

GENOTYPE BY ENVIRONMENT INTERACTION FOR HEAT TOLERANCE IN AUSTRALIAN HOLSTEIN DAIRY CATTLE

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SUMMARY

Genomic breeding values for heat tolerance in dairy cattle were first released in Australia in December 2017 to select animals with better tolerance to heat stress. It is also important to identify animals which perform well in a wide range of temperature and humidities, given the large seasonal and geographical variation in Australia. The aim of this study was to investigate the magnitude of genotype by environment interactions for heat tolerance in Australian Holsteins. A total of 2.5 million test-day milk yield records from 823,055 cows and 6,615 sires were included in the analysis. The heritability estimates at 5th and 95th percentile of temperature-humidity index (THI) were: 0.27 and 0.21, 0.21 and 0.14, and 0.19 and 0.14 for milk, protein and fat yield, respectively. The genetic correlations at the extreme THI values, that is THI = 60 and THI = 75 (equivalent to the temperature and relative humidity of around 20 °C and 45 and, 31 °C and 50, respectively) were: 0.87, 0.84, and 0.86 for milk, protein and fat, respectively. A re-ranking among sires was observed in different environments. These results could allow farmers to make decisions on whether to select sires which are best suited to specific environments, or those that are consistent across a range of environments.

INTRODUCTION

The desire to breed for robustness in the dairy industry is intensifying, driven in part by climate change. One of the key components of robustness is genotype by environment interactions ($G \times E$), which refers to the change in performance or a change in the ranking of animals in different environments. In Australia, dairying is carried out in a wide range of production systems and climatic conditions suggesting that re-ranking of genotypes may occur.

Various studies have demonstrated the presence of $G \times E$ due to heat stress in dairy cattle as reviewed by Carabaño *et al.* (2017). Previous studies in Australia using test-day records reported evidence of $G \times E$ for production traits due to heat stress for Australian Holsteins (Hayes *et al.* 2003; Haile-Mariam *et al.* 2008). These studies used first parity or whole lactation data.

Genetic selection for production traits in Australian dairy cattle has resulted in considerable genetic gains. However, this may have led to increased sensitivity to heat stress in dairy animals (Carabaño *et al.* 2017) and possibly increased $G \times E$ because of an unfavourable genetic correlation between heat tolerance and milk production traits (Ravagnolo *et al.* 2000). Nguyen *et al.* (2017) noted a declining genetic trend for heat tolerance in Australian Holstein and Jersey dairy cattle at a rate of 0.3%/year. This declining trend coupled with increasing temperature and frequency of heat events suggests the importance of revisiting the magnitude of changes in animal performance at different environmental temperature and humidities. The objective of this study was to investigate $G \times E$ for heat tolerance using test-day milk yield records in combination with temperature and humidity data from publicly available weather stations over a 15-year period.

MATERIALS AND METHODS

Test-day data. First lactation milk, protein and fat yield data (consisting of 6.6 million records for Holstein cows between 2003 to 2017) were obtained from DataGene (DataGene Ltd., Melbourne,

Australia). Data editing was as follows: (1) tests < 5d or > 305d days in milk (DIM) and herd test days with less than 10 cows were removed; (2) sires with daughters in less than 2 herds and herds using fewer than 2 sires were excluded and (3) only cows with at least 4 records were retained for analyses. The final dataset comprised 5.2 million records for 823,055 cows and 6,615 sires from 3,732 herds. The pedigree for these data included up to 15 generations.

Climate data. Climate data included hourly dry bulb and dew point temperature and relative humidity obtained from the Bureau of Meteorology (Melbourne, Australia) for 163 weather stations in Australia from 2003 to 2017. The pairwise distances between herds were calculated from geographical coordinates and assigned to the nearest weather station. Hourly temperature-humidity indexes (THI) for each weather station were calculated as follows (Yousef 1985): $THI = T_{db} + (0.36 T_{dp}) + 41.2$, where T_{db} = hourly dry bulb temperature (°C); T_{dp} is dew point temperature (°C) and $T_{dp} = (237.3b)/(1.0 - b)$, where $b = [\log(RH/100.0) + (17.27T_{db})/(237.3 + T_{db})]/17.27$, and RH = relative humidity. The THI values were then averaged for 24 hours to get the daily THI. The daily THI on the test day, 1, 2, 3, and 4th day before test day were then averaged and assigned to the test-day records.

Milk yield traits in Australia have been reported to begin declining at THI > 60 (Hayes *et al.* 2003; Nguyen *et al.* 2016). Therefore, the THI threshold was set at 60 in this study (i.e., if THI < 60 then THI = 60). A small proportion (0.004%) of tests obtained at THI \geq 75 were given a value of 75. This was to avoid unexpected trajectories as possible artefacts, which are often related to fitting polynomials with few extreme data points.

Statistical analysis. A univariate random regression sire model was applied to the data as follows: $y_{ijk} = \mu + HTD_i + YS_j + \sum_{n=1}^3 A_n X_n + \sum_{n=1}^8 D_n Z_n + \sum_{n=1}^2 P_n T_n + \sum_{n=0}^1 S_{kn} W_n + e_{ijk}$, where y_{ijk} is yield of milk in litres, fat or protein in kg from the i th herd test day, j th year season of calving, and daughter of the k th sire; μ is the intercept; HTD_i is the effect of the i th herd test day; YS_j is the effect of the j th year season of calving; X_n , Z_n , and T_n are the n th-order Legendre polynomials corresponding to age on day of test, DIM at test, and THI, respectively; A_n , D_n and T_n are the fixed regression coefficient of traits on age at test, DIM at test, and THI, respectively; S_{kn} is a random regression coefficient on THI for the k th sire; W_n is either the intercept ($n = 0$) or slope solution ($n = 1$) for heat load index (THI) for cows and sires; and e_{ijk} is the vector of residual effects. The following (co)variance structure was

assumed: $Var(S) = \begin{bmatrix} s_0 \\ s_1 \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{s_0}^2 & \mathbf{A}\sigma_{s_0s_1} \\ \mathbf{A}\sigma_{s_0s_1} & \mathbf{A}\sigma_{s_1}^2 \end{bmatrix}$, where \mathbf{A} is the relationship matrix for sires constructed

from pedigree data; s_0 , s_1 are the intercept and slope for sires; $\sigma_{s_0}^2$, $\sigma_{s_0s_1}$, $\sigma_{s_1}^2$ are (co)variance for sire effects of THI. Heterogeneous error variance was modelled for 10 DIM intervals over a lactation (DIM = 5–30, 31–60, 61–90, 91–120, 121–150, 151–180, 181–210, 211–240, 241–270, and 271–300) as follows: $Var(e) = \mathbf{R} = \text{diag}\{\mathbf{I}\sigma_{e_1}^2, \mathbf{I}\sigma_{e_2}^2, \dots, \mathbf{I}\sigma_{e_{10}}^2\}$, where $\sigma_{e_1}^2, \sigma_{e_2}^2, \dots, \sigma_{e_{10}}^2$ represents error variances and \mathbf{I} is the identity matrix. (Co)variance components were estimated using ASREML version 4.2 (Gilmour *et al.* 2015).

Calculation of genetic parameters. Additive genetic variances for sires were extracted from the diagonal elements of the covariance $\hat{\mathbf{G}}$ matrix calculated as $\hat{\mathbf{G}} = 4 * \mathbf{\Phi} Var(\hat{\mathbf{S}}) \mathbf{\Phi}'$, where $\mathbf{\Phi}$ is the matrix of Legendre polynomial functions for THI; $\hat{\mathbf{S}}$ is the sire (co)variance matrix. The genetic correlations were obtained from transforming the covariance $\hat{\mathbf{G}}$ matrix to a correlation matrix. The heritability as a function of THI was calculated as $h_i^2 = \frac{4 * \hat{\sigma}_{s(i)}^2}{\hat{\sigma}_{s(i)}^2 + \hat{\sigma}_e^2}$, where $\hat{\sigma}_{s(i)}^2$ is sire variance at i THI and $\hat{\sigma}_e^2$ is the average residual variance over the lactation. The estimated breeding value (EBV) for the sire i along the THI trajectory was calculated as $EBV_i = \theta_j * \hat{a}'_i$, where \hat{a}'_i is the vector of estimated random regression coefficients for the slope and intercept for sire i ; θ_j is the vector of Legendre polynomials evaluated at THI j . To examine the changes in performance along the THI trajectory, we estimated EBVs for sires with more than 1000 daughters with yield records.

RESULTS AND DISCUSSION

Table 1 shows genetic variances and heritability estimates at the 5th, 50th and 95th percentiles of THI. The genetic variance and heritability estimates decrease with increasing THI values. The heritability was greater for milk yield at the 5th and 95th percentiles (0.27 and 0.21) compared to protein yield (0.21 and 0.14) and fat yield (0.19 and 0.14).

Table 1. Additive genetic variances and heritabilities for milk, fat and protein yields at the 5th, 50th and 95th percentiles of the temperature-humidity index (THI)

	Additive genetic variance			Heritability		
	5 th	50 th	95 th	5 th	50 th	95 th
Milk (kg)	4.55	3.86	3.54	0.27	0.23	0.21
Fat (kg)	0.005	0.004	0.003	0.19	0.17	0.14
Protein (kg)	0.004	0.003	0.002	0.21	0.17	0.14

At the extremes of the trajectory of THI (i.e., THI 60 vs 75), the genetic correlations were 0.87, 0.84, 0.86 for milk, protein and fat, respectively (Figure 1). In the previous study, Hayes *et al.* (2003) reported smaller G × E estimates for milk (0.94), protein (0.92) and fat (0.90). Greater G × E in our study is likely in part due to increased sensitivity to heat stress in study population following continued selection for production traits over the years or a slight difference between the analyses; Hayes *et al.* (2003) included a random regression coefficient on THI for cows in their models.

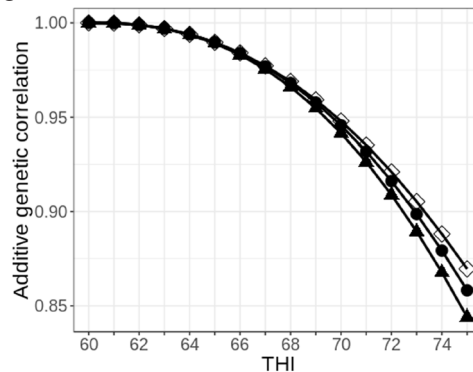


Figure 1. Additive genetic correlations for milk (□), protein (▲) and fat (●) yields at temperature-humidity index (THI) = 60 and those at THI up to 75

Reranking exists among sires, as seen from the differences in the reaction norms of EBVs for fat yield (Figure 2). Two groups of sires were identified based their EBVs at thermoneutral (THI = 60) and heat stress (THI = 75) conditions. The first group (shown in gray) are sires with above-average EBVs at THI = 60 and smaller EBVs at THI = 75 (i.e., environmentally sensitive sires). Daughters of these sires will likely produce less under heat stress conditions and therefore can be used in regions with the consistently low heat load. A more controlled environment, such as the provision of shade and diets designed to reduce core body temperature will be necessary if their daughters are to perform optimally under high heat load conditions.

The second group (Figure 2; shown in black) are sires with above-average and stable EBVs (i.e., resilient or robust sires); their performances are comparatively consistent and are well suited for variable environments. If the objective is to breed for robustness or resilience, then these sires are ideal candidates for selection. Australian dairying is predominantly pasture-based characterised by

Breeding Objectives

an array of factors including weather conditions which vary considerably between years as well as seasonal variability in feed quantity and quality feeds. Under these conditions and considering current trends towards extensive exchange of sires between regions or export of sires to other countries, it would be more beneficial to select for robust sires.

This study only considered first lactation data. Greater reranking is expected with later lactations due to relatively higher sensitivity to heat stress associated with greater milk yield in multiparous cows (Carabaño *et al.* 2017). This will be investigated in further studies.

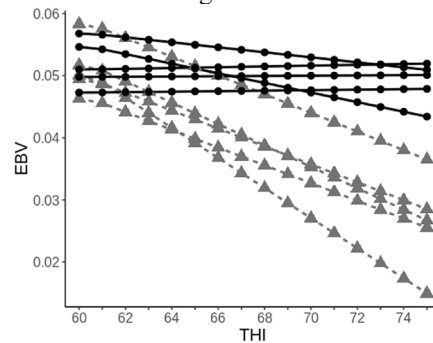


Figure 2. Estimated breeding values (reaction norms) along the THI for a sample of 10 sires with over 1000 daughters with fat yield records; the gray lines (▲) represent sires with above-average EBV at the thermoneutral conditions (THI = 60) and smaller EBV at heat stress conditions (THI = 75) whereas the black lines (●) are sires with above-average and stable EBVs

CONCLUSION

The results from this study indicate $G \times E$ due to heat stress exists at extreme THI for all the milk traits studied. The differences observed in the reaction norms (i.e., EBVs along the trajectory of THI) among the sires suggest that genetic variation in sire sensitivity to heat stress exist, which can be used to select animals that perform optimally in different environments.

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