pinzgau cattle populations. Archiv. Tierzucht. 57:1–12.

Peixoto, M. G. C. D., C. F. Poggian, R. S. Verneque, A. A. Egito, M. R. S. Carvalho, V. M. Penna, J. A. G. Bergmann, L. F. Viccini, and M. A. Machado. 2010. Genetic basis and inbreeding in the Brazilian Guzerat (*Bos indicus*) subpopulation selected for milk production. Livest. Sci. 131:168–174.

Pienaar, L., F. W. C. Neser, J. P. Grobler, M. M. Scholtz, and M. D. MacNeil. 2015. Pedigree analysis of the Afrikaner cattle breed. Anim. Genet. Res. 57:51–56.

R Core Team. 2017. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. URL https://www.R-project.org

Ramírez-Valverde, R., A. R. Delgadillo-Zapata, J. Domínguez-Viveros, J. A. Hidalgo-Moreno, R. Núñez-Domínguez, F. A. Rodríguez-Almeida, C. Reyes-Quiroz, and J. G. García-Muñiz. 2018. Análisis de pedigrí en la determinación de la diversidad genética de poblaciones bovinas para carne Mexicanas. Rev. Mex. Cien. Pec. 9:614–635.

Santana, M. L., Jr, P. S. Oliveira, J. P. Eler, J. P. Gutiérrez, and J. B. Ferraz. 2012. Pedigree analysis and inbreeding depression on growth traits in Brazilian Marchigiana and Bonsmara breeds. J. Anim. Sci. 90:99–108. doi:10.2527/jas.2011-4079

Scraggs, E., R. Zanella, A. Wojtowicz, J. F. Taylor, C. T. Gaskins, J. J. Reeves, J. M. de Avila, and H. L. Neibergs. 2014. Estimation of inbreeding and effective population size of full-blood Wagyu cattle registered with the American Wagyu Cattle Association. J. Anim. Breed. Genet. 131:3–10. doi:10.1111/jbg.12066

Steyn, J. W., F. W. C. Neser, C. Hunlun, and P. C. Lubout. 2012. Preliminary report: pedigree analysis of the Brangus cattle in South Africa. S. Afric. J. Anim. Sci. 42:511–514.

Sumreddee, P., S. Toghiani, E. H. Hay, A. Roberts, S. E. Agrrey, and R. Rekaya. 2019. Inbreeding depression in line 1 Hereford cattle population using pedigree and genomic information. J. Anim. Sci. 97:1–18. doi:10.1093/jas/sky385

Therneau, T. M., and J. Sinnwell. 2015. kinship2: pedigree functions. R package version 1.6.4. https://CRAN.R-project.org/package=kinship2

Trask, N. W. 1958. Managing a practical Polled Hereford herd. Memphis, TN: Polled Hereford World; p. 250.

Van Vleck, L. D. 1993. Selection index and introduction to mixed model methods for genetic improvement of animals: the green book. Boca Raton, FL, USA: CRC Press.

VanRaden, P. M. 2008. Efficient methods to compute genomic predictions. J. Dairy Sci. 91:4414–4423. doi:10.3168/jds.2007-0980

Worede, G. M., F. Forabosco, B. Zumbach, V. Palucci, and H. Jorjani. 2013. Evaluation of genetic variation in the international Brown Swiss population. Animal 7:1060–1066. doi:10.1017/S1751731113000281

Wright, S. 1922. Coefficients of inbreeding and relationship. Am. Nat. 56:330–338.

Yu, H., M. L. Spangler, R. M. Lewis, and G. Morota. 2017. Genomic relatedness strengthens genetic connectedness across management units. G3 (Bethesda). 7:3543–3556. doi:10.1534/g3.117.300151