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Energy partitioning and energy efficiency of two Holstein genotypes under a mixed pasture-based system during mid and late lactation

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ABSTRACT

The objective was to evaluate the effect of the Holstein genotype (North American Holstein *vs.* New Zealand Holstein; **NAH** *vs.* **NZH**, respectively) in a pasture-based system on heat production (**HP**), energy partitioning between maintenance and production (milk and tissue) and energy efficiency during two different stages of lactation. Twenty-eight Holstein dairy cows (14 cows of each genotype) with similar calving date (May 5, 2018 ± 23 days) were managed in a pasture-based system and supplemented with one third of the predicted total dry matter intake as concentrate. Heat production, retained energy in milk and tissue, metabolizable energy intake (**MEI**) and the proportion of MEI retained in milk + tissue (**RE/MEI**) were measured at 115 and 192 ± 19 days in milk and residual HP was estimated by the difference between measured HP and predicted HP based on NRC (2001) model according to body weight, body condition score and milk production. The NAH cows were 60 ± 15 kg heavier and produced 4.7 ± 1.0 kg/d more milk with lower percentages of fat and protein than NZH cows. However, there were no differences in fat or protein yield per day between genotypes. Metabolizable energy intake, retained energy in milk and tissue, HP and RE/MEI were not different between genotypes at 115 days in milk. Nevertheless, at 192 days in milk the MEI, HP and residual HP were lower in NZH than NAH, whereas RE/MEI was not different when both genotypes were managed under a pasture-based system with one third of the consumed diet as concentrate. The capacity of NZH cows to maintain the same RE/MEI than NAH cows at 192 days in milk despite of the lower MEI, was due to a lower metabolizable energy requirement for maintenance (853 *vs.* 729 kJ/body weight$^{0.75}$ per day for NAH and NZH, respectively). Indeed, the lower energy requirement for maintenance in NZH was associated with a lower fasting heat production since k_l were not different between genotypes. Thus, NZH cows could have a lower proportion of their body as protein mass or a lower relative mass of the internal organs involved with digestive and circulatory functions. However, further investigation is necessary to understand the differences in maintenance energy requirements between the Holstein genotypes.

1. Introduction

Pasture-based milk production systems have gained international interest during recent decades due to their economic benefits and their advantages in relation to environment care, animal welfare and product quality (Dillon, 2006). However, it has been reported that high-yielding Holstein cows are not able to express their full production potential under grazing systems. Hence, energy supplementation is necessary to reach milk yields greater than 30 kg/day or to maintain an adequate body condition score (**BCS**) that ensures a successful lactation (Kolver and Muller, 1998; Dillon et al., 2003). Nevertheless, Bargo et al. (2002) reported that high-yielding grazing dairy cows supplemented with 40% of the diet as concentrate also produced less milk than those fed with a balanced total mixed ration. Thus, the inclusion of grazed pasture in the diets of dairy cows clearly depresses milk yield even with high supplementation levels.

However, Holstein genotypes managed under grazing systems presented different responses in milk-solid production to concentrate supplementation which reflected their capacity to meet their energy demands from the grazed pasture (Horan et al., 2005). Historically, selection within the Holstein breed has been accompanied by an increase in the proportion of North American genes with the aim of

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increasing individual milk yield but, the interaction between cow genotype and production system indicates that dairy genotypes must be evaluated and selected within systems similar to those in which they will be managed (Dillon, 2006). Indeed, previous research has demonstrated that, under grazing systems New Zealand Holstein (**NZH**) cows had lower milk yield with greater milk-solid concentrations, mobilized less body reserves, had lower metabolic stress and better reproductive performance than North American Holstein (**NAH**) cows (Roche et al., 2006; Lucy et al., 2009). Moreover, NZH cows presented a reduced milk response to concentrate supplementation and greater efficiency in the use of pasture for milk production than NAH cows (Horan et al., 2005; Macdonald et al., 2008) which indicates a greater adaptability to grazing systems for NZH cows.

Milk production of grazing cows is often lower than predicted by different feeding systems (Agnew and Yan, 2000). Dong et al. (2015a) performed a meta-analysis of calorimetry chamber experiments and showed that, contrary to the recommendations of international feeding systems, metabolizable energy maintenance requirements (**MEm**) were not constant but increased with metabolizable energy intake (**MEI**) and with the proportion of the forage in the diet. The greater MEm could be related to dietary fiber concentration and to protein:energy imbalance from pastures (Bruinenberg et al., 2002). Moreover, MEm not only depends on the diet quality, but is also affected by animal physical activity (Agnew and Yan, 2000). Recently, it has been demonstrated that heat production of grazing dairy cows was 18 to 20% greater than non-grazing cows fed with the same pasture chopped indoors (Kaufmann et al., 2011; Dohme-Meier et al., 2014).

To our knowledge, only one study has reported the heat production (**HP**) of Holstein dairy cows of different genotypes (Swiss Holstein *vs.* NZH) grazing during late lactation and the authors concluded that similar milk yields and small differences in body weight (**BW**) and physical activity led to similar HP, expressed per kg $BW^{0.75}$, in both genotypes (Thanner et al., 2014). Further characterizing and quantifying heat production of diverging Holstein genotypes in a pasture-based system is key to accurately estimate energy requirements of grazing dairy cows (Dohme-Meier et al., 2014).

We hypothesized that when both genotypes are managed in a pasture-based system, NZH cows would have a greater energy efficiency, partitioning more energy towards milk production as consequence of a lower MEm than NAH cows. Thus, the objective of this experiment was to quantify and evaluate heat production, energy partitioning between maintenance and production (milk and tissue) and energy efficiency of two Holstein genotypes (NAH *vs*. NZH) in a pasture-based system during mid and late lactation.

2. Material and methods

The experiment was carried out in 2018 as a part of a larger grazing trial at the Experimental Station of the Instituto Nacional de Investigación Agropecuaria - "La Estanzuela" (Colonia, Uruguay; latitude: 34° 21′ 14″ S, longitude: 57° 41′ 43″ W). All the experimental procedures were approved by the INIA's Commission on Ethics in Use of Experimental Animals (file #INIA2017.2).

2.1. Animal management and experimental design

Twenty-eight autumn calving Holstein dairy cows, 14 NZH (547 ± 67 kg BW and 3.27 ± 0.20 BCS at calving) and 14 NAH (589 ± 43 kg BW and 2.95 ± 0.23 BCS at calving), with at least 87.5% proved ancestry belonging to their corresponding genotype (Mejoramiento y Control Lechero Uruguayo; https://www.mu.org.uy), were used in a complete randomized design. Cows were paired between genotypes according to calving date (May 5, 2018 ± 23 days) and lactation number (3.1 ± 0.8 lactations) and immediately after calving were managed as a contemporary group according with their genotype in mixed grazing system.

Throughout the experiment cows grazed *Dactylis glomerata* + *Medicago sativa* (75% of the time) and *Festuca arundinacea* (25% of the time) pastures in a rotational-grazing manner returning to defined grazing areas when the major part of the grass tillers had between 2.5 to 3 leaves. Pasture was offered in daily strips and cows of each genotype grazed separately to keep similar herbage allowance relative to their BW and also to ensure breeds behaved independently, and avoid dominance effects of NAH on NZH cows due to differences in BW (Phillips and Rind, 2002) that could affect animal performance and bias results.

Herbage mass was measured weekly in every paddock by a pasture meter with an infrared sensor which is capable of measuring sward height (C-Dax pasture meter; C-Dax Ltd, Turitea, New Zealand). The pasture meter was previously calibrated, and an equation was determined for each forage species to convert herbage height to herbage mass above 5 cm from ground level (Waller et al., 2017). On the other hand, pasture growth rate was estimated by the difference in herbage mass and the days elapsed between two consecutive measurements. Herbage allowance (kg DM/d per cow) was adjusted weekly, based on pasture growth rate in the grazing platform and on stocking rate with the objective that daily herbage allocation for the cow group was equal to the pasture growth rate of the grazing platform. When forage allowance was considered restrictive to reach the predicted DM intake, cows were restrictively supplemented with conserved forage (corn silage and pasture haylage mix; 80:20 ± 12% on DM basis, respectively) to ensure to reach the predicted DM intake according to the National Research Council (NRC) model for Dairy Cattle (2001). Conserved forages were offered in a feeding parlor immediately before the afternoon milking and DM intake was measured by the difference between the amount offered and refused. Moreover, pasture quality was maintained on the grazing platform by removing surplus pasture as haylage or through strategic use of mowing. Pasture herbage allowances and conserved forage supplementation were adjusted every week based on the weekly pasture growth. Also, cows were individually supplemented with concentrates during milking twice a day (0400 h and 1400 h) at a rate of 33% of predicted daily DM intake to ensure that cows of each genotype had the same proportion of concentrate in the diet (Table 1).

During HP measurement periods (from August 20 to September 10 and from November 6 to November 26; at 115 and 192 ± 19 days in

Table 1
Estimated group dry matter (DM) intake of pasture, concentrate and conserved forage (mean ± SD) for Holstein cows of two different genotypes and at two different stages of lactation.

	Stage of lactation			
	115 DIM		192 DIM	
Item	NZH	NAH	NZH	NAH
Estimated DM intake (kg/cow per day)				
Pasture[1]	8.1 ± 4.1	10.9 ± 4.4	7.9 ± 3.0	9.8 ± 2.1
Concentrate[2]	6.9 ± 0.2	7.7 ± 0.3	6.0 ± 0.4	6.9 ± 0.4
Conserved forage[2]	4.5 ± 2.4	3.1 ± 3.1	3.6 ± 1.6	4.0 ± 1.7
Total dry matter intake	19.6 ± 2.3	21.7 ± 1.6	17.6 ± 2.2	20.6 ± 1.4

DIM = Days in milk; NZH = New Zealand Holstein; NAH = North American Holstein
SD represents the variation between the measurement groups within each heat production measurement period.
[1] Calculated as (Metabolizable energy intake (MJ/d) – consumed concentrate (kg DM/d) × energy concentration of concentrate (MJ/kg DM) – consumed conserved forage (kg DM/d) × energy concentration of conserved forage (MJ/kg DM)) / energy concentration of pasture (MJ/kg DM).
[2] Estimated by the difference between the feed offered and refused.

Table 2
Forage allowance, pre and post-grazing herbage mass and height and forage disappearance of the pastures grazed during the experiment.

	Pasture							
	115 DIM		192 DIM			*P*-value		
Item	NZH	NAH	NZH	NAH	SEM	G	SL	G × SL
Forage allowance[1] (kg DM/100kg of BW)	2.49	2.37	2.76	2.62	0.19	0.513	0.176	0.955
Pre-grazing herbage mass[1] (kg DM/ha)	1512	1559	1495	1669	71	0.134	0.503	0.357
Pre-grazing herbage height (mm)	145	148	143	156	5			
Post-grazing herbage mass[1] (kg DM/ha)	545	518	424	620	40	0.040	0.808	0.006
Post-grazing herbage height (mm)	76	74	68	82	3			
Forage disappearance[1] (kg DM/ha)	916	1068	1082	1047	57	0.321	0.203	0.100
Forage disappearance (mm)	65	75	76	74	4			

DIM = Days in milk; NZH = New Zealand Holstein (n = 14); NAH = North American Holstein (n = 14); G = Genotype; SL = Stage of lactation.
[1] Herbage mass measured above 5 cm from ground level.

Table 3
Chemical composition and metabolizable energy concentration (mean ± SD) of the feedstuff offered during the experiment.

Item	Conserved forage	Concentrate	Pasture at 115 DIM	Pasture at 192 DIM
Dry matter (%)	40.0 ± 6.7	85.2 ± 0.6	18.4 ± 3.9	22.4 ± 1.7
Crude protein (% DM)	11.6 ± 1.8	22.2 ± 0.4	24.6 ± 2.8	22.6 ± 1.5
Neutral detergent fiber (% DM)	43.8 ± 2.6	28.7 ± 3.6	51.5 ± 3.1	49.9 ± 2.3
Acid detergent fiber (% DM)	28.0 ± 2.9	11.9 ± 1.4	31.6 ± 3.1	28.0 ± 1.3
Ash (% DM)	9.2 ± 1.8	8.4 ± 0.3	12.0 ± 0.5	12.0 ± 0.7
Metabolizable energy[1] (MJ/kg DM)	9.9 ± 0.4	12.2 ± 0.1	10.5 ± 0.2	10.5 ± 0.1

SD represents the variation between feedstuff samples.
[1] According to NRC (2001).

milk (**DIM**), mid and late lactation, respectively) cows grazed the same pasture (*Dactylis glomerata* + *Medicago sativa* or *Festuca arundinacea*) with similar pre-grazing structure and herbage allowance expressed as percentage of their BW (Table 2). Also, there were no differences in the chemical composition and energy concentration of the grazed pastures for each genotype (Table 3). Cows were given access to their daily herbage allowance after milking, with access to freshwater.

2.2. Data recording, sample collection and laboratory analysis

Daily milk production was measured using automatic milk meters synchronized to Dairy Plan software (Dairy Plan; GEA Farm Technologies, Düsseldorf, Germany). Milk samples for chemical composition were collected fortnightly from both am and pm milking and preserved with potassium dichromate 5% (Lactopol®, Grupo Benzo, Uruguay) and subsequently analyzed for fat, protein and lactose by a milk analyzer (Combi FOSS FT+, Foss Electric, HillerhØd, Denmark). Cow BW and BCS were recorded fortnightly. Cow BCS was recorded by the same trained operator according to a scale from 1 to 5 (1 represents an excessively thin cow and 5 represents an excessively fat cow; Edmonson et al., 1989) and BW was registered with an animal scale model AD-4406 (A&D Weighing, Tokyo, Japan).

Samples ($n = 20$) of weekly pre-grazed pastures were taken above 5 cm from ground level, dried at 60°C for 48 h, and composited by week and subsequently by month. Conserved forage samples were collected weekly in the feeding parlor and composited by month and a sample of concentrate was obtained during each measurement period. Composited samples were analyzed (Animal Nutrition Laboratory, INIA "La Estanzuela") for DM, crude protein (**CP**) and ash (AOAC, 1990) and neutral detergent fiber (**NDF**) and acid detergent fiber (**ADF**) (Ankom Technology Method, Macedon, NY, USA).

2.3. Heat production measurements

Heat production was measured by the heart rate (**HR**) – O_2 pulse (**O_2P**) technique (Brosh et al., 1998) which was validated to estimate HP for different ruminant species, diets and environmental conditions (Brosh, 2007) and recently used for measuring HP in grazing dairy cows (Jasinsky et al., 2019). During each HP measurement period (115 and 192 ± 19 DIM), cows were measured in three groups of eight or ten cows balanced according to genotype and DIM and each group was measured successively in a different week during four to five consecutively days.

The HR-O_2P technique is based on the indirect estimation of HP through O_2 consumption measurement and it was calculated assuming 20.47 kJ/L O_2 consumed (Nicol and Young, 1990). Oxygen consumption (**VO_2**) was calculated as $VO_2 = HR \times O_2P$ where O_2P is the amount of O_2 consumed per heartbeat. The HR was recorded using Polar® devices (Polar Electro Oy, Kempele, Finland), with a model H10 HR transmitter and a RCX3 data logger watch model. Both electronic devices were mounted on the animal using an elastic belt fitted around the thorax and behind the forelegs and conductive gel was used to ensure conductivity. The HR was recorded for at least 4 consecutive days every 5 second intervals. The O_2P was estimated as the ratio between O_2 consumption and HR when both were measured simultaneously for 12 min. Oxygen consumption was measured using a facemask open-circuit respiratory system (Fedak et al., 1981), and the accuracy of the system was checked gravimetrically by nitrogen injection (N_2 recovery) into the facemask (McLean and Tobin, 1990). The N_2 recovery at 115 DIM was 101 ± 2% and at 192 DIM was 103 ± 5%. The O_2P measurements were made once at each measurement period no more than 15 d before or after the 4 d-HR measurement.

During the VO_2 measurement the cow was immobilized in a cattle squeeze and a conical neoprene facemask was placed covering the mouth and nose to ensure that all the exhaled air by the cow entered the system. Inside the system, samples of the exhaled air were taken automatically in which O_2 concentration was measured by a paramagnetic O_2 analyzer model Servopro 1440 (Servomex®, Crowborough, East Sussex, UK). The air flux into the system was calculated by differential pressure measurement with a very low differential pressure transducer (Model 267; Setra; Boxborough; USA) and relative humidity and temperature within the system was recorded by HygroClip S electronic

sensor (Rotronic AG, Basserdorf, Switzerland) to estimate the VO_2 under standard conditions. Data were simultaneously recorded in 5 seconds intervals by a dataTaker DT 50 (dataTaker®, Rowville Melbourne, Victoria, Australia). Finally, VO_2 was estimated through the difference between the O_2 concentration of the exhaled air and the atmospheric O_2 concentration (20.95%), multiplied by the air flow and corrected to standard conditions of temperature, humidity and pressure. Thus, HP (kJ/$BW^{0.75}$/d) = HR (beats/min) × O_2P (mL O_2/kg $BW^{0.75}$/beat) × 20.47 (kJ/mL O_2) × 60 min/h × 24 h/d. Prior to VO_2 and HR measurements, cows were accustomed to wear the facemask and the elastic belt three times before the measurements to avoid biases in results as a consequence of working with stressed animals. We verified that cows were not stressed during the VO_2 measurement comparing the HR recorded during VO_2 measurement with the HR recorded during the four consecutively days at the same moment of the day.

2.4. Weather measurements

Temperature and relative humidity were recorded daily by an automatic meteorological station located 2 km from the experimental site. During the first measurement (at 115 DIM) period the average daily temperature, relative humidity and temperature humidity index (THI; Valtorta and Gallardo, 1996) were 11.8°C, 77% and 53, respectively. Whereas, in the second period (192 DIM) the average daily temperature, relative humidity and THI were 20.9°C, 69% and 67, respectively.

2.5. Calculations and statistical analysis

Retained energy in milk (**REmilk**) and retained energy in tissue (**REtissue**) were estimated by the equations reported by the NRC model for Dairy Cattle (NRC, 2001) using individual cow records. Retained energy in milk (REmilk) was calculated based on daily milk production and its composition, using 38.8, 22.8 and 16.5 MJ/kg for milk fat, crude protein and lactose, respectively according to the following equation [Eq. 1]:

$$\text{REmilk(MJ/d)} = 38.8 \times \text{kg fat/d} + 22.8 \times \text{kg crude protein/d} + 16.5 \times \text{kg lactose/d}; \quad (1)$$

Retained energy in tissue (REtissue) was calculated taking into account changes in BW and BCS. Using cow BW and BCS records, linear, quadratic and cubic models were tested for each cow and the more suitable models (based on adjusted-R^2) were selected to estimate the changes in BW and BCS during the measurement period according to corresponding DIM. Each cow had a model that represented its BW or BCS according to DIM along the entire lactation. Changes in BW during the measurement period was estimated by solving the integral of the model (BW as a function of DIM) to the DIM of each cow at the HP measurement. Estimation of tissue mobilization or repletion and its proportion of fat and protein according to the following equations [Eq. 2 – 6]:

$$\text{REtissue(MJ/d)} = \text{REtissue(MJ/kg tissue)} \times \text{change empty body weight(kg/d)}, \quad (2)$$

where

$$\text{Empty body weight (kg)} = \text{BW (kg)} \times 0.817, \quad (3)$$

and

$$\text{REtissue (MJ/kg tissue)} = \text{Proportion empty body fat} \times 39.3 + \text{Proportion empty body protein} \times 23.2, \quad (4)$$

where

$$\text{Proportion empty body fat} = 0.037683 \times BCS_{1-9}, \quad (5)$$

and

$$\text{Proportion empty body protein} = 0.200886 - 0.0066762 \times BCS_{1-9}; \quad (6)$$

Total retained energy (**RE**) was calculated by the sum of REmilk + REtissue and MEI was estimated as total RE + HP. Predicted HP was calculated from BW and total RE using the coefficients of 335 kJ/kg $BW^{0.75}$/d for maintenance requirement, 0.62 and 0.64 for efficiency of use of ME for maintenance (k_m) and lactation (k_l) and 0.82 and 0.75 for tissue loss and deposition (k_g), respectively (NRC 2001). Residual HP was estimated by the difference between the measured HP and predicted HP according the following equations [Eq. 7 - 8]:

$$\text{Residual HP} = \text{MEI} - ((335\text{kJ} \times BW^{0.75})/0.62 + \text{REmilk}/0.64 + \text{REtissue}/0.82), \text{ if REtissue} < 0 \quad (7)$$

or

$$\text{Residual HP} = \text{MEI} - ((335\text{kJ} \times BW^{0.75})/0.62 + \text{REmilk}/0.64 + \text{REtissue}/0.75), \text{ if REtissue} > 0. \quad (8)$$

Data were analyzed using the SAS software (SAS® University Edition, SAS Institute Inc., Cary, NC, USA). All variables were analyzed with a mixed model using repeated measurements by the MIXED procedure. The model included genotype (NZH *vs*. NAH), stage of lactation (115 *vs*. 192 DIM) and its interaction as fixed effects, group of measurement within stage of lactation as a random effect, and calving date as a covariate to take into account the differences in DIM between cows in each stage of measurement. The compound symmetric covariance structure was specified and the Kenward-Rogers procedure was used to adjust denominator of degrees of freedom. Univariate analyses were performed on all variables to check the normality of residuals and identify outlier data. Means were considered to differ when $P \leq 0.05$, and trends were identified when $0.05 < P < 0.10$.

Correlation analyses were performed using the CORR procedures and regressions between HP and MEI and between total RE and MEI were fitted as a linear mixed model using the MIXED procedure with cow genotype included as a fixed effect and cow as a random effect; as the effect cow genotype was significant; regressions within genotype were adjusted. Fasting heat production (**FHP**) was estimated with the intercept of the regression between HP and MEI, the k_l value was calculated by the slope of the regression between total RE and MEI, and MEm was calculated by FHP/k_l.

3. Results

3.1. Body weight, milk production and composition

The NAH cows were 60 ± 15 kg heavier ($P = 0.008$) than NZH cows and in average cows of both genotypes were 19 ± 15 kg heavier ($P < 0.001$) at 192 DIM than 115 DIM. The NAH cows produced 4.7 ± 1.9 kg/d more ($P < 0.001$) milk but with lower ($P \leq 0.050$) percentages of fat and protein than NZH cows (Table 4). Therefore, there were no differences in fat or protein yield between genotypes, but lactose yield was greater ($P < 0.001$) for NAH than NZH cows. There was a genotype by stage of lactation interaction for lactose ($P < 0.001$) as the percentage decreased ($P < 0.001$) from 115 to 192 DIM only in NZH cows (Table 4). Milk, fat, protein and lactose yields decreased ($P < 0.010$) from 115 to 192 DIM.

3.2. Partitioning and energy efficiency

The MEI did not differ between genotypes but was greater ($P = 0.008$) at 115 than 192 DIM and there was a genotype by stage of lactation interaction for MEI ($P = 0.004$) (Table 5). The MEI decreased 14% from 115 to 192 DIM for NZH cows, but only 7% for NAH cows, thus, MEI was greater for NAH than NZH cows at 192 DIM. Total RE and REmilk did not differ between genotypes but decreased ($P < 0.010$) from 115 to 192 DIM (Table 5). However, there was a trend for a

Table 4
Body weight, milk production and milk composition for Holstein cows of two different genotypes (G) and at two stages of lactation (SL).

	Genotype					*P*-value		
	115 DIM		192 DIM					
Item	NZH	NAH	NZH	NAH	SEM	G	SL	G × SL
Body weight (kg)	516	582	541	592	15	0.008	<0.001	0.289
Daily production (kg/d)								
Milk	27.4	32.5	20.2	25.1	1.9	<0.001	0.006	0.835
Fat	1.27	1.34	0.93	1.02	0.06	0.195	0.010	0.678
Protein	1.00	1.03	0.76	0.82	0.03	0.282	0.004	0.325
Lactose	1.34	1.55	0.95	1.20	0.06	<0.001	0.007	0.472
Milk composition (%)								
Fat	4.65	4.14	4.65	4.11	0.15	0.012	0.822	0.876
Protein	3.69	3.19	3.79	3.28	0.08	<0.001	0.330	0.845
Lactose	4.88[a]	4.79[ab]	4.70[b]	4.78[ab]	0.04	0.895	<0.001	<0.001

DIM = Days in milk; NZH = New Zealand Holstein (n = 14); NAH = North American Holstein (n = 14)
[ab] Means within a row with different superscripts differ ($P < 0.05$).

Table 5
Energy partitioning and energy efficiency for Holstein cows of two different genotypes (G) and at two different stages of lactation (SL).

	Genotype					*P*-value		
	115 DIM		192 DIM					
Item	NZH	NAH	NZH	NAH	SEM	G	SL	G × SL
Energy partitioning (kJ/BW$^{0.75}$ per day)								
MEI[1]	2011[ab]	2030[a]	1724[c]	1879[b]	45	0.117	0.008	0.004
Total RE[2]	842	816	607	649	32	0.808	0.006	0.062
REmilk[3]	872	859	619	651	31	0.764	0.003	0.170
REtissue[3]	-28	-44	-12	-2	15	0.739	0.209	0.218
HP[4]	1170[a]	1212[a]	1117[b]	1230[a]	27	0.029	0.303	0.045
Residual HP[5]	149	196	230	325	28	0.037	0.033	0.316
Energy efficiency								
RE/MEI	0.432	0.421	0.359	0.347	0.011	0.246	0.007	0.485
HR (beats/min)	79.0	78.2	75.7	75.6	1.1	0.731	0.065	0.602
O_2P (mL O_2/BW$^{0.75}$/beat)	0.504	0.527	0.501	0.552	0.010	0.030	0.369	0.087

DIM = Days in milk; NZH = New Zealand Holstein (n = 14); NAH = North American Holstein (*n* = 14); MEI = Metabolizable energy intake; Total RE = Total retained energy; REmilk = Retained energy in milk; REtissue = Retained energy in tissue; HP = Heat production; HR = Heart rate; O_2P = O_2 Pulse; BW = Body weight
[1] MEI = Total RE + HP.
[2] Total RE = REmilk + REtissue.
[3] According to NRC (2001).
[4] HP estimated by HR-O_2P technique (Brosh et al.,1998).
[5] Residual HP = difference between estimated HP and predicted HP according to NRC (2001).
[ab] Means within a row with different superscripts differ ($P < 0.05$).

genotype by stage of lactation interaction for total RE ($P = 0.062$) as the decrease from 115 to 192 was greater for NHZ than NAH cows (28 *vs.* 20%, respectively). There were no differences between genotype or stage of lactation for REtissue (Table 5).

Heat production was greater ($P = 0.029$) for NAH than NZH cows due to a greater ($P = 0.030$) O_2P (Table 5). Heart rate tended ($P = 0.065$) to decrease from 115 to 192 DIM while there was a tendency for genotype by stage of lactation interaction for O_2P ($P = 0.087$) as O_2P tended to be increase ($P = 0.098$) from 115 to 192 DIM for NAH cows but remained unchanged for NZH cows. Thus, there was genotype by stage of lactation interaction for HP ($P = 0.045$) as it decreased from 115 to 192 DIM only in NZH cows.

Residual HP was greater ($P = 0.037$) for NAH than NZH cows and it was greater ($P = 0.033$) at 192 than 115 DIM (Table 5). However, RE/MEI was not affected by genotype but was greater ($P = 0.007$) at 115 than 192 DIM (Table 5). The correlation of RE/MEI with residual HP was negative ($r = -0.772$; $P < 0.001$) and positive with MEI ($r = 0.612$; $P < 0.001$) (Fig. 1A and B). However, residual HP did not correlate with MEI ($r = 0.008$; $P = 0.970$) (Fig. 1C). Metabolizable energy intake correlated positively with total RE and HP and regression of these variables were significant for both genotypes (NZH total RE = -463 + 0.635 MEI; $r = 0.893$; $P < 0.001$; NAH total RE = -569 + 0.667 MEI; $r = 0.857$, $P < 0.001$) and HP (NZH HP = 463 + 0.365 MEI; $r = 0.752$; $P < 0.001$; NAH HP = 569 + 0.334 MEI; $r = 0.639$; $P < 0.001$) (Fig. 2). Moreover, FHP and k_l were 463 kJ/BW$^{0.75}$ per day and 0.635 for NZH and 569 kJ/BW$^{0.75}$ per day 0.667 for NAH, respectively and therefore MEm were 853 kJ/BW$^{0.75}$ per day for NAH and 729 kJ/BW$^{0.75}$ per day for NZH.

4. Discussion

Although our results indicated increased energy maintenance requirements - greater FHP and residual HP – for NAH than NZH cows, adjusted energy efficiency (total RE/MEI) was not different between Holstein genotypes. In spite of this, both, MEI and HP showed a deeper decrease from 115 to 192 DIM for NZH than NAH cows which decreased MEI in a lesser extent with no changes in HP. However, because the effects were in the same direction for both variables, there was no interaction for the energy efficiency.

Differences in MEI and energy partitioning (total RE – milk and

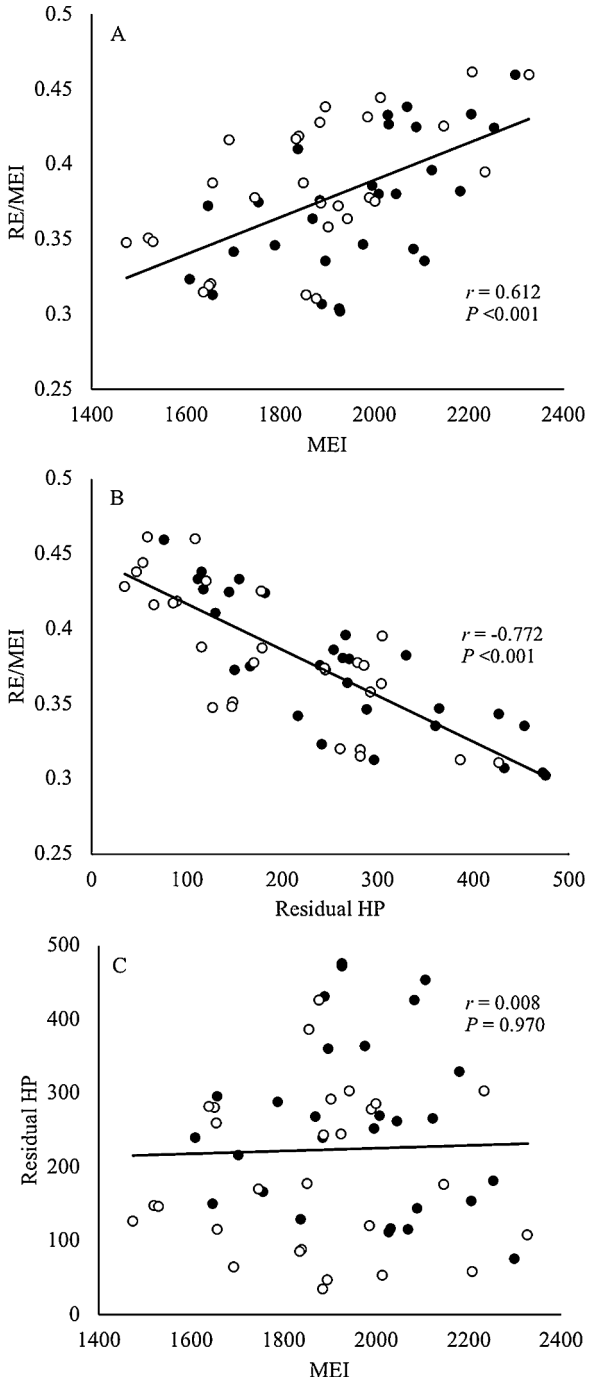

Fig. 1. (A) Relationship between RE/MEI (unitless) and Metabolizable energy intake (MEI; kJ/$BW^{0.75}$/d); (B) Relationship between RE/MEI and residual heat production (residual HP; kJ/$BW^{0.75}$/d); (C) Relationship between residual HP and MEI. Black circles (●) represent North American Holstein cows ($n = 14$) and open circles (○) represent New Zealand Holstein cows ($n = 14$).

tissue - and HP) between Holstein genotypes were not found during mid lactation (115 DIM) but during late lactation (192 DIM) the MEI and HP were greater in NAH cows compared to NZH cows. In contrast, Thanner et al. (2014) did not report differences in the daily energy intake or HP measured during 6 h when comparing NZH *vs.* Swiss Holstein at 176 ± 18 DIM and concluded that they were not able to find differences in HP due to the small differences between Holstein strains in milk production, BW and physical activity, and to the high variation between animals which could have been associated with the ^{13}C bicarbonate dilution technique used for HP estimation. Estimation of HP from VO_2 are more accurate than those solely from CO_2 production (McLean, 1972) as according to Brouwer equation (1965) the latter contributes approximately to 25% of HP whereas VO_2 contributes to 75% of HP.

In the present work, both genotypes decreased MEI when the lactation progressed (from 115 to 192 DIM) as well as milk yield. It was expected since cows consume feed to meet their energy needs and therefore the MEI is largely driven for the metabolic demands for milk production in dairy cows (Mertens, 1987). However, at 192 DIM, NAH cows had greater MEI than NZH cows probably as consequence of greater DM intake as estimated dietary ME concentration did not differ between groups (11.0 ± 0.1 MJ/kg DM). Indeed, based on MEI, concentrate and conserved forage DM intake and ME concentrations, estimated pasture forage intake was 7.9 ± 3.0 and 9.8 ± 2.1 kg DM/d for NZH and NAH, respectively. Therefore, total DM intake, expressed as a percentage of BW, was greater for NAH than NZH during late lactation, representing 3.48 and 3.26 ± 0.09 for NAH and NZH, respectively. The greater total DM intake and milk production of NAH than NZH cows during late lactation in this experiment are in the line with the results reported by McCarthy et al. (2007) who indicated that feed intake and milk yield are strongly correlated and therefore, dairy cows with higher milk production potential should have higher intake potential.

Although the greater MEI during late lactation for NAH than NZH cows was associated with greater milk production (208 *vs.* 180 g milk/kg$BW^{0.75}$/d), neither REmilk nor REtissue were different between genotypes at 192 DIM while HP was greater for NAH than NZH. Thus, NAH cows were not able to partition a greater proportion of MEI to energy in products (milk or tissue) compared to NZH cows, in turn the greater MEI was lost as HP.

The greater HP in NAH than NZH cows was due to an increased O_2P in the former ones because HR did not differ between genotypes. The HR values reported in this experiment are in line with those reviewed by Brosh (2007) for Holstein dairy cows although they were measured in confined cows during early and mid-lactation. On the other hand, the greater O_2P in NAH than NHZ cows could be explained by an increased energy demand (Brosh, 2007) associated with higher milk production which represents a greater metabolic demand. It has been reported that O_2P averaged 450 μL O_2/$BW^{0.75}$ per beat for confined high-yielding dairy cows between 30 and 160 DIM (Brosh, 2007). However, 1.12 to 1.21 fold-increases of O_2P have been reported as consequence of greater energy requirements in lactating *vs.* non-lactating or grazing *vs.* confined beef cows (Brosh, 2007). Thus, the O_2P determined in the present work is a reasonable value for grazing dairy cows during mid-late lactation.

Since total HP is a function of maintenance and production, either maintenance heat production (**HPm**), production heat production (**HPp**) or both may be responsible of driving total HP (Miron et al., 2008). Total RE did not differ between genotypes, thus, it can be expected that the greater HP determined for NAH cows was not due to HPp but to increased HPm. Indeed, linear regression of total HP on MEI indicated FHP (the intercept value when MEI is equal to zero) was 1.23-fold greater for NAH than NZH cows, suggesting increased basal metabolic rates in the former ones. Increased maintenance energy requirements of NAH cows were also evidenced in residual HP. Residual HP reflects HP associated to MEm after basal metabolism energy requirements (540 kJ/$BW^{0.75}$ per day) are discounted. Hence, the greater residual HP in NAH than NZH cows could be explained by increased basal metabolism energy requirement compared to the estimation based on the NRC (2001) model which is reflected in the greater FHP in NAH than NZH cows.

The differences in FHP could be related to a higher metabolic rate in NAH genotype as a result of genetic selection. The greater FHP of NAH than NZH cows may be associated with an increase in organ mass due to greater nutrient intake and therefore greater digestion, absorption, and circulatory activity as well as an increased body protein relative mass which results in higher energy costs associated with protein turnover

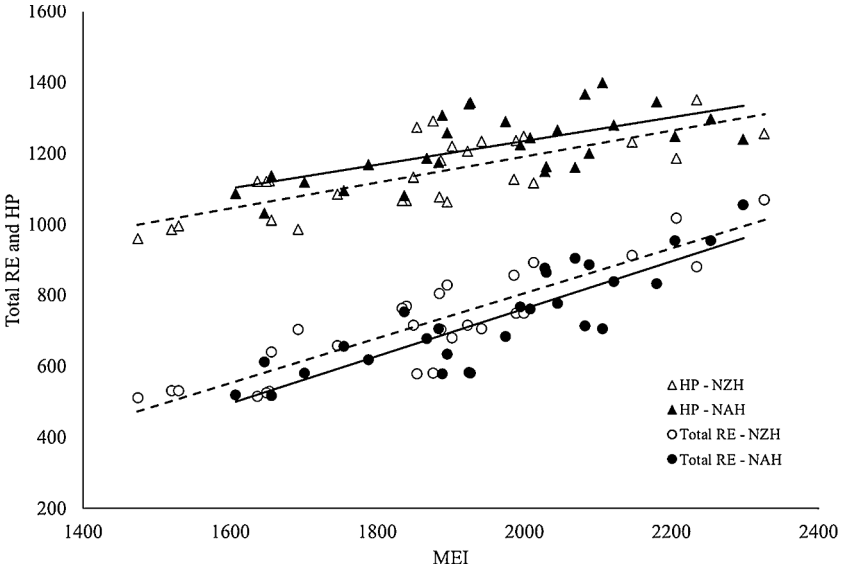

Fig. 2. Relationship between Heat production (HP; kJ/$BW^{0.75}$/d) and total Retained Energy (Total RE; kJ/$BW^{0.75}$/d) with Metabolizable Energy Intake (MEI; kJ/$BW^{0.75}$/d) in New Zealand Holstein (NZH, $n=14$) and North American Holstein (NAH, $n=14$). Solid lines represent the linear regression for HP and Total RE in NAH and dashed lines represent the linear regression for HP and Total RE in NZH. The HP-NAH = 569 + 0.334 MEI (R^2 = 0.41) and Total RE-NAH = -569 + 0.667 MEI (R^2 = 0.73). The HP-NZH = 463 + 0.365 MEI (R^2 = 0.57) and Total RE-NZH = -463 + 0.635 MEI (R^2 = 0.80).

(Oldham and Emmans, 1990; Agnew and Yan, 2000). We considered that in the present work, animal activity and thermoregulation did not affect MEm as the daily routine and grazing time did not differ between genotypes ($P > 0.100$; 374 *vs.* 357 min/d for NZH and NAH, respectively; Talmón et al., unpublished data) and cows were all managed in the same environment.

Energy efficiency (RE/MEI) decreased as lactation progressed due to a lower MEI that did not allow cows to "dilute" their maintenance energy requirements and therefore they partitioned a smaller proportion of the MEI to milk production (VandeHaar et al., 2016). However, the Holstein genotype did not affect RE/MEI which is explained because NAH cows were not able to retain a greater proportion of the MEI despite of their greater MEI at 192 DIM compared to NZH as consequence of their increased MEm.

On the other hand, the k_l values for both genotypes (0.67 *vs.* 0.63 for NAH and NZH, respectively) were close of k_l values reported by Moe and Tyrrell (1972) ($k_l=0.64$) and used in NRC (2001), Xue et al. (2011) for Holstein dairy cows fed with 30% of concentrate ($k_l=0.60$) and Dong et al. (2015a; 2015b) through a meta-analysis for high-producing Holstein dairy cows ($k_l=0.64$) or dairy cows consuming diets with >60% forage ($k_l=0.63$). Indeed, the negligible difference of 5% between genotypes on k_l was expected because it has been reported that cow genotype or milk yield would have a limited effect on k_l values when REmilk is adjusted by REtissue (Agnew and Yan, 2000; Xue et al., 2011). It would be more probable that partial efficiency of ME utilization for milk production (k_l) varies with diet composition because it is dependent on stochiometric and thermodynamic relationship between substrates and animal products (Baldwin, 1995) but in this experiment both genotypes received a similar diet.

The MEm in the present study (853 and 729 kJ/$BW^{0.75}$/d for NAH and NZH, respectively) were above maintenance energy requirements proposed by the NRC (2001) model (540 kJ/$BW^{0.75}$/d). Recently, underestimation of MEm proposed by NRC (2001) model for modern high producing dairy cows (Moraes et al., 2015) has been well documented through a multivariate analysis of more than a thousand complete energy balance data collected from respiration chamber trials. These authors indicated that dairy cows evaluated between 1984 and 1995 presented a MEm of 740 kJ/$BW^{0.75}$/d (700 to 780, 95% CrI) and being between 25 to 45% greater than MEm estimated for those evaluated between 1963 and 1983, highlighting the impact of the genetic progress on increased MEm. Moraes et al. (2015) data set was collected from the USDA Energy Metabolism Unit at Beltsville, Maryland, thus, it would be reasonable to compare their results only with those obtained from NAH cows in our work. Indeed, MEm was 15% greater for NAH cows in the present experiment than the one reported by Moraes et al. (2015) which could be associated to grazing activity energy requirements that do not exist when HP is measured in a respiration chamber. Thus, although HP measurements in respiration chambers is considered the gold standard, the O_2P technique has a great potential to estimate the HP on free-ranging animals (Oss et al., 2016).

Traditionally, the dairy industry has increased energy retention efficiency (RE/MEI), by driving MEI partitioning towards milk production. In this way, "diluting" maintenance requirements as milk production increases and feed intake does not increase to the same extent, has been the most important driver in improving feed efficiency in the past but, its effect decreases with each successive increment in milk production relative to BW and so it will be less important in the future (VandeHaar et al., 2016). Alternatively, individual energy efficiency, regardless of the "dilution of maintenance" effect, can be evaluated by estimating the residual HP (Aharoni et al., 2006). Moreover, as shown in the present study, cows with greater residual HP will have a decreased energy retention efficiency (RE/MEI) as a greater proportion of the consumed ME will be lost as heat. In addition, residual HP does not depend on MEI which would indicate that residual HP is defined mainly by each phenotype *per se* and is not dependent on the production or intake levels as RE/MEI. On the whole, residual HP could be a good selection tool to aim for a more efficient dairy cow since it is related with residual feed intake (Asher et al., 2018), which has been shown to have high ranking repeatability across different diets (Potts et al., 2015), lactations (Connor et al., 2013) and stages of lactation (Tempelman et al., 2015).

5. Conclusions

The NAH cows had a greater MEm than NZH cows and in both genotypes it was higher than the values proposed by NRC (2001) model while k_l were not different between genotypes and were in line with recent reports. Despite differences in MEm, energy efficiency (RE/MEI) was not affected by the Holstein genotype during the experiment. However, as lactation progressed the NZH cows decreased feed intake (both, DM and ME) associated with reduced milk yield when compared to NAH cows. Although NZH cows reduced their MEI during late lactation, their energy efficiency was similar to NAH cows as NZH cows decreased total HP due to lower MEm requirements when compared to NAH cows. Nevertheless, the presence of genotype by stage of lactation interaction for MEI and HP suggests that more measurements along lactation are necessary to conclude that both Holstein genotypes do not have differences in energy partitioning between milk and tissue as well

as in energy efficiency under pasture-based systems with high concentrate supplementation.

CRediT authorship contribution statement

Daniel Talmón: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Funding acquisition. **Mercedes Garcia-Roche:** Investigation, Writing - review & editing. **Alejandro Mendoza:** Conceptualization, Methodology, Resources, Writing - review & editing. **Diego A Mattiauda:** Writing - review & editing. **Mariana Carriquiry:** Conceptualization, Methodology, Formal analysis, Resources, Writing - review & editing, Supervision, Project administration.

Declaration of Competing Interest

None of the authors have any conflict of interest to declare.

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