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

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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, and 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 word: Beta distribution, inbreeding, relatedness, Hereford
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 effect 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. In the early 1900s Polled Hereford cattle became a recognized cattle breed, and with that came the breed’s own set of breeders and cattle herds. 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. An additional objective was to compare the average inbreeding coefficient of the Trask bulls to the average of all the cattle in their pedigrees. 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.
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.

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 ($A_{xy}$) is equal to two times the kinship coefficient matrix $\Theta_{xy}$.

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 $\sigma_{xy}$ 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 ($\beta$) distribution is a bivariate distribution with a parameter space of 0 to 1 (Bouguila et al., 2006; Olkin and Trikalinos, 2014). Two parameters, $\alpha$ and $\beta$ completely characterize this distribution. The first two moments of the $\beta$ distribution are:

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

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

and $\alpha$ and $\beta$ can be expressed as functions of moments and each other:

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

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

(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 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 $\alpha$ and $\beta$ parameters with each other and the distribution mean ($\mu$) were used to construct a grid of values for each parameter that preserved those relationships. Parameter values were successively altered in attempts to identify $\beta$ 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 $\beta$ 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 $\beta$ distributions (visually determined), those $\beta$ 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 $\mathbb{R}$ computing environment (once for each ancestor group).

Grids of parameter values were used to generate $\alpha$ and $\beta$ values that satisfied the above algebraic relationships of the parameters and the $\beta$ 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 $\beta$ distribution, that $\beta$ distribution was used to assess the 4th 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 $\mathbb{R}$ 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 $\mathbb{R}$ 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 $\beta$ with parameters $\alpha = 0.6493$ and $\beta = 5.6188$. This was not an excellent match as can be seen in Figure 1. The distribution of actual values had a higher peak than the plotted $\beta$ 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 $R_{xy}$ ($\mu = 0.15$) for the Trask Bull 26 with the Most Progeny 30 ancestors was located in the far-right tail of the distribution of the bootstrapped samples (Figure 2). The mean of the $R_{xy}$ bootstrap sample ($\mu = 0.104$) 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 ($\mu = 0.104$). Using this empirical distribution, the null hypothesis would be rejected ($P = 0.005$) in favor of an observed difference. 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 (Figure 3). The mean $R_{xy}$ of the Trask Bull 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 Bull 26 with the Key Trask 19 ancestors was positioned in the far tail of the distribution for the bootstrapped values (Figure 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 Bull 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 (26 Trask Bull 26 with Key AHA 15 ancestors) and the β($\alpha = 0.564$, $\beta = 7.081$) distribution were the most similar of all comparisons (Figure 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 Bull 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 Bull 26 with the Key AHA 15 ancestors is in the far right tail of the bootstrapped $R_{xy}$ distribution (Figure 6). The empirical $P$-value ($P < 0.0001$) authorized the rejection of the null hypothesis; the mean $R_{xy}$ of the (n = 26) Trask Bull 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.

**$F_x$ 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 β($\alpha = 0.468$, $\beta = 7.929$) distribution and the actual $F_x$ distribution of the entire pedigree matched reasonably well (Figure 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 Bull 26 did not differ from the overall $F_x$ mean ($P = 0.105$).

The plotted bootstrap samples are shown in Figure 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 reports of 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 (Scrags 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, b) 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), 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 Bull 26 group was much more related to the Key Trask 19 ancestors; this fact also casts doubt on the parameterization of the $R_x$ values with a $\beta(\alpha = 0.70716, \beta = 9.16)$ distribution (Figure 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 $\beta$ 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.
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| Animal Name                | AHA 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         |

\(^1\text{AHA: American Hereford Association}\)
Table 2. Hereford bulls classified as animals with the most progeny in the pedigree (Most Progeny 30)

| Animal name       | AHA\(^1\) 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          |

\(^1\)AHA: American Hereford Association
Table 3. Hereford bulls classified as important ancestors in Neil Trask lines of cattle (Key Trask 19)

| Animal name          | AHA\(^1\) 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                 |                      |                  |

\(^1\)AHA: American Hereford Association
Table 4. Hereford bulls classified as renowned with substantial influence on the breed (Key AHA 15)

| Animal name          | AHA\(^1\) 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                   |                      |                  |

\(^1\) AHA: American Hereford Association
