Interaction between adaptation and mitigation traits in Canadian Holsteins

G.R. Dodd[1], C.F. Baes[1], F.S. Schenkel[1], C. Machefert[1], I. Ampofo[1], B. Amini[1], V. Storing[1], A. Fleming[2], K. Lee[2], F. Malchiodi[1,3], C. Richardson[4], and F. Miglior[1,2]

[1] Centre for Genetic Improvement of Livestock, Department of Animal Biosciences, University of Guelph, Guelph, N1G 2W1 Ontario, Canada

[2] Lactanet, Guelph, N1K 1E5 Ontario, Canada

[3] Semex, 5653 Hwy 6, Guelph, N1H 6J2 Ontario, Canada

[4] AbacusBio International Ltd, Roslin Innovation Centre, Easter Bush Campus, University of Edinburgh, EH25 9RG Edinburgh, United Kingdom

Corresponding author: gdodd@uoguelph.ca

Abstract

In response to climate change, the dairy industry has shifted focus to reducing environmental impact and strengthening resilience. However, it is unclear how adaptation to environmental challenges and mitigation of environmental effects interact. This project aims to quantify the impact of selecting traits related to adaptation on profitability, health, efficiency, resilience, and environmental sustainability to inform selection of climate-smart dairy. Mitigation traits were defined as methane production (g/d), body maintenance requirements, and dry matter intake while adaptation traits were defined as heat tolerance with regards to production, fertility, and health. The first objective will be to quantify the direct effects of heat stress on production, fertility, health, and mitigation traits using a reaction norm approach to estimate heat tolerance. The second objective will be to estimate genetic correlations between mitigation traits and heat tolerance defined by production, fertility, and health traits. The third objective is to estimate genetic correlations among heat tolerance defined by all trait groups. Preliminary results have identified trait-specific heat stress thresholds for production, fertility, and mitigation traits ranging from THI 55 to 67, where fat yield was the most sensitive to environmental pressures and first service to conception was the least sensitive. Genetic correlations estimated between performance under thermoneutral conditions and heat tolerance for production traits were found to be moderately unfavorable (-0.27 to -0.31), indicating a trade-off between productivity and resilience. Weak and favorable genetic correlations were estimated between methane emissions and heat tolerance of production traits, with the strongest relationships observed between heat tolerance of fat yield and methane emissions (-0.05 to -0.16). These results highlight the need for balanced selection strategies to improve both productivity and heat tolerance, while suggesting that selection for reduced methane emissions is unlikely to adversely affect heat tolerance. These findings will inform climate-smart dairy selection strategies balancing profitability, resilience, and environmental impact.

Key words: environment, methane, heat tolerance

Introduction

Improving the environmental efficiency of dairy production is an important component of sustainable livestock production. Genetic selection provides a cumulative and permanent means of improving efficiency through traits related to greenhouse gas emissions and resource use, including methane efficiency, feed efficiency, and body maintenance requirements. In Canada, these traits have been incorporated into the Environmental Impact Sub-Index of the national Lifetime Performance Index (LPI), providing a genetic selection

framework for reducing the environmental footprint of dairy production (Van Doormaal et al., 2025).

Climate change presents a complementary challenge for the dairy industry. Increasing temperatures and more frequent heat stress events can negatively affect production, fertility, and health in dairy cattle (Bush et al., 2019; Polsky and von Keyserlingk, 2017; Yan et al., 2021; Campos et al., 2022b; Ishida et al., 2024; Dodd et al., 2026a). These effects vary among animals and traits, partly due to genetic differences in their ability to maintain performance under heat stress, commonly referred to as heat tolerance (Campos et al., 2022a; McWhorter et al., 2023). Previous research has demonstrated genetic variation in heat tolerance that could be exploited through selection for improved resilience. This is particularly relevant for Canadian Holsteins given increasing temperatures across Canada and the susceptibility of high-producing cattle to heat stress (Zhang et al., 2019; Hansen, 2004).

Despite opportunities to improve both environmental efficiency and heat tolerance, these objectives have largely been studied independently. Consequently, the genetic relationships between mitigation and adaptation traits remain poorly understood in Canadian Holsteins. Characterizing these relationships is necessary to determine whether selection for improved environmental efficiency could influence heat tolerance and to identify potential trade-offs or opportunities for balanced selection. Integrating these traits could therefore support the development of breeding strategies that improve both environmental efficiency and resilience to changing environmental conditions.

The objective of this project was to characterize the genetic basis of adaptation and mitigation in Canadian Holsteins and evaluate relationships among these traits. Specifically, the project aimed to 1) quantify direct effects of heat stress on production, health, fertility, and mitigation traits; 2) assess genetic relationships among adaptation and mitigation traits to identify potential trade-offs and opportunities for balanced selection; and 3) evaluate genetic relationships of heat tolerance among trait groups.

Materials and Methods

No approval by an Institutional Animal Care and Use Review Board was required because data were obtained from an existing database.

Data:

Phenotype data were provided by Lactanet Canada (Guelph, ON) comprising test-day records from first-lactation Canadian Holstein cows. Production traits included milk (MY; kg/d), fat (FY; g/d), and protein (PY; g/d) yields. Health traits included β-hydroxybutyrate (BHB; mmol/L) and somatic cell score (SCS). The fertility trait evaluated was days from first service to conception (FSTC; d). Mitigation traits included methane production predicted from mid-infrared spectral data (MP_{MIR}; g/d), body maintenance requirements (BMR; body weight^{75}), and dry matter intake (DMI; kg/d).

Weather data were extracted from the NASA POWER Database. Data included hourly records of ambient temperature (T; ˚C) and relative humidity (H; %) for each herd across the study period. Meteorological estimates in POWER are derived primarily from the NASA Modern-Era Retrospective Analysis for Research and Applications, Version 2 (MERRA-2), which combines observations from multiple sources, including satellites, surface observations, aircraft, radiosondes, ships, and buoys, with an atmospheric model through data assimilation. The data are provided at a spatial resolution of 0.5˚ latitude by 0.625˚ longitude. Herd coordinates were matched to the existing database of weather records, and date ranges from test dates and heat stress windows evaluated were used to extract the relevant records. Hourly temperature and

humidity index (THI) values were calculated using the equation reported by NRC (1971):

$$THI = (1.8*T) + 32 - (0.55 - (0.0055*H))*((1.8*T) - 26) \quad (1)$$

Daily THI values were generated by averaging across each 24-hour day and rounding to the tenths decimal place.

Phenotypic Analysis:

Phenotypic analyses were conducted to evaluate the impact of heat stress on production, fertility, health, and mitigation traits. Single trait animal models were fit for each trait to remove all known sources of environmental and genetic effects following the general structure of,

$$y = Xb + Za + Wu + Vo + e \quad (2)$$

where y is the phenotype, X is the design matrix for fixed effects in vector b, Z is the design matrix for additive genetic effects in vector a, W is the design matrix for additional random effects in vector u, V is the design matrix for permanent environment effects in vector o, and e is the vector of residuals. Fixed effects, presence of additional random effects, and presence of permanent environment effects varied between traits. Models implemented were based on the national evaluation models implemented by Lactanet Canada. The residual terms of these models capture variation in the phenotypes due to unknown sources, such as THI, and reflects the unexpected deviation in the phenotype after accounting for fixed and random effects.

For each trait, several temporal windows of effects were tested surrounding the test-day of the phenotype. Range of windows were based on previous studies and biological reasoning. Daily THI was averaged across each window and associated with the phenotypic record with windows ranging from ten days prior to two days after the test-day. Model residuals were plotted against the average THI generated from each of these windows to approximate the number and location of breakpoints. Thresholds of heat stress effects were identified using a segmented regression approach, where the relationship between THI and residuals is modeled by multiple linear functions. The breakpoints for each model were identified based on model fit, assessed by the adjusted coefficient of determination (R^2), visual inspection of the fitted regression line, and evaluation of associated pre- and post-breakpoint slopes.

Genetic Analysis:

Genetic analyses of heat tolerance were performed to estimate the heritability of traits under thermoneutral and heat stress conditions as well as to estimate the genotype by environment effect for the traits. The general model fit was

$$y=Xb+ Z_0a_0+ Z_1a_1+ Wu+ V_0o_0+ V_1o_1+ e \quad (3)$$

where y, X, b, W, u, and e are as defined above. The additive genetic and permanent environment effects were adjusted to include a slope and intercept term such that Z_0 is the incidence matrix for the random additive genetic intercept term in a_0, Z_1 is the incidence matrix for the random additive genetic slope term in a_1, V_0 is the incidence matrix for the random permanent environment intercept term in o_0, V_1 is the incidence matrix for the random permanent environment slope term in o_1. Slope terms (a_1 and o_1) were fit using a heat stress function,

$$HSF(Tr) = \max(0, Tr - th_t) \quad (4)$$

where r is each test-day record, Tr is the THI average associated with record r, and th_t is the THI threshold associated with each trait. Thresholds and windows for THI averages used in the genetic analysis were based on the best fit model identified in the phenotypic analysis. In this model, intercept terms (a_0 and o_0) represent thermoneutral production and slope terms (a_1

and o_1) represent heat tolerance, defined as the linear change per unit THI above the threshold.

Genetic correlations between the thermoneutral genetic intercept (a_0) and heat tolerance genetic slope (a_1) were estimated to evaluate the relationship between performance under thermoneutral conditions and the response to increasing THI above the trait-specific threshold defined by the heat stress function in Equation 4.

Correlation Analysis of Adaptation and Mitigation:

Genetic correlations were estimated among adaptation and mitigation traits to evaluate relationships between environmental resilience and mitigation potential and identify potential trade-offs in selection. Pairwise models were used to estimate correlations between the additive genetic effects of mitigation traits and the genetic intercept and slope terms of adaptation traits. Adaptation traits included production, health, and fertility traits and were modeled using the reaction norm approach described in Equation 3. Mitigation traits included MP_{MIR}, BMR, and DMI and were modeled using repeatability animal models. Thus, correlations with the adaptation intercept (a_0) represented relationships with thermoneutral performance, while correlations with the adaptation slope (a_1) represented relationships with heat tolerance. Correlations were considered significant when the absolute value of the estimate exceeded twice its standard error.

Preliminary Results & Discussion

Heat Stress Effects Varied Among Traits:

The THI threshold and window of susceptibility to heat stress differed among traits (Table 1). Production traits thresholds ranged from THI 55 for FY to THI 65 for MY. The highest estimated threshold was found for FSTC at THI 67. Windows of susceptibility also varied among traits, ranging from 2 d before through the test day for production traits to 3 d before through 2 d after the test day for FSTC. These differences demonstrate that the timing and magnitude of heat stress responses are trait-specific and support the use of trait-specific THI thresholds and exposure windows when evaluating heat tolerance. Detailed results for production and fertility traits are presented in Rockett et al. (2023b) and Dodd et al. (2026a), respectively. Results for MP_{MIR} (Amini et al., *in preparation*) and health traits (Campos et al., 2026; Storing et al., *in preparation*) are in preparation.

Table 1: Trait-specific temperature-humidity index (THI) thresholds and windows of susceptibility to heat stress. FSTC=first service to conception; MY=milk yield; FY=fat yield; PY=protein yield.

Trait	Units	Threshold	Window
FSTC	days	67	d-3 to d2
MY	kg/d	65	d-2 to d0
FY	g/d	55	d-2 to d0
PY	g/d	60	d-2 to d0

Genetic Variation in Heat Tolerance:

Genetic variation was identified for both thermoneutral performance and heat tolerance across the evaluated traits (Table 2). Heritability estimates for production traits ranged from 0.30 ± 0.01 to 0.22 ± 0.00 under thermoneutral conditions and from 0.24 ± 0.01 to 0.27 ± 0.01 under heat stress. These estimates indicate that genetic selection could be used to improve both overall production and the ability of animals to maintain performance under heat stress. Overall, the moderate heritability estimates under heat stress are consistent with previous studies in North American Holsteins (Campos et al., 2025; McWhorter et al., 2023) and indicate sufficient genetic variation to select for improved heat tolerance.

Genetic correlations between thermoneutral performance and heat tolerance were negative for all three production traits (Table 2). The strongest antagonistic relationship was observed for MY, followed by PY and FY. These results indicate an antagonistic genetic relationship between production potential and the ability to maintain performance under heat

stress. This is consistent with previous reports in Canadian and U.S. Holsteins (Campos et al., 2022a; Rockett et al., 2023a; McWhorter et al., 2023), which also reported a trade-off between production potential and heat tolerance. Thus, selection solely for increased production may compromise heat tolerance unless it is explicitly incorporated into breeding objectives.

Table 2: Heritabilities (h^2) and genetic correlations $r_{g(TN,HT)}$ among production traits under thermoneutral conditions and heat tolerance. Standard errors are shown in parentheses. Heritability of heat tolerance estimated at temperature-humidity index (THI) 75. TN = thermoneutral conditions; HT = heat tolerance; MY = milk yield; FY = fat yield; PY = protein yield.

Trait	TN h^2	HT h^2	$r_{g(TN,HT)}$
MY	0.30 (0.01)	0.26 (0.01)	-0.29 (0.05)
FY	0.22 (0.00)	0.24 (0.01)	-0.22 (0.03)
PY	0.22 (0.00)	0.27 (0.01)	-0.23 (0.03)

Genetic Correlations Between Adaptation and Mitigation:

Genetic correlations between MP_{MIR} and production traits were generally weak under both thermoneutral and heat stress conditions (Table 3). Under thermoneutral conditions, correlations were negligible for MY (-0.02 ± 0.02) and PY (-0.11 ± 0.02) and moderately unfavorable for FY (0.38 ± 0.02). Under heat stress, correlations were weak and favorable for all traits, ranging from -0.03 ± 0.04 for PY to -0.16 ± 0.04 for FY. These results indicate that selection for lower MP_{MIR} is unlikely to substantially affect MY or PY under either condition. The stronger association with FY suggests that selection for lower MP_{MIR} may be associated with a slight reduction in thermoneutral FY and a small improvement in the ability to maintain FY under heat stress. Results of this analysis are discussed in further detail in Dodd et al. (2026b).

Table 3: Genetic correlations between MIR-predicted methane production and production traits under thermoneutral conditions and heat tolerance. Standard errors are shown in parentheses. TN = thermoneutral conditions; HT = heat tolerance; MY = milk yield; FY = fat yield; PY = protein yield; MP_{MIR} = MIR-predicted methane production.

Trait	TN	HT
MY	-0.02 (0.02)	-0.10 (0.05)
FY	0.38 (0.02)	-0.16 (0.04)
PY	-0.11 (0.02)	-0.03 (0.04)

Conclusions

Heat stress responses were trait-specific, with differences in both the THI breakpoint and window of susceptibility among trait groups. Genetic variation was identified for both thermoneutral performance and heat tolerance of production traits, indicating potential for genetic selection to improve resilience to heat stress. The antagonistic relationship between thermoneutral production and heat tolerance further highlights the importance of including heat tolerance directly in breeding objectives rather than relying solely on selection for production. Positive genetic correlations among production traits indicate shared genetic control while supporting the inclusion of all traits in selection objectives. Generally weak relationships between heat tolerance of production traits and MP_{MIR} suggest that adaptation and mitigation can be improved with limited correlated responses. This project is ongoing and analyses are being completed across production (MY, FY, PY), health (BHB, SCS), fertility (FSTC), and mitigation traits (MP_{MIR}, BMR, DMI). Integration of these results will provide a comprehensive assessment of the genetic relationships among adaptation and mitigation traits to support the development of breeding strategies for more resilient and sustainable dairy cattle.

Acknowledgments

This study was part of Net-Zero Dairy Genome Project (NDGP; ICT-19401), Dairy Cluster 4 projects (Activities 8 & 13), AFC project (AFC-2025F3716R), AdaptMitigate Dairy Genome Project (ADGP; GAPP-1545773). We gratefully acknowledge all funding and support, as administered by Genome Canada (Ottawa, ON, Canada), Ontario Genomics (Toronto, ON, Canada), Genome Quebec (Montréal, QC, Canada), Genome Alberta (Calgary, ON Canada), Lactanet (Guelph, ON, Canada) and Dairy Farmers of Canada (Ottawa, ON, Canada) and contributions of Dairy Farmers of Ontario (Mississauga, ON, Canada), Dairy Farmers of Quebec (Montréal, QC, Canada), Alberta Milk (Edmonton, AB, Canada), Agricultural Funding Consortium (Edmonton, AB, Canada), Alberta Innovates (Edmonton, AB, Canada), Alberta Ministry of Technology and Innovation (Edmonton, AB, Canada), and Natural Sciences and Engineering Research Council of Canada (NSERC; Ottawa, ON, Canada). This research is supported by a contribution from the Dairy Research Cluster 4 partners (Lactanet Canada, Dairy Farmers of Canada, Semex Alliance, Holstein Canada and Agriculture and Agri-Food Canada) under the Sustainable Canadian Agricultural Partnership AgriScience Program. As per the research agreement, researchers maintain independence in conducting their studies, own their data, and report the outcomes regardless of the results. The decision to publish the findings rests solely with the researchers. No approval by an Institutional Animal Care and Use Review Board was required because data were obtained from an existing database. The authors have not stated any conflicts of interest.

References

Bush, E., N. Gillett, E. Watson, J. Fyfe, F. Vogel, and N. Swart. 2019. Understanding Observed Global Climate Change. Pages 24–72 in Canada's Changing Climate Report. Government of Canada.

Campos, I.L., T.C.S. Chud, G.A.O. Junior, C.F. Baes, Á. Cánovas, and F.S. Schenkel. 2022a. Estimation of Genetic Parameters of Heat Tolerance for Production Traits in Canadian Holsteins Cattle. Animals 12:3585. https://doi.org/10.3390/ani12243585.

Campos, I.L., T.C.S. Chud, H.R. Oliveira, C.F. Baes, A. Cánovas, and F.S. Schenkel. 2022b. Using publicly available weather station data to investigate the effects of heat stress on milk production traits in Canadian Holstein cattle. *Can. J. Anim. Sci.* 102:368–381. https://doi.org/10.1139/cjas-2021-0088.

Campos, I.L., R.E. Jahnel, F. Miglior, Z. Feng, A. Canovas, C.F. Baes, and F.S. Schenkel. 2025. Modeling heat tolerance for production traits in Canadian Holstein cattle. *J. Dairy Sci.* 108:9956–9966. https://doi.org/10.3168/jds.2025-26433.

Campos, I.L., R.E. Jahnel, H.R. Oliveira, F. Miglior, C.F. Baes, and F.S. Schenkel. 2026. Phenotypic and genetic analysis of somatic cell score response to heat stress in first lactation Holstein cattle. *J Anim Sci* skag252. https://doi.org/10.1093/jas/skag252.

Dodd, G.R., F. Miglior, F.S. Schenkel, I.L. Campos, R.E. Jahnel, and C.F. Baes. 2026a. Modeling heat stress effects on first service to conception rates in Canadian Holstein dairy cattle. *J. Dairy Sci.* 109:2727–2742. https://doi.org/10.3168/jds.2025-27171.

Dodd, G.R., F.S. Schenkel, C.F. Baes, F. Malchiodi, C. Richardson, and F. Miglior. 2026b. Genetic associations between mid-infrared-predicted methane production and heat tolerance of production traits in dairy cattle. *J. Dairy Sci.* 109:9677-9686. https://doi.org/10.3168/jds.2026-28568.

Hansen, P.J. 2004. Physiological and cellular adaptations of zebu cattle to thermal stress. *Animal Reproduction Science* 82–83:349–360. https://doi.org/10.1016/j.anireprosci.2004.04.011.

Ishida, S., A. Nishiura, T. Yamazaki, H. Abe, S. Nakagawa, Y. Nakahori, S. Yamaguchi, Y. Masuda, Y. Saito, R. Tatebayashi, T. Osawa, C.-H. Huang, and K. Hagiya. 2024. Effects of heat stress on predicted energy balance, fat-to-protein ratio, and milk β-hydroxybutyrate in first-lactation Holstein cattle in Hokkaido, Japan. *Animal Science Journal* 95:e70013. https://doi.org/10.1111/asj.70013.

McWhorter, T.M., M. Sargolzaei, C.G. Sattler, M.D. Utt, S. Tsuruta, I. Misztal, and D. Lourenco. 2023. Single-step genomic predictions for heat tolerance of production yields in US Holsteins and Jerseys. *J. Dairy Sci.* 106:7861–7879. https://doi.org/10.3168/jds.2022-23144.

NRC, (National Research Council). 1971. A Guide to Environmental Research on Animals. National Academy of Sciences.

Polsky, L., and M.A.G. von Keyserlingk. 2017. Invited review: Effects of heat stress on dairy cattle welfare. *J. Dairy Sci.* 100:8645–8657. https://doi.org/10.3168/jds.2017-12651.

Rockett, P.L., I.L. Campos, C.F. Baes, D. Tulpan, F. Miglior, and F.S. Schenkel. 2023a. Genetic evaluation of heat tolerance in Holsteins using test-day production records and NASA POWER weather data. *J. Dairy Sci.* 106:6995–7007. https://doi.org/10.3168/jds.2022-22776.

Rockett, P.L., I.L. Campos, C.F. Baes, D. Tulpan, F. Miglior, and F.S. Schenkel. 2023b. Phenotypic analysis of heat stress in Holsteins using test-day production records and NASA POWER meteorological data. *J. Dairy Sci.* 106:1142–1158. https://doi.org/10.3168/jds.2022-22370.

Van Doormaal, B., C. Jaton, H. Sweett, P.G. Sullivan, A. Fleming, F. Miglior, and C.M. Richardson. 2025. Modernizing Canada's Lifetime Performance Index (LPI). Interbull Bulletin 203–212.

Yan, G., K. Liu, Z. Hao, Z. Shi, and H. Li. 2021. The effects of cow-related factors on rectal temperature, respiration rate, and temperature-humidity index thresholds for lactating cows exposed to heat stress. *Journal of Thermal Biology* 100:103041. https://doi.org/10.1016/j.jtherbio.2021.103041

Zhang, X., G. Flato, M. Kirchmeier-Young, L. Vincent, H. Wan, X. Wang, R. Rong, J. Fyfe, G. Li, and V.V. Kharin. 2019. Changes in Temperature and Precipitation Across Canada. Pages 112–193 in Canada's Changing Climate Report. Government of Canada.