Genetic evaluations for growth heat tolerance in Angus cattle[1]

H. L. Bradford,[2] B. O. Fragomeni, J. K. Bertrand, D. A. L. Lourenco, and I. Misztal

Department of Animal and Dairy Science, University of Georgia, Athens 30605

ABSTRACT: The objectives were to assess the impact of heat stress and to develop a model for genetic evaluation of growth heat tolerance in Angus cattle. The American Angus Association provided weaning weight (WW) and yearling weight (YW) data, and records from the Upper South region were used because of the hot climatic conditions. Heat stress was characterized by a weaning (yearling) heat load function defined as the mean temperature–humidity index (THI) units greater than 75 (70) for 30 (150) d prior to the weigh date. Therefore, a weaning (yearling) heat load of 5 units corresponded to 80 (75) for the corresponding period prior to the weigh date. For all analyses, 82,669 WW and 69,040 YW were used with 3 ancestral generations in the pedigree. Univariate models were a proxy for the Angus growth evaluation, and reaction norms using 2 B-splines for heat load were fit separately for weaning and yearling heat loads. For both models, random effects included direct genetic, maternal genetic, maternal permanent environment (WW only), and residual. Fixed effects included a linear age covariate, age-of-dam class (WW only), and contemporary group for both models and fixed regressions on the B-splines in the reaction norm. Direct genetic correlations for WW were strong for modest heat load differences but decreased to less than 0.50 for large differences. Reranking of proven sires occurred for only WW direct effects for the reaction norms with extreme heat load differences. Conversely, YW results indicated little effect of heat stress on genetic merit. Therefore, weaning heat tolerance was a better candidate for developing selection tools. Maternal heritabilities were consistent across heat loads, and maternal genetic correlations were greater than 0.90 for nearly all heat load combinations. No evidence existed for a genotype × environment interaction for the maternal component of growth. Overall, some evidence exists for phenotypic plasticity for the direct genetic effects of WW, but traditional national cattle evaluations are likely adequately ranking sires for nonextreme environmental conditions.

Key words: beef cattle, genotype × environment interaction, heat stress, reaction norm, weight

INTRODUCTION

Because beef cattle are raised in extensive conditions, growth can vary across production environments. Genotype × environment interactions have been reported for weaning weight (**WW**) and yearling weight (**YW**; Butts et al., 1971; Bertrand et al., 1987). Part of this interaction could be attributed to genetic differences in heat tolerance, an economically important trait for livestock producers in some regions. In the beef industry, total economic losses from heat stress are estimated to be greater than $360 million annually (St.-Pierre et al., 2003). Heat stress reduces feed intake, growth, milk production, and pregnancy percentage (Nardone et al., 2006). Angus has been reported to experience greater physiological effects of heat stress than *Bos indicus* and tropically adapted *Bos taurus* breeds (Hammond et al., 1996). With Angus dominating the U.S. beef industry, improving heat tolerance can have a large economic impact nationally and can increase the use of Angus genetics in regions with greater heat stress.

Currently, selection tools for improving heat tolerance or adaptability are not routine in U.S. national cattle evaluations. Hair shedding scores were proposed as an indicator trait for heat tolerance (Gray et

al., 2011) but are not commonly collected. Producers have limited options for decreasing heat stress in cow–calf production systems, and with intense selection for production traits in Angus cattle (AAA, 2016), the consequences for adaptability are unknown. Heat stress has been characterized using methods developed by Ravagnolo and Misztal (2000) and has been successfully implemented in dairy cattle (Freitas et al., 2006; Bohmanova et al., 2007; Aguilar et al., 2009) and swine (Zumbach et al., 2008a; Fragomeni et al., 2015). The purpose of this study was to investigate the existence of heat stress on growth in Angus cattle and to develop a model for genetic evaluation using routinely measured, economically relevant traits to improve heat tolerance.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not needed as data were obtained from preexisting databases.

Animal Data

The American Angus Association (**AAA**; St. Joseph, MO) provided WW and YW data in August 2015. Contemporary groups were the concatenation of sex, owner-defined group codes, weigh date, and herd. Yearling contemporary group also included weaning contemporary group. Data were edited to include weights recorded in 2005 or after, multiple-sire contemporary groups with at least 35 animals for WW or 20 animals for YW, and a known owner zip code. Embryo transfer calves were removed because of extensive use of cooperator herds in the Angus breed, and some of those calves' geographic locations would be inaccurate. Phenotyped animals had 3 ancestral generations included in the pedigree.

Based on Leighton et al. (1982), records were assigned to regions of the United States to coincide with similar climate and environmental conditions (Fig. 1). Bradford et al. (2016) used the same region boundaries and presented more detailed regional and seasonal data descriptions. Data from the Upper South region were used for genetic analyses because of the number of records (Bradford et al., 2016) and the expectation of meaningful heat stress in this area. Data descriptions are summarized in Table 1.

Weather Data

Freitas et al. (2006) demonstrated that off-farm weather data were adequate for approximating on-farm weather conditions. Airport weather stations were assigned to herds based on the owner's zip code. Minimum, mean, and maximum distances of the
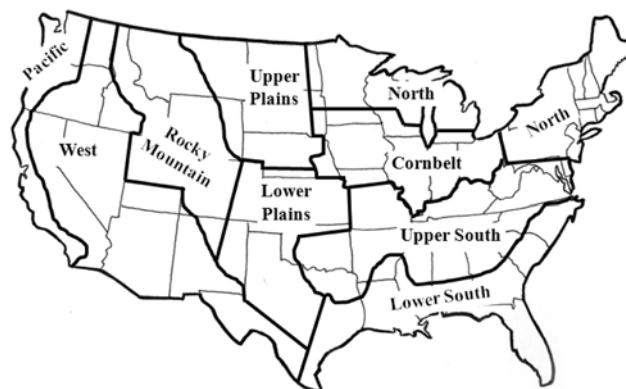

Figure 1. Boundaries for region assignments in the United States.

weather station from the herds were 4, 61, and 140 km for WW and 4, 59, and 144 km for YW, respectively. Based on the weather station associated with each contemporary group, maximum daily temperature (°C) and minimum relative humidity (%) were obtained for a given number of days prior to the weigh date using the weatherData (Narasimhan, 2014) package in R (R Core Team, 2015). Data were used to calculate daily temperature–humidity index (**THI**):

$$\mathrm{THI}_i = \mathrm{temp}_i - [0.55 - (0.0055 \times \mathrm{rh}_i)] \times (\mathrm{temp}_i - 14.5),$$

in which THI_i was THI for the ith day prior to the weigh date, temp_i was maximum temperature (°C), and rh_i was minimum relative humidity (%). This index adjusted temperature based on the relative humidity.

Heat load functions were developed to quantify weaning and yearling heat stress (Ravagnolo and Misztal, 2000). For these functions, a common threshold represented the THI at which growth began to decrease, and heat stress effects were assumed cumulative for a number of days prior to data collection. The threshold and days were determined as in Zumbach et al. (2008a) by selecting the combination with the greatest R^2 for each trait (data not shown). The thresholds were 75 and 70 THI for WW and YW, respectively. Heat load accumulated for 30 d before weaning and 150 d before yearling weigh dates. Therefore, WW and YW heat loads were defined, respectively, as

$$H_{\mathrm{W}j} = \mathrm{maximum}(0, \ \textstyle\sum_{i=0}^{30} \mathrm{THI}_{ij} - 75) \ \text{and}$$

$$H_{\mathrm{Y}j} = \mathrm{maximum}(0, \ \textstyle\sum_{i=0}^{150} \mathrm{THI}_{ij} - 70)$$

in which $H_{\mathrm{W}j}$ was the weaning heat load ($H_{\mathrm{Y}j}$ was yearling heat load) for contemporary group j and THI_{ij} was the THI on the ith day prior to the weigh date. When THI was less than the threshold, heat stress was not expected to affect growth. Therefore, if average THI was less than

Table 1. Descriptive statistics for weaning weights (WW) and yearling weights (YW) for Angus in the Upper South region

Item	WW	YW
Mean, kg	255	430
SD, kg	48	90
Animals	82,669	69,040
Pedigree animals	169,291	149,963
Contemporary groups	1,549	2,071

the threshold, the contemporary group had 0 heat load. If the mean THI was greater than the threshold, the entire contemporary group had a positive heat load. Heat load was greater than 0 for 46% of WW and 44% of YW.

Univariate Models

Separate univariate models were used for WW and YW as a proxy for the Angus growth national cattle evaluation. The model for WW was

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{W}\mathbf{m} + \mathbf{M}\mathbf{p} + \mathbf{e},$$

in which $\mathbf{y}$ was a vector of WW; $\boldsymbol{\beta}$ contained solutions for fixed effects of linear age covariate (d), age-of-dam class (2, 3, 4, 5 to 10, or ≥ 11 yr; BIF, 2008), and weaning contemporary group; $\mathbf{u}$ was a vector of direct genetic effects; $\mathbf{m}$ was a vector of maternal genetic effects; $\mathbf{p}$ was a vector of maternal permanent environmental effects; $\mathbf{e}$ was a vector of random residuals; and $\mathbf{X}$, $\mathbf{Z}$, $\mathbf{W}$, and $\mathbf{M}$ were incidence matrices relating records to fixed, direct genetic, maternal genetic, and maternal permanent environmental effects, respectively. Likewise, the model for YW was

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{W}\mathbf{m} + \mathbf{e},$$

in which $\mathbf{y}$ was a vector of YW; $\boldsymbol{\beta}$ contained solutions for fixed effects of linear age covariate (d) and yearling contemporary group; and all other effects were the same as previously defined. Maternal permanent environment was not significant ($P < 0.01$) for YW. For all models, the covariance between direct and maternal genetic effects was assumed to be 0 as used by the AAA. Variance components were estimated with animal models using average information REML (AIREML) implemented in the BLUPF90 family of programs (Misztal et al., 2015).

Reaction Norm Models

Reaction norms were used to determine how genetic predictions changed as a function of heat load. Heat load was transformed to first degree B-splines

with an interior knot at 0 and no explicit intercept. The knot was placed at 0 because more than half of the heat loads were 0. Therefore, the first spline functioned as the intercept and the second was the linear slope for heat load. The B-splines were modeled as

$$S_{0ij} = [(H_i \text{ maximum} - H_{ij})/ H_i \text{ maximum}]I(H_{ij} \neq 0) + I(H_{ij} = 0) \text{ and}$$

$$S_{1ij} = (H_{ij}/H_i \text{ maximum})I(H_{ij} \neq 0),$$

in which S_{0ij} was the heat load intercept for trait i and contemporary group j, S_{1ij} was the heat load slope, H_i maximum was the maximum heat load for the trait, H_{ij} was the heat load, $I(H_{ij} = 0)$ was an indicator variable equal to 1 if heat load was 0 and equal to 0 otherwise, and $I(H_{ij} \neq 0)$ was an indicator variable equal to 1 if heat load was greater than 0 and equal to 0 otherwise.

The following random regression model was used:

$$y_{ijkl} = \text{fixed}_i + \sum_{a=0}^{1} F_a S_{aj} + \sum_{a=0}^{1} D_{al} S_{aj} + \sum_{a=0}^{1} M_{ak} S_{aj} + \sum_{a=0}^{1} P_{ak} S_{aj} + e_{ijkl},$$

in which y_{ijkl} was the WW for animal l with fixed effects i, heat load j, and dam k; fixed$_i$ were the fixed effects for linear age covariate (d), age-of-dam class (2, 3, 4, 5 to 10, or ≥ 11 yr; BIF, 2008), and contemporary group; a was the degree of the B-spline for heat load (0 intercept and 1 linear slope); S_{aj} was the heat load B-spline; F_a was a fixed regression coefficient; D_{al} was a direct genetic random regression coefficient; M_{ak} was a maternal genetic random regression coefficient; P_{ak} was a maternal permanent environmental random regression coefficient; and e_{ijkl} was a random residual. The YW model was the same but with fixed effects of linear age covariate (d) and contemporary group and no maternal permanent environmental effects.

Direct WW heritabilities were calculated as

$$h^2 = \mathbf{z}'\mathbf{V_d}\mathbf{z}/(\mathbf{z}'\mathbf{V_d}\mathbf{z} + \mathbf{z}'\mathbf{V_m}\mathbf{z} + \mathbf{z}'\mathbf{V_p}\mathbf{z} + v_e),$$

in which h^2 was the heritability for a specific heat load (0 to 10); $\mathbf{z}$ was a vector containing the intercept and slope B-splines for the given heat load; $\mathbf{V}$ were covariance matrices for the direct genetic (d), maternal genetic (m), and maternal permanent environmental (p) effects; and v_e was the residual variance. Maternal heritabilities were calculated with the maternal variance components in the numerator. Heritabilities for YW were calculated without the maternal permanent environmental variance components.

Validation

Validations used predictivity for the direct effect in all models as in Legarra et al. (2008). Validation data included young animals born in 2012 or after, and analyses had 18,474 and 13,683 young animals for WW and YW, respectively. Of those young animals, 7,763 and 6,341 had a heat load greater than 0 for WW and YW, respectively. Phenotypes were corrected for all fixed effects for a given model, and the corrected phenotypes were correlated with EBV from an evaluation excluding young animals' phenotypes. For the reaction norm, EBV were calculated based on the actual heat load each young animal experienced. Additionally, proven sires ($n = 1,048$ for WW and $n = 878$ for YW) with at least 25 progeny were used to compare rankings between models. For both direct and maternal effects, Spearman rank correlations were evaluated across models and within the reaction norm using different heat loads.

RESULTS AND DISCUSSION

Heat load distributions are illustrated for WW and YW (Fig. 2). A WW heat load of 1°C corresponded to 76°F THI, and the same YW heat load corresponded to 71° THI. Therefore, heat load values were not directly comparable between traits. No heat load was observed for more than half of WW and YW, and heat stress was not expected to negatively affect the growth of those animals. Few records had large heat loads; consequently, results for large heat loads were less accurate because few producers raised cattle in these conditions. More extreme yearling heat loads were expected because the threshold THI was less than for weaning, but weaning heat loads were more extreme when considering the underlying THI.

One challenge was appropriately quantifying heat stress in beef cattle. The methods used to define heat load have been successfully used in dairy cattle (Ravagnolo and Misztal, 2000; Aguilar et al., 2009) and swine (Zumbach et al., 2008b; Fragomeni et al., 2015). These species were both raised in confinement systems with less variation in production environments from farm to farm than existed for beef cattle. Because beef cattle typically harvest their own forages, heat load was confounded with seasonal changes in forage type, quantity, and quality including fescue toxicosis (Paterson et al., 1995). Confounding may also exist between calving season and heat load because of the seasonality of calving in some regions (Bradford et al., 2016). Yearling weight was used instead of actual postweaning gain. The number of days between weaning and yearling weigh dates was the same for all animals in a postweaning gain contemp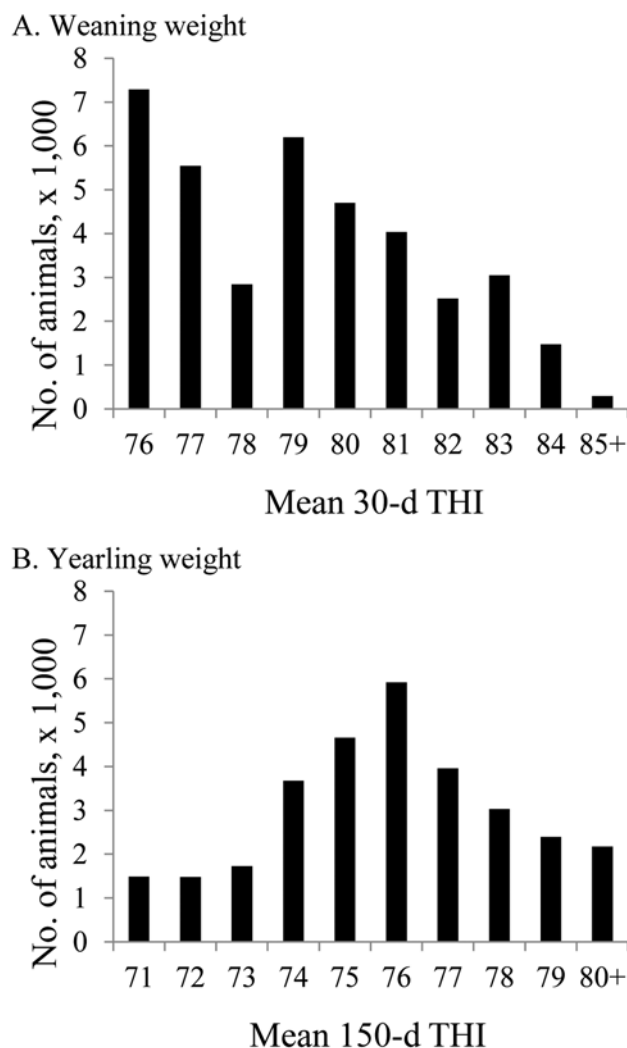orary group and was confounded with heat load. Approaches exist to distinguish heat load and contemporary group but require assuming heat load accumulates for the animal's lifetime (Santana et al., 2015). Although heat stress may decrease growth for a period, animals will likely have compensatory gain after the heat stress has subsided. In addition, off-farm weather data were used as an approximation for on-farm conditions. On-farm data were not available to validate this estimate although off-farm data were acceptable for more intensively managed dairy cattle (Freitas et al., 2006).

Heritabilities were estimated with univariate and reaction norm models. Univariate direct heritabilities (SD) were 0.24 (0.01) for WW and 0.32 (0.01) for YW. Previous estimates were greater for both traits in Angus (Costa et al., 2011), but our WW direct result was closer to the 0.20 heritability used by the AAA (2016). The univariate results were most similar to the reaction norms with intermediate heat loads (Fig. 3). Weights were most

Figure 2. Distributions of mean temperature–humidity index (THI) for weaning (A) and yearling (B) weights for Angus in the Upper South region. Graphs exclude 44,747 weaning and 38,540 yearling weights with mean THI less than the respective threshold.

heritable for no heat load and least heritable for intermediate heat load. Other beef cattle studies also had greater heritability for more favorable environmental conditions (Cardoso and Templeman, 2012; Santana et al., 2015). Conversely, carcass weight during heat stress was most heritable in swine (Zumbach et al., 2008b; Fragomeni et al., 2015). The heritability estimates from the current study indicated breeders could make genetic improvement by selecting for the direct genetic component of weight in heat-stressed conditions.

Maternal heritabilities increased with increasing heat load (Fig. 3). Univariate maternal heritabilities (SD) were 0.07 (0.01) for WW and 0.12 (0.01) for YW, and reaction norm heritabilities were similar, especially with little or no heat load. Previous estimates were greater for WW and similar for YW (Costa et al., 2011). The AAA uses a WW maternal heritability of 0.14 (AAA, 2016). In Brazilian beef breeds, maternal WW heritabilities from the reaction norm were similar in magnitude but quadratic in shape (Santana et al., 2015). Differences in the definition and amount of heat load could contribute to the dissimilarities between studies. In dairy cattle, milk production also had greater heritability with increasing heat stress (Ravagnolo and Misztal, 2000; Aguilar et al., 2009).

Correlations between slope and intercept were all positive and indicative of a favorable relationship between greater growth in environments both with and without heat stress. The direct genetic correlations (SD) were 0.30 (0.002) for WW and 0.71 (0.06) for YW, and the maternal genetic correlations (SD) were 0.87 (0.001) for WW and 0.96 (0.07) for YW. The correlations indicated that greater growth without heat stress was positively related to growth during heat stress with a very strong relationship for the maternal effects. These correlations were previously reported to be moderately negative for WW direct ($r = -0.30$ to -0.43) and negative or no different from 0 for WW maternal ($r = -0.17$ to -0.37; Santana et al., 2015), which suggested phenotypic plasticity existed for growth traits. Differences between studies could result from differences in breeds, random regression models, heat load definitions, or the complexity of modeling maternal traits. Selecting Angus cattle for greater growth should result in increased weight across environmental temperatures in the Upper South region.

Direct genetic correlations are summarized as a heat map for the WW and YW reaction norms (Fig. 4). Weaning weight correlations were strong when heat loads differed by at most 5, but for large heat load differences, direct correlations were less than 0.50, indicating growth was not the same trait between these environments. Conversely, results for YW indicated no environmental differences for the direct effect. Phenotypic analyses of
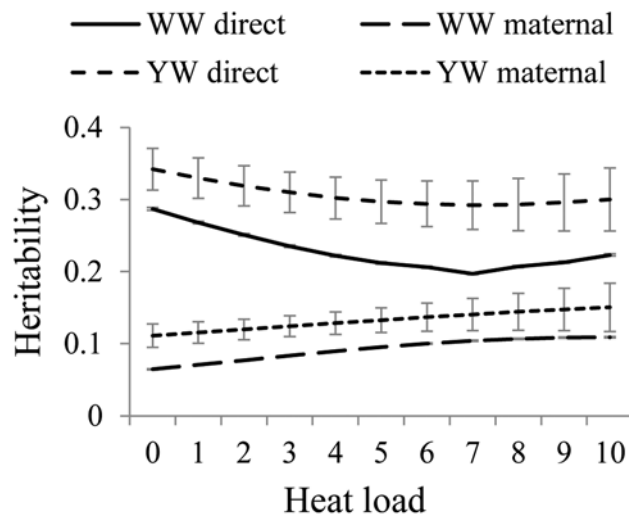

Figure 3. Direct and maternal heritabilities ± 2 SD for weaning weight (WW) and yearling weight (YW) using a reaction norm on heat load for Angus in the Upper South region.

these data suggested no seasonal differences for WW or YW in the Upper South region (Bradford et al., 2016). These results align well with the lack of genotype × environment interaction for YW. Heat load was defined for a longer period for YW, and cattle may have acclimatized to heat stress during the 150 d (Robinson et al., 1986) resulting in no detectable genotype × environment interaction. Santana et al. (2015) studied 3 beef breeds with similar WW direct results for Brangus, stronger correlations for Nellore, and weaker correlations for Tropical Composite. The correlation strength may be related to the adaptability of the breed to hot environments, causing weaker correlations for less-adapted breeds. Weaning weights were only considered distinct traits for no heat load or large heat load; however, few seed stock animals were raised in these extreme environments.

Results for maternal correlations differed from the direct correlations (Fig. 4), and WW and YW had similar results. All maternal correlations were greater than 0.85, indicating little change in the maternal component across heat loads. Strong genetic correlations existed for dairy milk production across a similar range of THI (Ravagnolo and Misztal, 2000). Dairy and beef cows have a large difference in their genetic potential for milk production, and heat stress was expected to affect dairy cows more, resulting in weaker genetic correlations in dairy cattle because of their greater production. Although one component of the maternal genetic effect is milk production, this effect included other genetic factors associated with the growth of the dam's offspring such as nurturing ability and milk quality. Additionally, the calf could be compensating for any decrease in milk production by consuming creep feed or other forages to maintain weight gain (McMorris and Wilton, 1986). Conversely, Santana et al. (2015) had weaker maternal
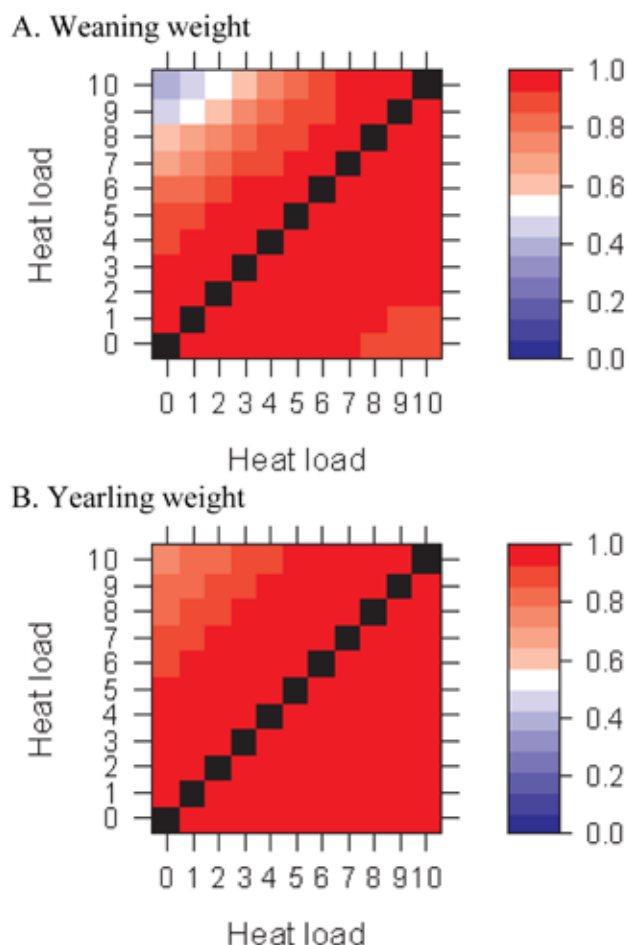
A. Weaning weight

B. Yearling weight

Figure 4. Heat map of direct (above diagonal) and maternal (below diagonal) genetic correlations from the reaction norm on heat load for weaning (A) and yearling (B) weight in Angus in the South region.

Table 2. Spearman rank correlations for sires with at least 25 progeny for direct genetic (above diagonal) and maternal genetic (below diagonal) effects for weaning and yearling weights using univariate or reaction norm models for Angus in the Upper South region

Model	Uni[1]	Reaction norm[2]		
		H = 0	H = 5	H = 10
Weaning weight (n = 1,048)				
Uni		0.98	0.98	0.79
H = 0	0.99		0.95	0.71
H = 5	0.98	0.99		0.89
H = 10	0.96	0.97	0.99	
Yearling weight (n = 878)				
Uni		0.99	0.99	0.95
H = 0	0.99		0.98	0.91
H = 5	0.99	0.99		0.98
H = 10	0.99	0.99	0.99	

[1]Uni = univariate model.

[2]Reaction norm model with heat loads (H) of 0, 5, or 10°C.

genetic correlations than direct genetic for 2 of 3 breeds. Santana et al. (2015) had data from fewer farms and did not include the maternal permanent environmental effect for 1 breed because of limited repeated records per dam. The breed with no maternal permanent environmental effect had the strongest maternal genetic correlations (Santana et al., 2015), so perhaps our model did not sufficiently distinguish between maternal genetic and maternal permanent environmental effects as a result of relatively few offspring per dam (average number = 1.7). These results indicate selection for the maternal genetic component of weight should be effective despite any environmental heat stress.

Rank correlations were strong between the univariate and reaction norm (Table 2), and proven sires were nearly identically ranked between models for the maternal effects. Some reranking occurred between the univariate and reaction norm with extreme heat load for WW direct, and selection decisions for the direct effect could slightly differ depending on the heat load for WW. Carcass weights in swine had slightly weaker correlations between the univariate and reaction norm

models and substantially weaker correlations within the reaction norm, suggesting swine had a greater physiological response to heat stress (Zumbach et al., 2008b). Rank correlations were stronger for YW than WW, potentially resulting from the lesser yearling THI threshold and selection after weaning. The single-trait YW models did not account for sequential culling after weaning. Despite some reranking of sires, the univariate models were adequately identified the best growth sires across environmental conditions.

Reaction norms for proven bulls were inspected to visualize how EBV changed as a function of heat load. From the univariate evaluation, 10 proven bulls were chosen with the largest and smallest WW EBV, and the same procedure was used for YW. The bulls with the largest EBV were important to the breed, as producers would be considering these bulls when selecting for greater growth. The 2 groups of bulls were distinct across heat loads for both traits (Fig. 5). Although both traits have a similar amount of reranking, WW had a greater magnitude difference between EBV for minimum and maximum heat load. Generally, the expected WW for these bulls' offspring would be different during heat stress, resulting in regional or seasonal differences in progeny performance.

Predictivity was used to compare the models' accuracies. Predictive abilities for the univariate and reaction norm based on the actual heat load were r = 0.17 and r = 0.20, respectively, for WW and r = 0.22 and r = 0.20, respectively, for YW. The univariate WW correlation was less than in Lourenco et al. (2015) for traditional, multiple-trait BLUP (r = 0.34) in the same Angus population. No predictivity difference was expected because heritability estimates were similar between models. Only the direct genetic effect could be

assessed using predictivity, as difficulties arise for a maternal effect, because the maternal genetic effect was 1 generation back and required corrected phenotypes for the dam instead of the individual (Lourenco et al., 2015). Based on predictive abilities, the univariate model was performed for WW and YW.

For producers with operations in extreme heat stress conditions, opportunities exist to make greater genetic progress with environment-specific WW EBV. Genetic correlations between environments indicate WW was not the same trait depending on heat stress. Although rank correlations were strong across environments, progeny of some proven bulls in Fig. 5 would be expected to have a greater than 20 kg WW difference between no heat load and maximum heat load, and this difference would have a large economic impact for producers who market calves at weaning. Therefore, some breeders could use a heat tolerance genetic evaluation to fine tune selection decisions in the Upper South region. Identifying the elite bulls for hot environments would enable Angus producers to stimulate demand for these genetics and to market those bulls to commercial cattlemen in the Upper South, potentially for a premium.

Many considerations exist for the implementation of a heat tolerance genetic evaluation for growth traits in beef cattle. The weatherData package (Narasimhan, 2014) has data retrieval inconsistencies, which are concerning for large-scale, routine heat load calculations. Occasionally, weather information was available, but the package reported no data and located the data on another attempt. If heat tolerance was implemented, the opportunity could exist for producers to submit zip codes specific to where cattle were raised to reduce the inevitable inaccuracies in assigning cattle to geographic locations. Another issue is the presentation of the EPD, as publishing the slope coefficients creates difficulty in interpretation because solutions are based on splines. Ideally, heat tolerance EPD would be disseminated to producers through decision support tools to customize predictions to an individual environment. Beef producers are not accustomed to obtaining genetic predictions in this manner, and the alternative is to provide EPD based on preselected heat load or loads. Publishing both traditional and heat tolerance WW EPD could create additional confusion for cattlemen when comparing the 2 results. Either way, a large education effort would be needed for successful implementation.

In modern beef production enterprises, cattlemen consider many economically relevant traits in their breeding objectives. The methodology from this study requires heat tolerance to be assessed by trait. Between WW and YW, WW was better for assessing growth heat tolerance because of weaker genetic correlations across environments and more producers marketing calves
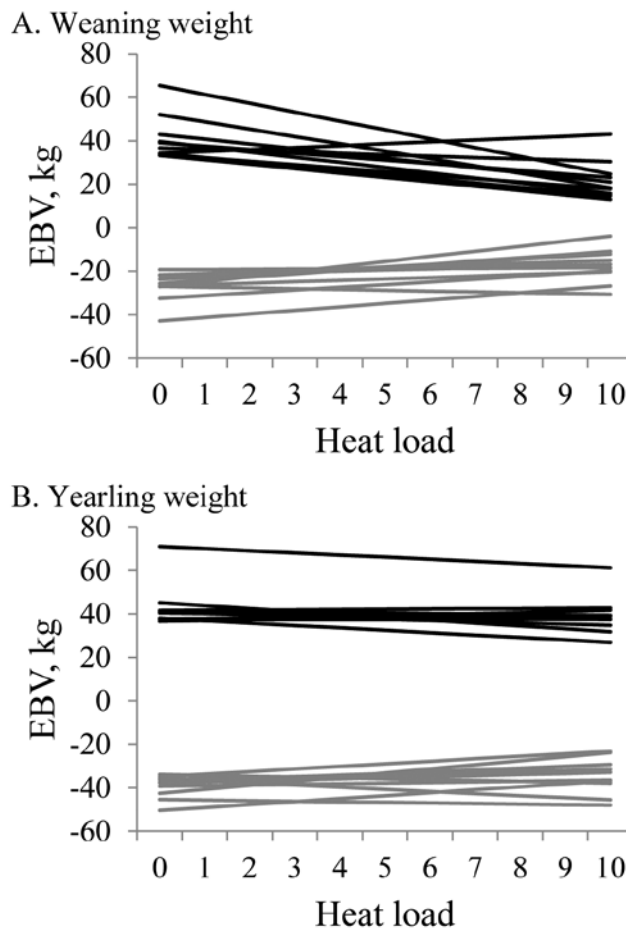

Figure 5. Reaction norms for the 10 proven bulls with the greatest (black) or least (gray) weaning (A) or yearling (B) weight direct EBV from the univariate analysis for Angus in the Upper South region.

at weaning than yearling. Carcass traits are important to the industry, but breed associations do not typically have information regarding the geographic location of animals during the finishing phase, limiting the ability to evaluate heat tolerance. On the other hand, heat stress is expected to affect female and male reproductive traits, making these traits a logical next step for evaluating heat tolerance. Yet female reproduction is best assessed when whole herd reporting is used to consistently account for every female. Ideally, heat tolerance for all of these traits could be combined into an index to provide producers with comprehensive, easy-to-use selection tools.

Conclusions

Selection tools for improving heat tolerance in growth traits were developed in Angus cattle. Some evidence exists for phenotypic plasticity for the WW direct genetic effects, indicating potential for users of Angus genetics in extreme environments to make greater genetic improvement by using environment-specific genetic predictions. The maternal component of growth can be selected with similar selection

response despite environmental heat stress. Further research is needed for the heat tolerance of other traits in beef cattle to develop a systematic understanding of the genetic mechanisms controlling adaptability. These conclusions assume that heat load directly quantifies the amount of heat stress.

LITERATURE CITED

Aguilar, I., I. Misztal, and S. Tsuruta. 2009. Genetic components of heat stress for dairy cattle with multiple lactations. J. Dairy Sci. 92:5702–5711. doi:10.3168/jds.2008-1928

American Angus Association (AAA). 2016. Genetic trend EPD and $Value by birth year. http://www.angus.org/Nce/GeneticTrends.aspx. (Accessed 9 March 2016.)

Bertrand, J. K., J. D. Hough, and L. L. Benyshek. 1987. Sire × environment interactions and genetic correlations of sire progeny performance across regions in dam-adjusted field data. J. Anim. Sci. 64:77–82. doi:10.2527/jas1987.64177x

Beef Improvement Federation (BIF). 2008. Guidelines for uniform beef improvement programs. 9th ed. BIF, Raleigh, NC.

Bohmanova, J., I. Misztal, and J. B. Cole. 2007. Temperature-humidity indices as indicators of milk production losses due to heat stress. J. Dairy Sci. 90:1947–1956. doi:10.3168/jds.2006-513

Bradford, H. L., B. O. Fragomeni, J. K. Bertrand, D. A. L. Lourenco, and I. Misztal. 2016. Regional and seasonal analyses of weights in growing Angus cattle. J. Anim. Sci. (in press). doi:10.2527/jas.2016-0683

Butts, W. T., M. Koger, O. F. Pahnish, W. C. Burns, and E. J. Warwick. 1971. Performance of two lines of Hereford cattle in two environments. J. Anim. Sci. 33:923–932. doi:10.2527/jas1971.335923x

Cardoso, E. F., and R. J. Templeman. 2012. Linear reaction norm models for genetic merit prediction of Angus cattle under genotype by environment interaction. J. Anim. Sci. 90:2130–2141. doi:10.2527/jas.2011-4333

Costa, R. B., I. Misztal, M. A. Elzo, J. K. Bertrand, L. O. C. Silva, and M. Łukaszewicz. 2011. Estimation of genetic parameters for mature weight in Angus cattle. J. Anim. Sci. 89:2680–2686. doi:10.2527/jas.2010-3574

Fragomeni, B. D., S. Tsuruta, D. A. L. Lourenco, K. Gray, Y. Huang, and I. Misztal. 2015. Genomic mitigation of seasonality effect on carcass weight in commercial pigs. J. Anim. Sci. 93(Suppl. S3):847. (Abstr.)

Freitas, M. S., I. Misztal, J. Bohmanova, and J. West. 2006. Utility of on- and off-farm weather records for studies in genetics of heat tolerance. Livest. Sci. 105:223–228. doi:10.1016/j.livsci.2006.06.011

Gray, K. A., T. Smith, C. Maltecca, P. Overton, J. A. Parish, and J. P. Cassady. 2011. Differences in hair coat shedding, and effects on calf weaning weight and BCS among Angus dams. Livest. Sci. 140:68–71. doi:10.1016/j.livsci.2011.02.009

Hammond, A. C., T. A. Olson, C. C. Chase Jr., E. J. Bowers, R. D. Randel, C. N. Murphy, D. W. Vogt, and A. Tewold. 1996. Heat tolerance in two tropically adapted *Bos taurus breeds, Senepol* and *Romosinuano*, compared with Brahman, Angus, and Hereford cattle in Florida. J. Anim. Sci. 74:295–303.

Legarra, A., C. Robert-Granié, E. Manfredi, and J. Elsen. 2008. Performance of genomic selection in mice. Genetics 180:611–618. doi:10.1534/genetics.108.088575

Leighton, E. A., R. L. Willham, and P. J. Berger. 1982. Factors influencing weaning weight in Hereford cattle and adjustment factors to correct records for these effects. J. Anim. Sci. 54:957–963. doi:10.2527/jas1982.545957x

Lourenco, D. A. L., S. Tsuruta, B. O. Fragomeni, Y. Masuda, I. Aguilar, A. Legarra, J. K. Bertrand, T. S. Amen, L. Wang, D. W. Moser, and I. Misztal. 2015. Genetic evaluation using single-step genomic best linear unbiased predictor in American Angus. J. Anim. Sci. 93:2653–2662. doi:10.2527/jas.2014-8836

McMorris, M. R., and J. W. Wilton. 1986. Breeding system, cow weight and milk yield effects on various biological variables in beef production. J. Anim. Sci. 63:1361–1372. doi:10.2527/jas1986.6351361x

Misztal, I., S. Tsuruta, D. A. L. Lourenco, I. Aguilar, A. Legarra, and Z. Vitezica. 2015. Manual for BLUPF90 family of programs. http://nce.ads.uga.edu/wiki/lib/exe/fetch.php?media=blupf90_all2.pdf. (Accessed 1 April 2016.)

Narasimhan, R. 2014. weatherData: Get weather data from the Web. R package version 0.4.1. https://CRAN.R-project.org/package=weatherData. (Accessed 1 April 2016.)

Nardone, A., B. Ronchi, N. Lacetera, and U. Bernabucci. 2006. Climatic effects on productive traits in livestock. Vet. Res. Commun. 30(Suppl. 1):75–81. doi:10.1007/s11259-006-0016-x

Paterson, J., C. Forcherio, B. Larson, M. Samford, and M. Kerley. 1995. The effects of fescue toxicosis on beef cattle productivity. J. Anim. Sci. 73:889–898.

Ravagnolo, O., and I. Misztal. 2000. Genetic component of heat stress in dairy cattle, parameter estimation. J. Dairy Sci. 83:2126–2130. doi:10.3168/jds.S0022-0302(00)75095-8

R Core Team. (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. (Accessed 10 January 2016.)

Robinson, J. B., D. R. Ames, and G. A. Milliken. 1986. Heat production of cattle acclimated to cold, thermoneutrality and heat when exposed to thermoneutrality and heat stress. J. Anim. Sci. 62:1434–1440. doi:10.2527/jas1986.6251434x

Santana, M. L., Jr., A. B. Bignardi, J. P. Eler, and J. B. S. Ferraz. 2015. Genetic variation of the weaning weight of beef cattle as a function of accumulated heat stress. J. Anim. Breed. Genet. 133:92–104. doi:10.1111/jbg.12169

St.-Pierre, N. R., B. Cobanov, and G. Schnitkey. 2003. Economic losses from heat stress by US livestock industries. J. Dairy Sci. 86(E. Suppl.):E52–E77. doi:10.3168/jds.S0022-0302(03)74040-5

Zumbach, B., I. Misztal, S. Tsuruta, J. P. Sanchez, M. Azain, W. Herring, J. Holl, T. Long, and M. Culbertson. 2008a. Genetic components of heat stress in finishing pigs: Development of a heat load function. J. Anim. Sci. 86:2082–2088. doi:10.2527/jas.2007-0523

Zumbach, B., I. Misztal, S. Tsuruta, J. P. Sanchez, M. Azain, W. Herring, J. Holl, T. Long, and M. Culbertson. 2008b. Genetic components of heat stress in finishing pigs: Parameter estimation. J. Anim. Sci. 86:2076–2081. doi:10.2527/jas.2007-0282