1 Genomic-polygenic evaluation for ultrasound and weight traits in Angus-Brahman
2 multibreed cattle with the Illumina3k chip
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Abstract

The objectives of this study were to estimate the proportion of additive genetic and phenotypic variances explained by the SNP markers in the Illumina3K chip for 4 postweaning ultrasound carcass and weight traits, to compare rankings of calf predicted additive genetic values with 3 models, and to evaluate trends of calf predictions as Brahman fraction increased from 0 to 1. Traits were postweaning ultrasound measures of ribeye area (UREA), backfat thickness (UFAT), intramuscular fat (UPIMF), and body weight at time of ultrasound (UW). Models were genomic-polygenic, genomic, and polygenic. Phenotypes and genotypes were from 623 bulls, heifers, and steers ranging in breed composition from 100% Angus to 100% Brahman fed for 90 d at a GrowSafe automated feeding facility from 2006 to 2010. Variance components were estimated with Markov Chain Monte Carlo procedures (option VCE, program GS3) using a single-trait genomic-polygenic model. Fixed effects were contemporary group (year-pen), age of dam, sex of calf, age of calf, Brahman fraction of calf, and heterozygosity of calf. Random effects were additive SNP, animal polygenic, and residual effects. Models without polygenic effects were used for genomic predictions, and without additive SNP effects for polygenic predictions. Fractions of additive genetic variances explained by the SNP in the Illumina3K chip were 9% for UREA, 38% for UBF, 6% for UPIMF, and 8% for UW. Phenotypic variance fractions explained by Illumina3K SNP were 3.7% for UREA, 9.7% for UBF, 3.2% for UPIMF, and 4.6% for UW. Substantially higher rank correlations existed between genomic-polygenic and polygenic models (0.89 to 0.99) than between genomic-polygenic and genomic (0.64 to 0.79), and genomic and polygenic (0.51 to 0.65) models. Genomic-polygenic, genomic, and polygenic predicted values tended to decrease as Brahman fraction of calf increased suggesting that calves with higher percentage

Brahman grew more slowly and had less desirable ultrasound carcass traits. However, there were calves with high, medium, and low predicted genetic values across the Angus-Brahman spectrum, suggesting that selection of animals with desirable postweaning ultrasound carcass and growth traits using a genomic-polygenic strategy would be effective in this multibreed population. Insofar as this multibreed herd represents commercial operations in Florida and the Southern region of the US, selection of commercial calves for these postweaning traits would likely increase their rate of improvement in Brahman and Brahman crossbred populations.

Key words: cattle, genomic, multibreed, polygenic, ultrasound

1. Introduction

Acceptable carcass and meat quality characteristics are major economic factors for beef cattle enterprises. This aim is particularly challenging for producers in the Southern US due to the widespread use of *Bos taurus*-Brahman crossbred cattle needed to withstand the hot and humid conditions of the region. Brahman cattle have some carcass and meat quality characteristics (e.g., ribeye area, marbling, tenderness) that are less desirable than those of *Bos taurus* breeds (Elzo et al., 2012a; Johnson et al., 1990; Pringle et al., 1997; Wheeler et al., 2010). Consequently, identification of animals with optimal carcass characteristics in *Bos taurus*-Brahman populations is of primary interest. However, carcass and meat quality traits are expensive and labor intensive to measure. A cost effective alternative to increase the amount of phenotypic information on carcass traits is ultrasound. Carcass traits measured by real-time ultrasound are closely related to actual carcass traits at slaughter and with total meat yield (Houghton and Turlington, 1992; Perkins et al., 1992). Another alternative to help identify animals with desirable carcass characteristics is the use

of genotype data. The development of marker chips has allowed the utilization of genotypic and phenotypic information to predict the genetic merit of animals (Meuwissen et al., 2001; Matukumalli et al., 2009). However, the elevated cost of high-density marker chips for cattle (e.g., Illumina50K, IlluminaHD) has prevented their widespread use. Low-density chips such as the Illumina GoldenGate Bovine3K BeadChip (Illumina3K heretofore; Illumina, 2011a) provide a reasonable alternative to genotyping. However, the low proportion of additive genetic variance explained by markers in these chips has made it necessary to include a polygenic term in the models (Goddard, 2009; Snelling et al., 2011; Elzo et al., 2012b).

A multibreed Angus-Brahman herd was developed at the University of Florida (UF) in 1989 to conduct genetic research on economically important traits applicable to *Bos taurus*-Brahman populations under subtropical conditions. Thus, the objectives of this study were: 1) to estimate the proportion of additive genetic and phenotypic variances explained by the SNP markers in the Illumina3K chip for 4 postweaning ultrasound carcass and body weight traits, 2) to compare rankings of calves evaluated with genomic-polygenic, genomic, and polygenic models for these 4 traits, and 3) to evaluate trends of additive polygenic, genomic, and genomic-polygenic predicted values as Brahman fraction increased from 0 to 1 in the UF multibreed Angus-Brahman herd.

2. Materials and methods

2.1. Animals, data, and traits

The University of Florida Institutional Animal Care and Use Committee (IACUC number D477) approved the research protocol utilized in this project. Animals used in the study belonged to the multibreed Angus-Brahman (MAB) herd of the University of Florida.

Cattle were classified into six mating groups according to their expected Angus (A) and Brahman (B) breed composition: Angus = (1.0 to 0.80) A (0.0 to 0.20) B, ¾ A ¼ B = (0.79 to 0.60) A (0.21 to 0.40) B, Brangus = (0.625) A (0.375) B, ½ A ½ B = (0.59 to 0.40) A (0.41 to 0.60) B, ¼ A ¾ B = (0.39 to 0.20) A (0.61 to 0.80) B, and Brahman: (0.19 to 0.0) A (0.81 to 1.00) B. Mating was diallel (Elzo and Wakeman, 1998). Sires from each breed group (3 to 5 sires per year) were mated across dams from all breed groups. In addition, one or more sires were repeated in two years to generate connectedness over time.

Three postweaning ultrasound carcass measurements and one body weight record were obtained from 623 calves born between 2006 and 2010 (90 Angus, 123 ¾ A ¼ B, 114 Brangus, 154 ½A ½B, 69 ¼ A ¾ B, and 73 Brahman). There were 56 bulls, 310 heifers, and 257 steers in the dataset. Calves were produced by 64 sires (12 Angus, 11 ¾ A ¼ B, 14 Brangus, 8 ½ A ½ B, 8 ¼ A ¾ B, and 11 Brahman) and 330 dams (53 Angus, 61 ¾ A ¼ B, 52 Brangus, 74 ½ A ½ B, 42 ¼ A ¾ B, and 47 Brahman).

Postweaning traits were ultrasound ribeye area (UREA, cm^2), ultrasound percent of intramuscular fat (UPIMF, %), ultrasound backfat thickness (UBF, cm), and body weight at the time ultrasound measurements were taken (UW, kg). Ultrasound traits were collected by a trained technician at the end of a 70-day feed efficiency trial using an Aloka 500 ultrasound system (Hitachi Aloka Medical, Ltd., Wallinford, Connecticut, USA). Ultrasonic images were analyzed with UICS Scanning Software by Walter and Associates, LLC (Ames, Iowa, USA) to obtain phenotypic records of UREA, UBF, and UPIMF. Live weight (UW) was obtained at the same time as ultrasound traits were measured.

2.2. Feeding and management

Calves were born at the Beef Research Unit of the University of Florida from December to March and remained at the unit until weaning in August. After weaning calves were fed a preconditioning diet for 3 to 6 weeks. This diet comprised concentrate (1.6 kg to 3.6 kg per day; 14.0 % CP; 488 Pellet, Medicated Weaning Ration, Lakeland Animal Nutrition, Lakeland, Florida; and soy hull pellets), bahiagrass (*Paspalum notatum*) hay, and ad libitum access to a mineral supplement (UF University Special Hi-Cu Mineral, University of Florida, Animal Science Department, Gainesville, Florida). Subsequently, calves were moved to the Feed Efficiency Facility of the Institute of Food and Agricultural Sciences of the University of Florida (UFEF) in Marianna, Florida, for a period of 90 days to conduct a postweaning feed efficiency trial. The trial lasted for 70 d after an initial adjustment period of 21 d.

Calves were individually identified using half-duplex passive transponder ear tags (Allflex USA Inc., Dallas-Fort Worth, TX) upon arrival at the UFEF. Subsequently, calves within sire group (A, ¾ A ¼ B, Brangus, ½ A ½ B, ¼ A ¾ B, and B) by sex (bull, heifer, and steer) subclasses were randomly allotted to pens (108 m^2/pen; 2 GrowSafe nodes per pen). The stocking rate was 15 animals per pen and 7.5 animals per GrowSafe node on average. Feed at UFEF was offered ad libitum. Feed included various percentages of whole corn or corn gluten, cottonseed hulls, molasses, chopped grass hay, and a vitamin-mineral-protein supplement (FRM, Bainbridge, GA). The mean dry matter, crude protein, net energy for maintenance, and net energy for gain from 2006 to 2010 were 12.9%, 89.2%, 1.6 mcal/kg DM, and 1.0 mcal/kg DM. Phenotypic individual feed intake was collected in real-time using GrowSafe software, and body weights were recorded every 2 weeks.

2.3. Tissue sampling and genotyping

Vacutainer tubes coated with EDTA (10 mL) were used to collect blood samples from calves at weaning, and kept at 4°C before sending them to New Mexico State University (NMSU) for processing and storage at -80 °C. Processing at NMSU involved centrifugation for 30 min at 1,875 g at 4°C, recovery of white blood cell supernatant (i.e., buffy coat), and PBS added to a volume of 1.0 mL (Beauchemin et al., 2006). Subsequently, 0.05 mL of each was sent to GeneSeek (Gene Seek, Inc., Lincoln, NE, USA) to obtain genotypes for markers in the Illumina GoldenGate Bovine3K BeadChip (Illumina, 2011a).

2.4. Genomic-Polygenic Variance Components

Additive genomic and polygenic variance components were obtained for each trait using a genomic-polygenic univariate animal model (VanRaden, 2008; Legarra et al., 2008; Snelling et al., 2011). The model, in matrix notation, was as follows:

$$y = Xb + Za + Tu + e$$

Where y was a vector of records (UREA, UPIMF, UBF, or UW), b was a vector of unknown fixed effects: contemporary group (year-pen), age of dam, sex of calf, age of calf, Brahman fraction of calf, and heterozygosity of calf, a was an unknown random vector of additive marker SNP effects (AS), u was an unknown random vector of animal additive polygenic effects (AP), e was a vector of residuals, X was a known incidence matrix relating records in vector y to fixed effects in vector b, Z was a known incidence matrix relating observations in vector y to marker SNP effects in vector a through the number of "2" alleles (0, 1 or 2) in each marker SNP locus represented in the Illumina3K chip, and T was a known incidence matrix relating records in vector y to animal additive polygenic effects in vector u. The AP effects were assumed to have mean zero and covariance matrix

155 = A * additive polygenic variance, where A is the additive relationship matrix. The AS
156 effects were assumed to have null expected value and covariance matrix = I * additive SNP
157 variance, where I is the identity matrix. Residual effects were assumed to have mean zero
158 and covariance matrix = I * residual variance.

159 Monte Carlo Markov Chain (MCMC) procedures were used to compute variance
160 components and heritabilities for all traits. Computations were performed using the VCE
161 option of software GS3 (Legarra, 2009; Number of iterations = 120,000; Burn-in = 20,000;
162 Thinning = 100; Correction = 10,000). Prior values for additive polygenic and residual
163 variances for each trait were obtained by computing restricted maximum likelihood
164 estimates (REML) estimates with program ASREML (Gilmour et al., 2006) using
165 univariate polygenic animal models. These univariate polygenic models included all the
166 effects in the genomic-polygenic model, except for AS effects. Preliminary values for
167 additive SNP variances were computed using the expression $\mathrm{VSNP} = \frac{\widehat{V_g}}{\sum_{i=1}^{2899} 2p_i(1-p_i)}$
168 (Habier et al., 2007; VanRaden, 2008; Gianola et al., 2009; Legarra et al., 2009; Aguilar et
169 al., 2010), where $\widehat{V_g}$ was the REML estimate of additive polygenic variance obtained with
170 ASREML, p_i is the frequency of the "2" allele in the i^{th} marker SNP locus of the
171 Illumina3K chip, and 2899 was the total number of SNP considered herein. All SNP
172 markers in the Illumina3K chip, except for BTB-00291093 were included in the analysis.
173 This marker was excluded because it provided no genotypic information for any of the
174 animals in the population. A total of 1,200 MCMC samples were obtained with GS3, each
175 one with a value of additive SNP (VSNP), additive polygenic (VAPO) and residual (VRES)
176 for each trait. Then, VAGO, total additive genetic variances (VGTot), and phenotypic
177 variances (Phenvar) were computed for each MCMC sample as follows: 1) $\mathrm{VAGO} =$

178 VSNP $* \sum_{i=1}^{2899} 2p_i(1-p_i)$, 2) VGTot = VAGO + VAPO, and 3) Phenvar = VAGO +
179 VAPO + VRES. These variance components were used to obtain heritabilities and ratios of
180 VAGO to VGtot and VAGO to Phenvar. These last two ratios were computed to estimate
181 the proportion of genetic and phenotypic variances accounted for by the 2,899 markers in
182 the Illumina3K chip. Finally, estimates and dispersions of each variance component and
183 variance ratio in the Angus-Brahman multibreed population for UREA, UPIMF, UBF, and
184 UW were obtained as means and standard deviations of their values across the 1,200
185 MCMC samples.
186
187 *2.5. Genomic-polygenic, genomic, and polygenic predictions*
188 Best linear unbiased predictions of AP and AS were obtained by solving the mixed
189 model equations using a Gauss-Seidel iterative algorithm (option BLUP in program GS3;
190 Legarra, 2009). Values of VAGO, VAPO and VRES needed for the mixed model
191 equations were those computed using genomic-polygenic univariate animal models as
192 described above. A convergence criterion of 10^{-4} was used to solve the mixed model
193 equations for UREA, UPIMF, UBF, and UW with the genomic-polygenic, genomic and
194 polygenic models.
195 Calf genomic-polygenic predictions for all traits were computed as $\widehat{GPBV_j} =$
196 $p_{B_j}(B-A)^0 + \widehat{AP_j} + \sum_{i=1}^{2899} w_{ij} * \widehat{AS_i}$, where $\widehat{GPBV_j}$ is the additive genomic-polygenic value
197 of calf j, p_{B_j} is the expected fraction of Brahman in calf j, $(B-A)^0$ is the estimate of the
198 difference between the Brahman and Angus slopes, $\widehat{AP_j}$ is the additive polygenic value of
199 calf j, w_{ij} is the number of copies (0, 1 or 2) of the second allele in SNP locus i of calf j,
200 and $\widehat{AS_i}$ is the BLUP of the substitution effect of allele 2 for allele 1.

Calf genomic predictions for all traits were computed using a genomic model (i.e., a genomic-polygenic model without polygenic effects). Calf predicted additive genomic values were computed as follows: $\widehat{GBV}_j = p_{B_j}(B - A)^0 + \sum_{i=1}^{2899} w_{ij} * \widehat{AS}_i$, where ($\widehat{GBV}_j$) = predicted additive genomic value of calf j, and all the other elements were as defined above, but computed using a genomic model.

Predicted additive polygenic values were obtained using a polygenic animal model, i.e., a genomic-polygenic model without the AS effects. Thus, the predicted additive polygenic value for the j^{th} calf ($\widehat{PBV}_j$) was obtained as follows: $\widehat{PBV}_j = p_{B_j}(B - A)^0 + \widehat{AP}_j$, where terms were as previously defined.

To assess the impact of the inclusion of genomic information on calf rankings based on predicted values, Spearman rank correlations among calf rankings from genomic-polygenic, genomic and polygenic models were computed using the CORR procedure of SAS (SAS Institute Inc., Cary, NC).

To determine trends of $\widehat{GPBV}$, $\widehat{GBV}$ and $\widehat{PBV}$ on Brahman fraction of calf for UREA, UBF, UPIMF and UW, linear regressions of calf predictions on Brahman fraction of calf were computed with the REG procedure of SAS.

Lastly, predicted SNP values for UREA, UBF, UPIMF, and UW from the genomic-polygenic model were standardized, i.e., divided by the standard deviations of the predicted SNP values (SDSNP) and plotted against chromosome number to study their distribution across chromosomes and their relative importance across traits.

3. Results and discussion

223 Number of calves, means and standard deviations for each breed group and the
224 complete dataset are presented in Table 1. Number of calves per breed group ranged from
225 67 (¼ A ¾ B for UPIMF) to 154 (½ A ½ B for UREA, UBF and UW). The range of means
226 per breed group went from 55.7 cm^2 (Brahman) to 62.6 cm^2 (¼ A ¾ B) for UREA, from
227 0.61(¾A¼B) to 0.68 cm (¼ A ¾ B) for UBF, from 2.55 (¼ A ¾ B) to 3.3% (A) for
228 UPIMF, and from 317.9 kg (B) to 356.2 kg (¾ A ¼ B) for UW. Overall means were 58.9
229 cm^2 for UREA, 0.63 cm for UBF, 2.89% for UPIMF, and 346.3 kg for UW.
230
231 *3.1. Genomic and polygenic variance components*
232 Posterior means and standard deviations for additive genomic, polygenic, and total
233 genetic as well as phenotypic variances estimated using genomic-polygenic models are
234 shown in Table 2. The value $\sum_{i=1}^{2899} 2p_i(1-p_i)$ required for the computations of VAGO
235 estimates was equal to 1,223.38. The VSNP values were $1.7*10^{-3} \pm 1.4*10^{-3}$ cm^4 for
236 UREA, $1.8*10^{-6} \pm 1.1*10^{-6}$ cm^2 for UBF, $1.5*10^{-5} \pm 1.3*10^{-5}$ % for UPIMF and 0.05 ±
237 0.04 kg^2 for UW. Thus, the VAGO estimates were 2.06 ± 1.70 cm^4 for UREA, 0.002 ±
238 0.001 cm^2 for UBF, 0.02 ± 0.02% for UPIMF and 56.7 ± 45.55 kg^2 for UW. For
239 comparison purposes, Table 2 also shows additive genetic (VGPO) and phenotypic
240 variances (PhenVarPO) from polygenic models. Estimates of VGPO tended to be similar
241 or smaller than VGTot values suggesting that genomic-polygenic models tended to account
242 for a larger fraction of the genetic variation in this multibreed herd than polygenic models.
243 *3.2. Heritability ratios*
244 Heritabilities of UREA, UBF, UPIMF and UW computed using genomic-polygenic
245 models are presented in Table 3. The heritability for UREA was moderate (0.39 ± 0.10)
246 and within the range of values for US Angus yearling bulls and heifers (0.28 ± 0.03 to 0.45

247 ± 0.09; Hassen et al., 2004; MacNeil and Northcutt, 2008), but higher estimates for US
248 Angus steers (0.18 ± 0.06 to 0.29; Kemp et al., 2002; MacNeil and Northcutt, 2008).
249 Similarly, the UREA heritability value was also within the range of estimates for Angus
250 bulls and heifers in Australia (0.37 to 0.46; Reverter et al., 2000), Brangus cattle in the US
251 (0.29 ± 0.04 to 0.63 ± 0.11; Fortes et al., 2012; Moser et al., 1998; Peters et al., 2012;
252 Stelzleni et al., 2002), and Nellore cattle in Brazil (0.34 to 0.46; Yokoo et al., 2008;
253 Pinheiro et al., 2011).

254 The UBF heritability estimate (0.25 ± 0.08) was within the range of values reported
255 for Brangus in the US (0.11 ± 0.03 to 0.40 ± 0.11; Fortes et al., 2012; Moser et al., 1998;
256 Peters et al., 2012; Stelzleni et al., 2002) and Nellore cattle in Brazil (0.20 ± 0.05 to 0.52;
257 Yokoo et al., 2008; Pinheiro et al., 2011). Conversely, UBF heritability values here were
258 lower than estimates for Angus bulls (0.39 ± 0.03; MacNeil and Northcutt, 2008), heifers
259 (0.46 ± 0.04; MacNeil and Northcutt, 2008), and steers (0.26 ± 0.08 to 0.39; Kemp et al.,
260 2002; MacNeil and Northcutt, 2008) in the US and Angus heifers in Australia (0.47;
261 Reverter et al., 2000).

262 The heritability estimate for UPIMF obtained here (0.53 ± 0.12) was higher than
263 values obtained for Angus bulls (0.38 ± 0.03), heifers (0.40 ± 0.03), and steers (0.26 ± 0.09)
264 in the US (MacNeil and Northcutt, 2008), Angus bulls (0.18) and heifers (0.47) in Australia
265 (Reverter et al., 2000), Brangus cattle in the US (0.16 to 0.42 ± 0.10; Fortes et al., 2012;
266 Moser et al., 1998; Peters et al., 2012; Stelzleni et al., 2002), and Angus steers in the US
267 (0.31 ± 0.03; MacNeil et al., 2010).

268 The high heritability estimate for UW (0.54 ± 0.11) was comparable to estimates in
269 the upper range of values found in the literature (0.27 ± 0.04 to 0.53; Fortes et al., 2012;
270 Moser et al., 1998; Peters et al., 2012; Snelling et al., 2010; Stelzleni et al., 2002). The

271 heritabilities for UREA, UPIMF, UBF, and UW obtained here suggested that there may be
272 substantial additive genetic variation available in the multibreed Angus-Brahman
273 population to effectively select for these traits.

274 Heritabilities computed using polygenic models (Table 3) were similar to those
275 computed with genomic-polygenic models for UREA but lower for UBF, UPIMF, and UW
276 suggesting that genomic-polygenic models tended to explain a larger fraction of the genetic
277 variation in this multibreed population.

278 *3.3. Additive genomic to additive genetic and to phenotypic variance ratios*

279 The VAGO to VGTot ratios were low for all traits, except for UBF (Table 3).
280 Similarly, VAGO to phenotypic variance (Phenvar) ratios (Table 3) were low for all traits.
281 Values of VAGO to VGTot ranged from 0.06 ± 0.05 for UPIMF to 0.38 ± 0.17 for UBF.
282 These ratios were all lower than those obtained for feed efficiency and postweaning gain
283 traits (0.11 ± 0.09 to 0.25 ± 0.17) in this multibreed population (Elzo et al., 2012b).
284 Estimates of VAGO to Phenvar ratios ranged from 0.032 ± 0.027 for UPIMF to 0.097 ±
285 0.056 for UBF. Thus, the proportion of phenotypic variance accounted for by the SNP in
286 the Illumina Bovine3K chip suggested that only a small fraction of the total variation for
287 ultrasound traits was accounted for by the 2,899 markers from the Illumina3K chip.

288 The values of VAGO to Phenvar ratios for UREA (0.037 ± 0.030), UBF (0.097 ±
289 0.056), UPIMF (0.032 ± 0.027), and UW (0.08 ± 0.06) were substantially lower than the
290 values obtained for UREA (0.22), UBF (0.17), UPIMF (0.28), and 365-d weight (0.19) in a
291 population of Brangus heifers (n = 748 to 761) using 53,692 SNP loci from the Illumina
292 BovineSNP50 chip (Peters et al., 2012). Similarly, VAGO to Phenvar ratios here were
293 somewhat lower than values estimated for UREA (0.057; 14 QTL), UBF (0.207), and
294 UPIMF (0.066; 14 QTL) in a population of 418 *Bos taurus* crossbred steers in Canada

using a customized panel of 4,592 SNP markers (Nalaila et al., 2012). The lower VAGO to Phenvar fractions obtained with the 2,899 SNP from the Illumina3K chip here compared to the higher ratios with the 53,692 SNP of the Illumina BovineSNP50 chip (Illumina, 2011b) seem reasonable. However, both sets of values were substantially lower than the complete accountability of the genetic variation for feed efficiency and postweaning growth traits in a population of 1,159 crossbred steers from the Cycle VII of the USMARC Germplasm Evaluation Project with the Illumina BovineSNP50 chip (Snelling et al., 2011). When Snelling et al. (2011) tested subsets of the BovineSNP50 chip, they found out that significant SNP ($P < 0.0001$) accounted for 0.22 (postweaning gain) to 0.51 (metabolic midtest body weight) of the additive genetic variance. These results from Snelling et al. (2011) and those of Nalaila et al. (2012) suggest that a reduced set of SNP from high density marker chips that are highly associated with QTL may be sufficient to account for most of the variation for these quantitative traits. However, disagreement between the VAGO to Phenvar ratios obtained by Peters et al. (2012) and Snelling et al. (2011) for postweaning weight traits suggest that the additive genetic variance accounted for by SNP markers from the Illumina BovineSNP chip will vary depending on the genetic architecture of the population. Thus, results from one cattle population may not apply to cattle populations with different breed composition, linkage disequilibrium patterns (Snelling et al., 2011), and living under different environmental conditions.

3.4. Ranking of animals evaluated with genomic-polygenic, genomic, and polygenic models

Table 4 shows the Spearman rank correlations among rankings based on predictions of calf genomic-polygenic, genomic, and polygenic values for UREA, UBF, UPIMF and UW. All rank correlations were highly significant ($P < 0.0001$). The highest correlations

were between rankings of animals from genomic-polygenic and polygenic models (0.99 for UREA, 0.89 for UBF, 0.99 for UPIMF, and 0.99 for UW). The lowest correlations among animal rankings were those between BLUP from polygenic and genomic animal models (0.58 for UREA, 0.51 for UBF, 0.60 for UPIMF, and 0.65 for UW). Rank correlations between BLUP from genomic-polygenic and genomic models were in between (0.65 for UREA, 0.79 for UBF, 0.64 for UPIMF and 0.70 for UW). Rank correlations among models for ultrasound carcass and weight traits were similar to those obtained for feed efficiency and postweaning gain traits with the Illumina3K chip in this multibreed population (Elzo et al., 2012b), and with the Illumina BovineSNP50 chip in a crossbred cattle population at USMARC (Snelling et al., 2011). Rank correlations indicated that the incorporation of genomic information from the Illumina Bovine3K chip to the polygenic model had little impact on the ranking of animals in this population. Except for UBF, BLUP rankings from genomic-polygenic and polygenic models were nearly identical. Conversely, the largest amount of re-ranking occurred between calves ranked by their BLUP from polygenic and genomic models. Thus, rank correlations among BLUP from the 3 models suggested that a genomic-polygenic model would need to be used instead of a genomic model to evaluate and select animals in this population. It could be argued that some genetic progress could be made by using the Illumina3K chip to evaluate animals using genomic models in commercial cattle populations without data or pedigree. However, the low rank correlations between BLUP from genomic-polygenic and genomic or between polygenic and genomic models obtained here suggests that a large number of animals would need to be genotyped to increase the chance of identifying superior ones. This will likely increase costs beyond the potential benefits to be obtained by genomic selection in these populations. Alternatively, in populations with records and pedigree

343 information, the Illumina3K or other low density chips could be used in combination with
344 higher density chips, and perform imputation (Gengler et al., 2007; Howie et al., 2009;
345 Weigel et al., 2010; Sargolzaei et al., 2011; VanRaden et al., 2011) to the higher density
346 chip before conducting a genomic-polygenic evaluation. Considering the amount of
347 genetic variation accounted for by the Illumina BovineSNP50 chip, the results of Snelling
348 et al. (2011) would suggest this to be a potentially favorable alternative, but the results of
349 Peters et al. (2012) would suggest otherwise. The higher cost of the Illumina BovineSNP50
350 and other higher density chips would preclude their use in most commercial beef cattle
351 operations in the US. Use of low-density chips followed by imputation may, however, be a
352 reasonable alternative to increase the accuracy of evaluation of valuable young animals in
353 beef cattle operations that can genotype large numbers of animals.
354
355 *3.5. Predicted SNP values*
356 Predicted SNP values ranged from -0.0131 to 0.0135 cm^2 for UREA, -0.0006 to
357 0.0007 cm for UBF, -0.0010 to 0.0011% for UPIMF and from -0.083 to 0.079 kg for UW.
358 Predicted SNP values for all traits were divided by their corresponding SDSNP to compare
359 SNP effects across traits. The SDSNP were equal to 0.0410 cm^2 for UREA, 0.0013 cm for
360 UBF, 0.0039% for UPIMF and 0.0021 kg for UW. Figure 4 shows standardized predicted
361 SNP values for UREA ordered by chromosome. Similar figures were constructed for all
362 traits. Once the predicted SNP values were standardized, distribution frequencies were
363 constructed for each trait. Table 5 shows the distribution frequencies with the marginal
364 relative and absolute frequencies according to various SDSNP fractions around the mean.
365 Most SNP predictions for UREA, UBF, UPIMF and UW were within the range of -0.4 to
366 0.4 SDSNP. Only one trait, UBF, had 2 predicted SNP values between 0.4 and 0.5 SDSNP.

All traits, except UPIMF, had SNP with predicted values below -0.3 and above 0.3 SDSNP. The trait with the largest number of SNP beyond ± 0.3 SDSNP was UBF (n = 30; 1.04%), followed by UW (n = 11; 0.38%), and UREA (n = 5; 0.08%). Lowering the threshold to ± 0.2 SDSNP increased the number and percentage of SNP beyond this range to 191 (6.59%) for UBF, 146 (5.03%) for UW, 39 (1.25%) for UREA, and 33 (1.14%) for UPIMF. Thus, a larger number of SNP markers in the Illumina3K chip were in linkage disequilibrium with QTL affecting UBF and UW than UREA and UPIMF. A supplemental file containing the Illumina3K index number, SNP name, NCBI SNP identification, chromosome number, SNP location within chromosome, SNP predicted value and SNP predicted value divided by the SDSNP of the trait is available at http://www.sciencedirect.com/science/journal/xx. The number and percentage of SNP beyond ± 0.2 SDSNP for UBF here was larger than corresponding values for all feed efficiency and postweaning gain traits in this same population (Elzo et al., 2012b). However, values for UW were similar to those for postweaning gain (n = 144; 4.96%) and feed conversion ratio (n = 116; 4.01%), and values for UREA and UPIMF were similar to those for RFI (n = 17, 0.59%) and DFI (n = 12; 0.41%; Elzo et al., 2012b).

Standardized predicted SNP values were plotted against chromosome number for all traits to visualize the location of influential SNP markers across the genome. Figure 4 shows this plot for UREA. As with feed efficiency and postweaning gain traits (Elzo et al., 2012b), there were SNP with values beyond ± 0.1 SDSNP across all chromosomes for all traits. Conversely, SNP with predicted values above and below 0.2 SDSNP existed in all chromosomes except 4, 6, 11, 17, 18, 23, 26, 27, and 28 for UREA, all chromosomes except 4, 11, 12, 14, 17, 18, 20, 21, 23, and 29 for UPIMF, all chromosomes for UBF, and all chromosomes except 21 and 29 for UW. This distribution pattern of SNP associated

391 beef carcass traits located throughout the genome was also found for ultrasound traits by
392 Nalaila et al. (2012) and Peters et al., (2012). The same pattern has also been found for
393 meat and carcass traits (Bolormaa et al., 2011b), and growth and feed efficiency traits
394 (Bolormaa et al., 2011a; Mujibi et al., 2011a, b; Snelling et al., 2010, 2011; Elzo et al.,
395 2012b; Peters et al., 2012) lending support to the assumption that quantitative traits are
396 affected by large numbers of alleles of small effect spread across the genome.
397
398 *3.6. Trends for genomic-polygenic, genomic, and polygenic predictions from Angus to*
399 *Brahman*
400 The multibreed population contained calves from 100% Angus to 100% Brahman
401 that had high, medium and low predicted genomic-polygenic, genomic, and polygenic
402 values for UREA, UBF, UPIMF and UW. Calf genomic-polygenic, genomic, and
403 polygenic predictions tended to decrease as Brahman fraction of calf increased. Linear
404 regression coefficients (Table 6) were negative for all models for UBF ($P < 0.0001$) and
405 UW ($P = 0.0252$ to $P < 0.0001$), but only for genomic models for UREA ($P < 0.0001$) and
406 UPIMF ($P = 0.0107$). All other regression coefficients were non-significant. To
407 graphically illustrate these trends in calf predicted values from Angus to Brahman, Figures
408 1, 2, and 3 show predicted additive genomic-polygenic values, predicted genomic values,
409 and predicted polygenic values for all evaluated calves ordered by their expected Angus
410 and Brahman breed composition. Trends in calf predicted values indicate that UREA,
411 UBF, and UW tended to decrease as Brahman fraction of the calf increased. This negative
412 trend also existed for UPIMF for the genomic model. Smaller ribeye areas and lower
413 marbling are undesirable under the current standards of carcass quality in the US. Small
414 ribeye areas are associated with lower meat yield (i.e., higher yield grades) and lower

415 marbling scores are associated with lower quality grades both of which carry discounts
416 under current US grid pricing system (DiCostanzo and Dahlen, 2000; Greer and Trapp,
417 2000). However, there was a sizeable amount of variation for all ultrasound traits among
418 calves of all breed compositions including Brahman, suggesting that selection for desirable
419 UREA, UBF, UPIMF, and UW could be pursued in this Angus-Brahman multibreed
420 population. Feeding and management in this herd was similar to commercial beef cattle
421 populations in Florida, and Angus, Brangus, and Brahman sires were brought from the
422 Angus, Brangus, and Brahman national populations. Thus, to the extent that this
423 multibreed herd represents commercial cattle herds of similar breed composition in Florida
424 and the Southern region of the US, a genomic-polygenic evaluation and preliminary
425 selection of bull and heifer calves postweaning for UREA, UBF, and UPIMF would be an
426 important step to accelerate the rate of improvement of Brahman and Brahman crossbred
427 cattle for carcass traits.
428
429 **4. Conclusions**
430 The low fractions of additive genetic and phenotypic variances accounted for by the
431 SNP in the Illumina3k chip and the high rank correlations between predictions from
432 genomic-polygenic and polygenic models for postweaning ultrasound carcass and weight
433 traits suggested that it would be economically difficult to justify using this chip in
434 commercial Angus-Brahman multibreed cattle operations. The substantial amount of
435 genetic variation for postweaning ultrasound carcass and weight traits suggested that
436 selection for these postweaning traits would be advantageous to speed up the improvement
437 of Brahman and Brahman crossbred cattle populations under subtropical conditions.
438

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Table 1

Numbers of calves, means and standard deviations per breed group and total

	Trait[a]											
	UREA, cm^2			UBF, cm			UPIMF, %			UW, kg		
Breed group	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
Angus	89	59.7	13.2	89	0.66	0.40	90	3.30	1.55	90	349.6	57.2
¾ A ¼ B	123	59.5	12.6	123	0.61	0.36	122	3.15	1.55	123	356.2	63.4
Brangus	114	58.1	11.0	114	0.62	0.37	114	2.87	1.43	114	344.6	50.5
½ A ½ B	154	58.4	11.8	154	0.63	0.38	153	2.74	1.53	154	351.1	57.2
¼ A ¾ B	69	62.6	12.1	69	0.68	0.41	67	2.56	1.49	69	346.9	48.9
Brahman	73	55.7	9.6	73	0.62	0.40	73	2.64	1.61	73	317.9	46.2
Total	622	58.9	11.9	622	0.63	0.38	619	2.89	1.54	623	346.3	56.2

[a]UREA = ultrasound rib eye area; UBF = ultrasound backfat; UPIMF = ultrasound percent intramuscular fat; UW = ultrasound weight.

598 **Table 2**

599 Posterior means and standard deviations for additive genomic, polygenic, total genetic and
600 phenotypic variances

	Trait[a]			
Variance[b]	UREA, cm^4	UBF, cm^2	UPIMF, $\%^2$	UW, kg^2
VAGO	2.06 ± 1.70	0.002 ± 0.001	0.02 ± 0.02	56.7 ± 45.6
VAPO	20.14 ± 6.00	0.004 ± 0.002	0.29 ± 0.08	612.2 ± 148.6
VGTot	22.20 ± 6.35	0.006 ± 0.002	0.31 ± 0.08	668.9 ± 158.1
Phenvar	56.30 ± 3.58	0.022 ± 0.001	0.59 ± 0.04	1227.3 ± 81.7
VGPO	23.34 ± 6.96	0.004 ± 0.002	0.22 ± 0.07	614.8 ± 155.1
PhenVarPO	60.34 ± 4.02	0.026 ± 0.002	0.71 ± 0.05	1218.9 ± 86.3

601 [a]UREA = ultrasound rib eye area; UBF = ultrasound backfat; UPIMF = ultrasound percent
602 intramuscular fat; UW = ultrasound weight.
603 [b]VAGO = additive genomic variance; VAPO = additive polygenic variance; VGTot = total
604 genetic variance = VAGO + VAPO; Phenvar = phenotypic variance; VGPO = additive
605 genetic variance from a polygenic model; PhenVarPO = phenotypic variance from a
606 polygenic model.
607

608 **Table 3**

609 Posterior means and standard deviations for additive genetic and genomic variance ratios

	Trait[a]			
Variance Ratios[b]	UREA	UBF	UPIMF	UW
VAGO/VGTot	0.09 ± 0.07	0.38 ± 0.17	0.06 ± 0.05	0.08 ± 0.06
VAGO/Phenvar	0.037 ± 0.030	0.097 ± 0.056	0.032 ± 0.027	0.046 ± 0.036
Heritability	0.39 ± 0.10	0.25 ± 0.08	0.53 ± 0.12	0.54 ± 0.11
HeritabilityPO	0.38 ± 0.10	0.17 ± 0.07	0.30 ± 0.09	0.50 ± 0.10

610 [a]UREA = ultrasound rib eye area; UBF = ultrasound back fat; UPIMF = ultrasound percent
611 intramuscular fat; UW = ultrasound weight.
612 [b]VAGO = additive genomic variance; VGTot = VAGO + VAPO; Phenvar = phenotypic
613 variance; HeritabilityPO = heritability from a polygenic model.
614

Table 4

Spearman rank correlations for animals evaluated using genomic-polygenic, genomic, and polygenic models

	Trait[a]			
Correlation[b]	UREA	UBF	UPIMF	UW
GP Model, G Model	0.65	0.79	0.64	0.70
GP Model, P Model	0.99	0.89	0.99	0.99
G Model, P Model	0.58	0.51	0.60	0.65

[a]UREA = ultrasound rib eye area; UBF = ultrasound back fat; UPIMF = ultrasound percent intramuscular fat; UW = ultrasound weight.

[b]GP Model = genomic-polygenic model; G Model = genomic model; P Model = polygenic model. All correlations were significant ($P < 0.0001$).

Table 5

Number and percentage of standardized predicted SNP values from the genomic-polygenic model

	Trait[a]							
	UREA		UBF		UPIMF		UW	
SDSNP Range[b]	N	%	N	%	N	%	N	%
-0.3 to -0.4	2	0.07	11	0.38	0	0	6	0.21
-0.2 to -0.3	14	0.48	78	2.69	15	0.52	65	2.24
-0.1 to -0.2	276	9.52	419	14.45	245	8.45	359	12.38
0 to -0.1	1098	37.88	954	32.91	1217	41.98	1018	35.12
0 to 0.1	1190	41.05	920	31.74	1170	40.36	1006	34.7
0.1 to 0.2	296	10.21	415	14.32	234	8.07	370	12.76
0.2 to 0.3	20	0.69	83	2.86	18	0.62	70	2.41
0.3 to 0.4	3	0.1	17	0.59	0	0	5	0.17
0.4 to 0.5	0	0	2	0.07	0	0	0	0

[a]UREA = ultrasound rib eye area; UBF = ultrasound back fat; UPIMF = ultrasound percent intramuscular fat; UW = ultrasound weight.

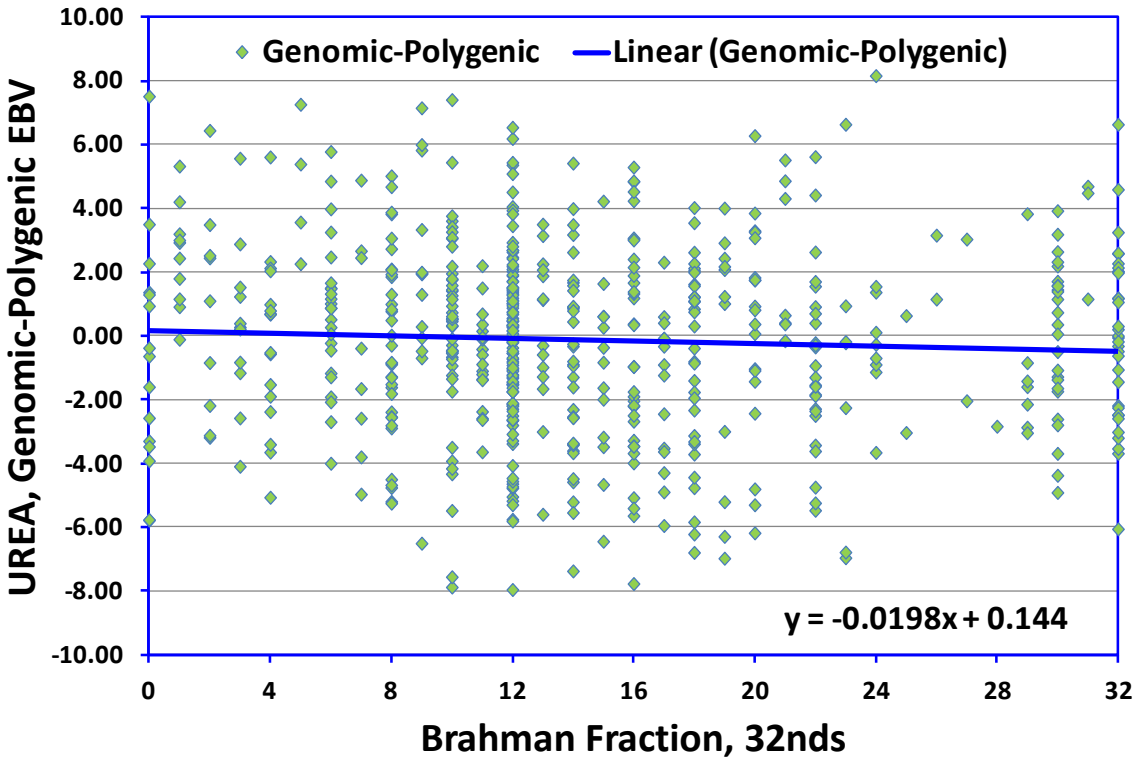
[b]SDSNP = additive SNP standard deviation.

630 **Table 6**

631 Linear regression coefficients for genomic-polygenic, genomic, and polygenic predictions
632 on Brahman fraction of calf

	Trait[a]			
Effect	UREA	UBF	UPIMF	UW
Genomic-Polygenic	-0.0198	-0.0011	0.0024	-0.0023
	P = 0.1778	P < 0.0001	P = 0.2222	P = 0.0133
Genomic	-0.0127	-0.0015	-0.0008	-0.0017
	P < 0.0001	P < 0.0001	P = 0.0107	P < 0.0001
Polygenic	-0.0136	-0.0007	0.0019	-0.0020
	P = 0.3321	P < 0.0001	P = 0.3256	P = 0.0252

633 [a]UREA = ultrasound rib eye area; UBF = ultrasound back fat; UPIMF = ultrasound percent
634 intramuscular fat; UW = ultrasound weight.
635

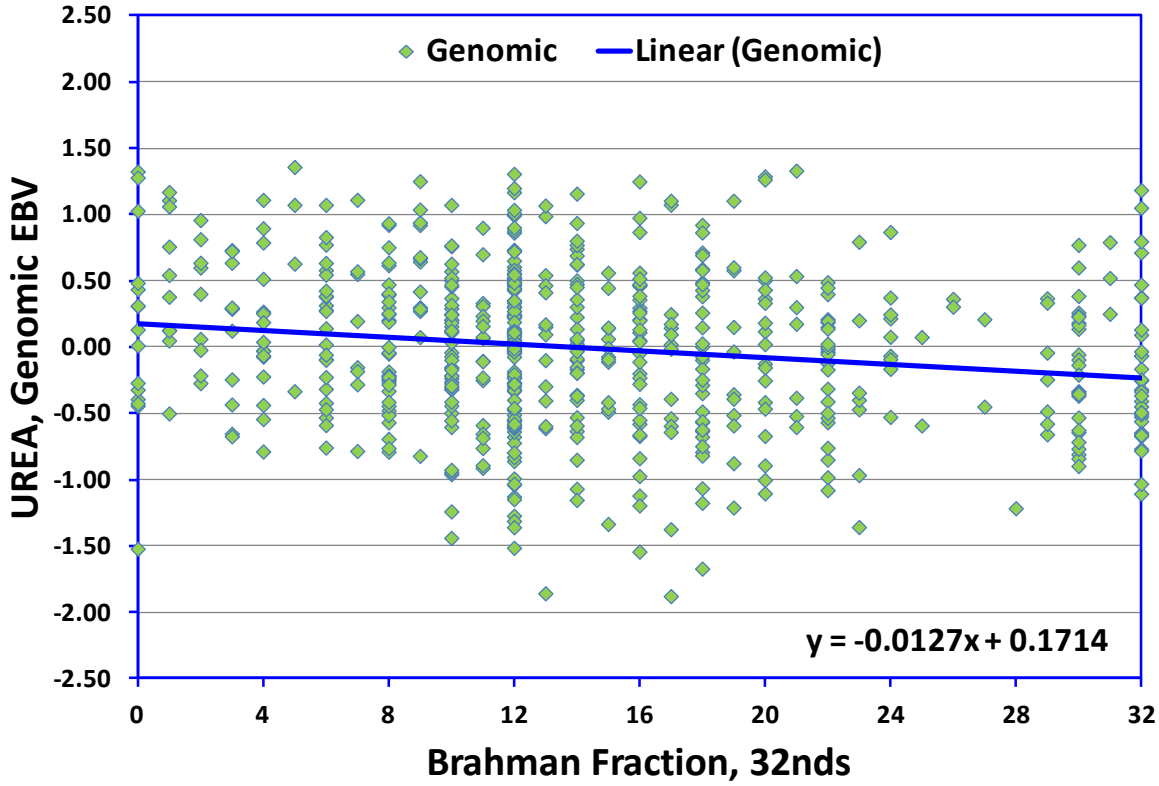


636

637 **Fig. 1.** Predicted additive genomic-polygenic values (EBV) for UREA as a function of

638 Brahman fraction of calf

639

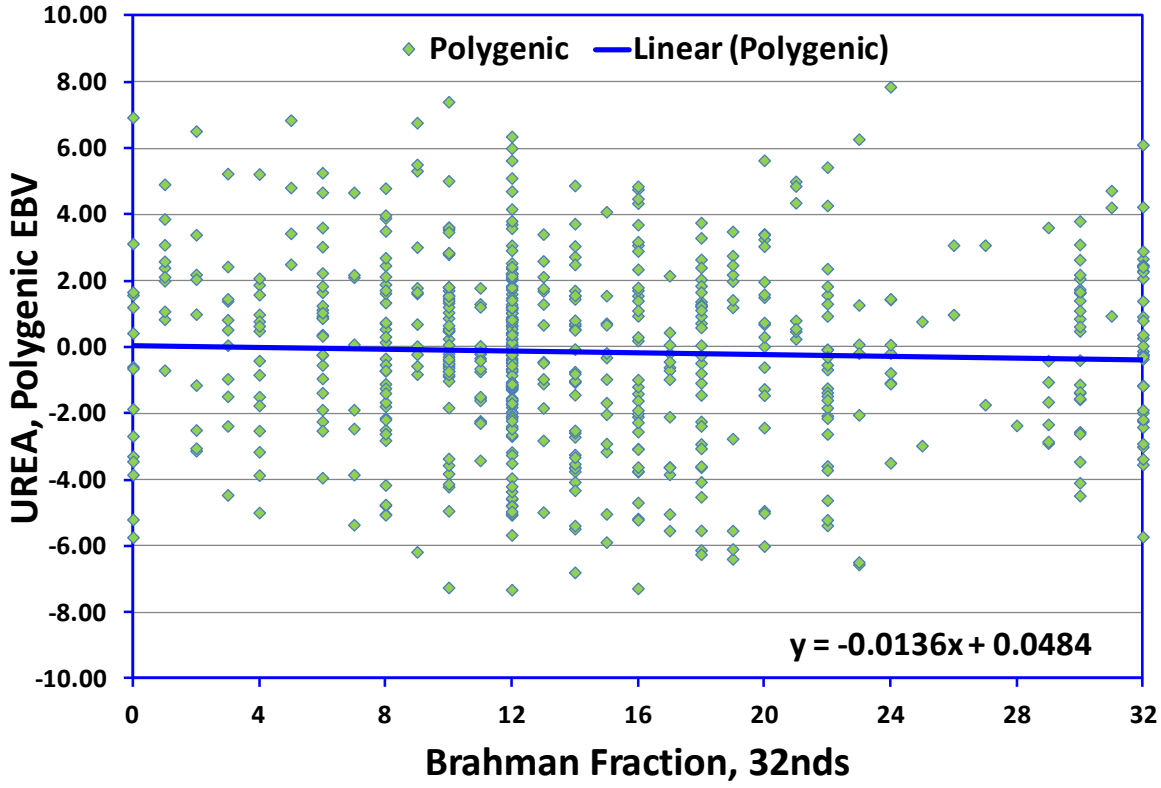


640

641 **Fig. 2.** Predicted additive genomic values (EBV) for UREA as a function of Brahman

642 fraction of calf

643



644

645 **Fig. 3.** Predicted additive polygenic values (EBV) for UREA as a function of Brahman
646 fraction of calf

647

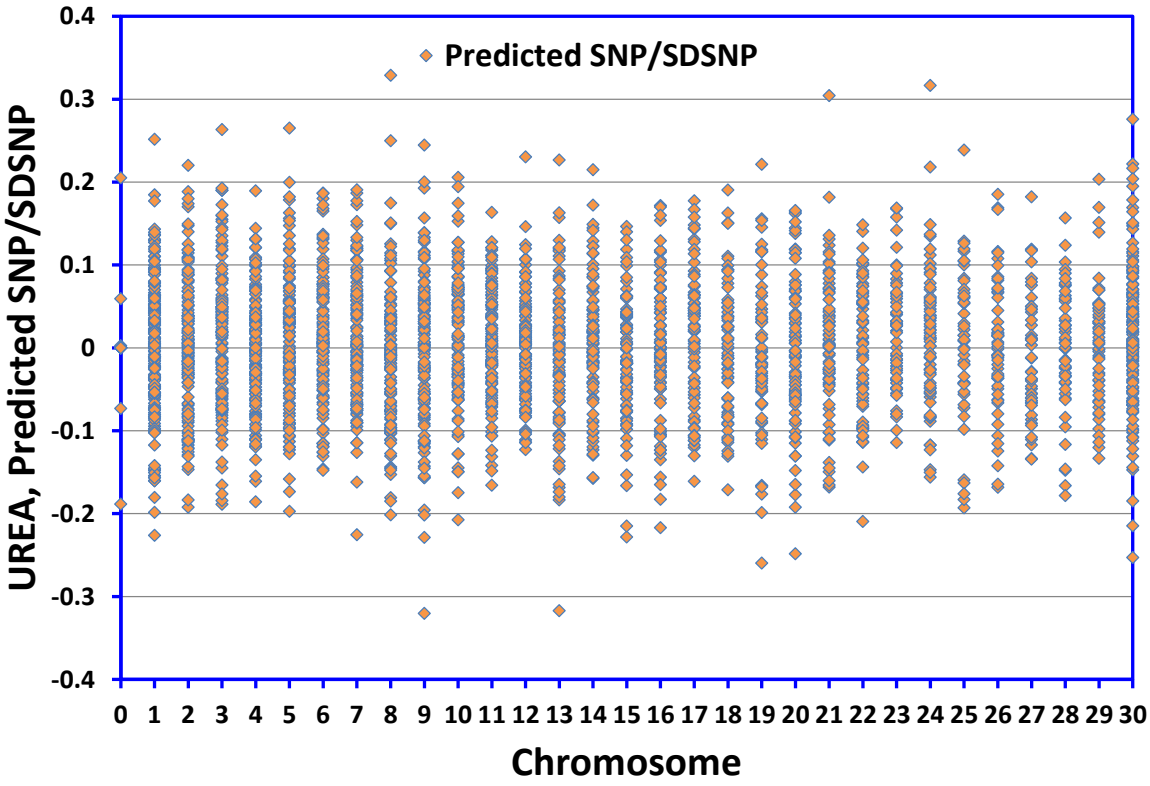


Fig. 4. Standardized predicted SNP values associated with UREA by chromosome number (0 = unassigned; 30 = X chromosome)