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Holstein strain affects energy and feed efficiency in a grazing dairy system

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ABSTRACT

Context. Improving the partitioning of the energy consumed by dairy cows towards milk-solid production is a priority in grazing diary systems because energy efficiency has been associated with sustainability. Different selection criteria in the Holstein breed have led to divergent Holstein strains with different suitability to grazing systems. **Aim.** The objective of this work was to quantify and evaluate the energy partitioning between maintenance and milk production of two divergent Holstein strains (New Zealand Holstein and North American Holstein) in a grazing system without supplementation of concentrate. **Methods.** New Zealand Holstein and North American Holstein cows, nine of each, in mid-lactation (183 ± 37 days in milk, mean ± s.d.) were allocated in a randomised block design and evaluated under grazing conditions. The cows were managed under a daily strip-grazing system and grazed perennial ryegrass as the only source of nutrients. After an adaptation period of 14 days, heat production, retained energy in milk and metabolisable energy intake were measured over 7 days, and animal behaviour was simultaneously recorded. **Key results.** Milk yield did not differ between Holstein strains, but fat and protein content were greater for New Zealand than North American Holstein cows; consequently, retained energy in milk was 13% greater for the former strain. Heat production did not differ between Holstein strains, but metabolisable energy intake (kJ/bodyweight$^{0.75}$.day) was greater for New Zealand than North American Holstein cows, which was associated with a greater pasture dry matter intake relative to their body weight. Both feed and energy efficiency were greater for New Zealand than North American Holstein cows. **Conclusions.** The results supported that the New Zealand Holstein strain has greater energy and feed efficiency, demonstrating that it could be more suitable to be managed under a grazing dairy system without supplementation than the North American Holstein strain. **Implications.** The New Zealand Holstein strain may be suited to selection as a dairy cow with the capacity to fulfil energy requirements from pasture, which is a key factor to improve production efficiency of grazing dairy systems.

Keywords: dairy cattle, dairy cows, dairy nutrition, feed conversion efficiency, grazing, heat production, Holstein–Friesian, pasture-based system.

Introduction

Interest in grazing dairy systems has increased in many temperate and subtropical regions of the world because of their reduced complexity of installation, requirement for capital infrastructure and cost per unit of product compared with intensive systems, as well as their potential for accessing high-value markets due to perceived animal welfare benefits (Roche *et al.* 2017). However, despite these advantages, and probably because of land use competition, grazing systems account for only 10% of the world's milk production (Steinfeld and Mäki-Hokkonen 1995). Therefore, most of the research, technology developments and animal genetic selection criteria have not been focused on these systems.

The existence of interaction between animal genotype and the production system in which they are managed is well documented (Veerkamp *et al.* 1994; Horan *et al.* 2005;

McCarthy *et al.* 2007; Macdonald *et al.* 2008). In pasture-based systems, the ability of the grazing animal to consume sufficient quantities of forage in order to satisfy its requirements is a key factor for increasing milk production (Dillon 2006). Therefore, the selection of a dairy cow able to achieve a high herbage intake to maximise the amount of forage in its diet and efficiently convert that forage into milk is critical to successful dairy grazing systems (McCarthy *et al.* 2007).

The Holstein breed is one of the most popular dairy breeds world-wide, and divergent strains selected according to the production system in which they are managed can be identified. On one hand, the New Zealand Holstein (NZH) strain has been selected to be managed under pasture-based systems focusing on a dairy cow with a low body weight (BW), low maintenance requirements and medium milk yield but with high milk-solid contents. On the other hand, the North American Holstein (NAH) strain has been selected to be managed in indoor systems, resulting in a dairy cow with greater BW and maintenance requirements and greater milk yield potential but with lower milk-solid contents than the NZH strain (Miglior *et al.* 2005). Kolver *et al.* (2002) reported that when both strains were fed only with pasture, NHZ cows had greater dry matter intake (DMI) and efficiency at producing 1 kg milk solid per unit metabolic BW ($BW^{0.75}$), without differences in the total milk-solid yield per cow in the lactation, compared with NAH cows.

Recently, we reported that when grazing dairy cows were supplemented with concentrate at the rate of one-third of the daily diet, maintenance energy requirement expressed per unit $BW^{0.75}$ was less for NZH than NAH cows, which allowed them to maintain a similar partitioning of the energy consumed towards milk and tissue despite their reduced metabolisable energy intake (MEI) during mid-lactation (Talmón *et al.* 2020). This diet could have favoured the NAH cow because of its greater response to concentrate supplementation (McCarthy *et al.* 2007), which indicates that NAH cows have less capacity to meet their energy requirements than NZH cows when they are fed a pasture-only diet. Therefore, it is expected that the differences between strains decrease when the proportion of pasture in the diet is lower. In this context, we hypothesised that when both Holstein strains were managed in a grazing system without supplementation, the NZH cows would achieve greater DM and energy intake per kg BW than NAH cows, which, together with their lower maintenance energy requirements, would lead to a greater partitioning of the consumed energy into milk-solid production for NZH than NAH cows. Thus, the aim of this work was to evaluate and quantify the energy partitioning between maintenance and milk production of these two divergent Holstein strains (NZH vs NAH) in a grazing system without supplementation.

Materials and methods

Animals and experimental design

The experiment was performed during spring 2019 at the Experimental Station of the Instituto Nacional de Investigación Agropecuaria, 'La Estanzuela' (INIA; Colonia, Uruguay; 34°21′14″S, 57°41′43″W). All of the experimental procedures were previously approved by the INIA's Commission on Ethics in the Use of Experimental Animals (File #INIA2017.2).

The experiment was of a randomised block design and lasted 35 days with three successive periods: a transition period of 14 days, and an experimental period comprising 14 days of adaptation and 7 days of measurement. Eighteen Holstein, nine NAH and nine NZH cows, selected from the experimental station dairy herd were balanced according to lactation number (3.0 ± 1.6 and 3.2 ± 1.5 for NAH and NZH, respectively; values are mean ± s.d. unless indicated), days in milk (DIM), and milk yield and assigned to three blocks. Each block was composed of two sub-paddocks, one per genetic strain, with three cows per sub-paddock. Experimental cows had >87.5% of their genes belonging to their corresponding strain, and the economic and productive breeding index was on average 106 ± 11 for NAH and 122 ± 6 for NZH cows. NAH cows had a 305-day expected progeny difference of: +90 ± 132 kg for milk yield, +4.7 ± 7.6 kg for fat yield, +0.02% ± 0.12% for fat content, +4.8 ± 3.6 kg for protein yield, and +0.03% ± 0.07% for protein content. NZH cows had a 305-day expected progeny difference of: −77 ± 180 kg for milk yield, +4.8 ± 5.1 kg for fat yield, +0.11% ± 0.08% for fat content, +5.8 ± 5.8 kg for protein yield, and +0.12% ± 0.05% for protein content (Mejoramiento y Control Lechero Uruguayo, https://www.mu.org.uy). Cows calved in autumn 2019 (5 May 2019 ± 37 days) and were managed as a contemporary group under a grazing system with individual and variable concentrate supplementation based on their milk production until the beginning of the experiment.

At the start of the transition period, NAH and NZH cows were producing 36.7 ± 8.6 and 30.2 ± 9.1 kg milk/day and were supplemented with 6.0 ± 1.2 and 5.3 ± 1.7 kg DM concentrate/day, respectively. During the transition period, supplementation was gradually decreased (by 20% every 3 days) until the end of the period, when cows were fed only with grazing pasture. During the adaptation period, cows were offered a similar diet (only grazing pasture) and were managed in the same conditions as during the measurement period. At the end of the adaptation period, NAH cows had average values of BW 571 ± 79 kg, body condition score (BCS) 3.0 ± 0.34 units (on a 1–5 scale; Edmonson *et al.* 1989) and DIM 179 ± 38; NZH cows had values of BW 526 ± 64 kg, BCS 3.1 ± 0.37 units and DIM 186 ± 36.

Experimental period: daily routine, grazing management and weather conditions

Cows were milked twice daily at 06:30 and 16:00 hours and had access day and night to a pasture paddock (19.5 h, from 1730 to 0600 hours and from 0845 to 1545 hours), with free access to fresh water, which was 450 m from the milking parlour. The pasture was a first-year tetraploid perennial ryegrass (*Lolium perenne* L. cv. Halo; PGG Wrightson Seeds, Montevideo, Uruguay) with herbage mass of 3673 ± 194 kg DM/ha and herbage allowance of 31 ± 4 kg DM/cow.day (mean ± s.e.m.), which was considered non-restrictive to maximise pasture DM intake (Pérez-Prieto and Delagarde 2013). Chemical composition of the pasture is presented in Table 1. The paddock was divided into six sub-paddocks, one per replicate, in which herbage mass was measured every day by cutting five pasture samples of 50 cm by 50 cm above 5 cm from ground level. A strip-grazing system was used, and every day after the morning milking, cows accessed a fresh strip delimited with electric fences. Five weeks before the start of the measurement period, the pasture was intensively grazed and fertilised with 70 kg nitrogen (N)/ha to achieve a good-quality vegetative structure of the pasture during the experiment.

Weather conditions were registered by an automatic meteorological station (Campbell Scientific, Logan, UT, USA) placed 1500 m from the milking parlour. During the experimental period, the mean temperature was 19.4°C ± 0.7°C (25.3°C ± 2.0°C maximum and 14.8°C ± 1.4°C minimum temperature), and the mean relative humidity was 73% ± 10% (91% ± 8% maximum and 51% ± 16% minimum relative humidity). The average temperature humidity index (Valtorta and Gallardo 1996) was 66 ± 1, which did not indicate the presence of heat stress conditions.

Table 1. Chemical composition and gross energy concentration of the perennial ryegrass offered during the measurement period.

Pasture component	Value
Dry matter (DM, g/kg)	149
Chemical composition (g/kg DM)	
Crude protein	130
Neutral detergent insoluble crude protein	42
Acid detergent insoluble crude protein	16
Ether extract	40
Non-fibre carbohydrates[A]	211
Neutral detergent fibre	522
Acid detergent fibre	327
Lignin	39
Ash	139
Gross energy (MJ/kg DM)	16.0

[A] Calculated as 1000 − crude protein − ether extract − neutral detergent fibre − ash.

Data recording, sample collection and laboratory analysis

Daily milk yield was measured individually by using automatic milk meters synchronised to Dairy Plan software (Dairy Plan; GEA Farm Technologies, Düsseldorf, Germany). Samples for milk composition were collected on 3 days during the measurement period (Days 2, 4 and 6) from both milkings and preserved with 5% potassium dichromate (Lactopol; Grupo Benzo, Montevideo, Uruguay). Milk fat, protein and lactose were analysed in a milk analyser (Combi FOSS FT+; Foss Electric, Hillerhød, Denmark). Cow BW was recorded at start and the end of the measurement period by using an animal scale (model ID3000; Tru-Test, Auckland, New Zealand) immediately after the morning milking.

Heat production (HP) was measured in each cow by indirect calorimetry using the heart rate (HR)–oxygen pulse technique (Brosh 2007), which consists of estimating the animal's oxygen consumption by measuring the HR throughout several days and the oxygen consumed per heartbeat (O_2P) as described by Talmón *et al.* (2020). Briefly, cow HR was recorded for six consecutive days (Day 1–6 of the measurement period) every 5 s, using Polar devices (Polar Electro Oy, Kempele, Finland), with a model H10 HR transmitter and an RCX3 datalogger watch, mounted on the animal with an elastic belt fitted around the thorax and behind the forelegs. On Days −1 and 7, cow O_2P was measured through the simultaneous measurement of HR and oxygen consumption for 12 min, by means of a facemask open-circuit respiratory system (Fedak *et al.* 1981). During the days of O_2P measurement, N_2 recovery was determined three times (before, at midpoint and after O_2P determinations) and averaged 0.98 ± 0.02.

In order to estimate organic matter digestibility (OMD) as per Comerón and Peyraud (1993), faecal samples were collected immediately after defecation for each cow while they were observed in the grazing paddock (two samples per cow; one morning and one afternoon) on Days 4, 5 and 6 of the measurement period and frozen at −20°C until analysis. Subsequently, samples were defrosted and dried at 60°C in an air-forced oven to constant weight and then ground using a 2-mm sieve. Ground faecal samples were pooled per cow by mixing equal amounts from each subsample to be analysed for faecal N and acid detergent fibre (ADFom) (AOAC 2000).

Ingestive (grazing, ruminating) and postural (lying, standing) behaviours were registered for five consecutive days (Days 2–6 of the experimental period) by visual observation through scan sampling every 10 min from when cows entered a new paddock until sunset (for 9.5 h). Thus, 57 behavioural recordings were performed per day for each cow. The animal was considered grazing when the head was in the pasture or when it was chewing grass, ruminating when it was chewing regurgitated boluses of feed, lying down when it was in sternal or lateral decubitus positions, and standing when it was supported with the four legs on the ground. Time spent per activity (min) was calculated assuming that the activity recorded was maintained during the time until the next observation. Lengths of the first morning and afternoon grazing session were calculated assuming the end of the session when the cow did not graze for two consecutively observations. At Days 3 and 5, during grazing activity, bite rate was determined in 10-min intervals by counting the number of bites during 1 min (Chilibroste *et al.* 2012). In addition, nine cows (five NZH and four NAH) were mounted with an activity collar (Moonitor; Tel Aviv, Israel) to record animal activity (eating or resting) every 5 min, 24 h per day from Day 1 to Day 6.

Samples of pasture of the pre-grazed paddock were collected daily above 5 cm from ground level. Samples were dried for 3 days at 60°C by an air-forced oven, ground using a 1-mm sieve and subsequently combined in a unique representative sample of the pasture used during the measurement period. The composite sample was analysed for 105°C DM, crude protein, ether extract, ash, neutral detergent fibre, ADFom, acid detergent lignin, neutral detergent insoluble crude protein, acid detergent insoluble crude protein and gross energy (AOAC 2000).

Calculations and statical analyses

Estimation of HP was based on HR and O_2P (Eqn 1); retained energy in milk (REmilk) was calculated based on the individual records of daily milk yield and composition (Eqn 2); and because retained energy in tissue was assumed negligible, MEI was estimated as the sum of REmilk plus HP:

$$\begin{aligned}\mathrm{HP}\ (\mathrm{kJ/kg\ BW^{0.75}.day}) &= \mathrm{HR}\ (\mathrm{beats/min})\\ &\quad \times \mathrm{O_2P}\ (\mathrm{mL\ O_2/kg\ BW^{0.75}.beat})\\ &\quad \times 20.47\ (\mathrm{J/mL\ O_2})/1000\ (\mathrm{J/kJ}) \times 60\ (\mathrm{min/h})\\ &\quad \times 24\ (\mathrm{h/day})\end{aligned} \tag{1}$$

$$\begin{aligned}\mathrm{REmilk}\ (\mathrm{MJ/day}) &= 38.8 \times \mathrm{kg\ fat/day} + 22.8\\ &\quad \times \mathrm{kg\ crude\ protein/day} + 16.5 \times \mathrm{kg\ lactose/day}\end{aligned} \tag{2}$$

Residual HP was calculated as the difference between measured and predicted HP, which was calculated using the coefficients 540 kJ ME/kg $BW^{0.75}$.day for maintenance energy requirement and 0.64 for the efficiency of use of ME for lactation (*kl*). Therefore, residual HP was calculated according to the following equation (Eqn 3):

$$\begin{aligned}\mathrm{Residual\ HP}\ (\mathrm{kJ/kg\ BW^{0.75}.day}) &= \mathrm{MEI}\ (\mathrm{kJ/kg\ BW^{0.75}.day})\\ &\quad - (540\ \mathrm{kJ/BW^{0.75}} + \mathrm{REmilk}\ (\mathrm{kJ/kg\ BW^{0.75}.day})/0.64)\end{aligned} \tag{3}$$

Pasture OMD was estimated based on faecal N and ADFom (Eqn 4) (Comerón and Peyraud 1993); and pasture digestible energy (DE) was calculated based on pasture OMD and assuming that the ash fraction does not contain energy (Eqn 5):

$$\begin{aligned}\mathrm{OMD}\ (\mathrm{kg\ digestible\ OM/kg\ total\ OM}) &= 0.791 + 0.0334\\ &\quad \times \mathrm{faecal\ N}\ (\mathrm{\%OM}) - 0.0038 \times \mathrm{faecal\ ADFom}\ (\mathrm{\%OM})\end{aligned} \tag{4}$$

$$\begin{aligned}\mathrm{DE}\ (\mathrm{MJ/kg\ DM}) &= \mathrm{gross\ energy}\ (\mathrm{MJ/kg\ DM})/\\ &\quad ((100 - \mathrm{ash}\ (\mathrm{\%DM}))/100)\\ &\quad \times \mathrm{OMD}\ (\mathrm{kg\ digestible\ OM/kg\ total\ OM})\end{aligned} \tag{5}$$

Pasture ME was estimated considering the pasture DE according to the NRC (2001) equation (Eqn 6):

$$\mathrm{ME}\ (\mathrm{MJ/kg\ DM}) = 4.23 \times \mathrm{DE}\ (\mathrm{MJ/kg\ DM}) - 1.88 \tag{6}$$

Pasture DMI was calculated according to Eqn 7:

$$\begin{aligned}\mathrm{DMI}\ (\mathrm{kg\ DM/day}) &= \mathrm{MEI}\ (\mathrm{kJ/kg\ BW^{0.75}.day})\\ &\quad \times \mathrm{BW^{0.75}}/1000(\mathrm{kJ/MJ})/\mathrm{ME}\ (\mathrm{MJ/kg\ DM})\end{aligned} \tag{7}$$

Energy corrected milk (ECM) was calculated according to the equation reported by Kirchgeßner (1997) (Eqn 8):

$$\begin{aligned}\mathrm{ECM}\ (\mathrm{kg/day}) &= \mathrm{milk\ yield}\ (\mathrm{kg/day})\\ &\quad \times ((0.39 \times \mathrm{fat\%} + 0.24 \times \mathrm{protein\%} + 0.17\\ &\quad \times \mathrm{lactose\%})/3.17)\end{aligned} \tag{8}$$

and feed efficiency was calculated according to Eqn 9:

$$\mathrm{Feed\ efficiency} = \mathrm{ECM}\ (\mathrm{kg/day})/\mathrm{DMI}\ (\mathrm{kg/day}) \tag{9}$$

Data were analysed using SAS software (SAS University Edition; SAS Institute, Cary, NC, USA). Univariate analyses were performed on all variables to check the normality of the residuals and identify outlier data. Productive variables were analysed with a mixed model, which included Holstein strain (NZH vs NAH) as fixed effect, block as a random effect, and calving date as a covariate:

$$Y_{ikl} = \mu + S_i + \beta_k + \mathrm{CD} + \varepsilon_{ikl},$$

where Y_{ikl} is the analysed variable, μ is the mean of the experiment, S_i is the Holstein strain effect, β_k is the block effect and CD is calving date.

Animal behaviour variables and HP were analysed with a mixed model with repeated measurements including Holstein strain (NZH vs NAH), time of measurement and their interaction as fixed effects, block and day of measurement as a random effects, and calving date as a covariate:

$$Y_{ijklm} = \mu + S_i + T_j + ST_{ij} + \beta_k + D_l + \mathrm{CD} + \varepsilon_{ijklm},$$

where T_j is the time of measurement in the day and D_l is the day of measurement.

Results

Milk production and composition

Daily milk yield and percentage of lactose did not differ ($P \geq 0.22$) between Holstein strains, whereas both fat and protein percentages were greater ($P < 0.01$) for NZH than NAH cows (Table 2). Nevertheless, ECM yield did not differ ($P = 0.13$) between Holstein strains but milk energy concentration was greater ($P < 0.01$) for NZH than NAH cows (Table 2).

Organic matter digestibility, pasture intake and energy partitioning

The OMD was not different ($P = 0.31$) between Holstein strains, and therefore, nor were DE and ME concentration of the pasture (Table 3). Moreover, pasture DMI expressed as kg/day did not differ ($P = 0.81$) between Holstein strains; however, expressed as kg DM/100 kg BW, it was greater for NZH than NAH cows ($P = 0.04$), and expressed as g DM/kg $BW^{0.75}$, it tended to be greater for NZH than NAH cows ($P = 0.08$; Table 3).

MEI, expressed per unit $BW^{0.75}$, was 10% greater ($P = 0.05$) and REmilk was 25% greater ($P = 0.01$) for NZH than NAH cows. Despite differences in REmilk, there were no differences ($P = 0.39$) in HP between the Holstein strains, which led to a greater ($P = 0.05$) energy efficiency for NZH cows than NAH cows (Table 3). Moreover, residual HP expressed per unit $BW^{0.75}$ did not differ ($P = 0.75$) between strains and averaged 135 ± 36 kJ/kg $BW^{0.75}$.day, being greater than zero in both (Table 3).

On the other hand, none of the variables that refer to energy partitioning were different between the Holstein strains when expressed in MJ/cow day (Table 4).

Table 2. Milk yield, milk composition and energy corrected milk for New Zealand Holstein (NZH) and North American Holstein (NAH) cows during the measurement period.

	NZH	NAH	s.e.m.	*P*-value
Milk yield (kg/day)	17.2	16.7	1.2	0.76
Fat (%)	4.60	3.82	0.18	<0.01
Protein (%)	3.48	3.14	0.11	<0.01
Lactose (%)	4.65	4.53	0.06	0.22
Energy in milk[A] (MJ/kg milk)	3.35	2.97	0.08	<0.01
Energy corrected milk[B] (kg/day)	18.5	15.8	1.3	0.13

[A] According to NRC (2001).
[B] According to Kirchgeßner (1997).
s.e.m., standard error of the mean.

Table 3. Organic matter digestibility, pasture intake, energy partitioning, and energy and feed efficiency for New Zealand Holstein (NZH) and North American Holstein (NAH) cows during the measurement period.

	NZH	NAH	s.e.m.	*P*-value
Organic matter digestibility[A] (%)	72.0	71.2	1.0	0.31
Metabolisable energy of pasture[B] (MJ/kg DM)	9.75	9.62	0.16	0.31
Pasture DM intake expressed as:				
(kg/day)	16.6	16.3	0.8	0.81
(kg/100 kg BW)	3.18	2.86	0.10	0.04
(g/kg $BW^{0.75}$)	152	139	5	0.08
Feed efficiency (ECM/pasture DMI)	1.09	0.96	0.08	0.04
Energy partitioning (kJ/kg $BW^{0.75}$.day)				
Metabolisable energy intake[C]	1489	1347	47	0.05
Heat production[D]	963	922	33	0.39
Retained energy in milk[E]	519	416	37	0.01
Energy efficiency[F]	0.346	0.308	0.02	0.05
Residual heat production[G]	127	143	36	0.75
Heart rate (beats/min)	67.8	66.8	1.5	0.63
O_2P (mL O_2/kg $BW^{0.75}$.beat)	0.480	0.469	0.014	0.59

[A] Comerón and Peyraud (1993).
[B] According to NRC (2001), based on the digestible energy content of the pasture estimated from its gross energy content and organic matter digestibility.
[C] Calculated as heat production + retained energy in milk.
[D] Measured using O_2P technique (Brosh 2007).
[E] Based on NRC (2001).
[F] Calculated as retained energy in milk/metabolisable energy intake.
[G] Difference between measured and predicted heat production without activity requirements (NRC 2001).
DM, dry matter; BW, body weight; DMI, DM intake; ECM, energy corrected milk; O_2P, oxygen pulse; s.e.m., standard error of the mean.

Table 4. Energy partitioning expressed as MJ/day for New Zealand Holstein (NZH) and North American Holstein (NAH) cows during the measurement period.

	NZH	NAH	s.e.m.	*P*-value
Metabolisable energy intake[A]	163.0	157.3	8.0	0.62
Heat production[B]	105.3	107.8	5.4	0.75
Retained energy in milk[C]	57.4	49.2	4.0	0.13
Residual heat production[D]	13.8	17.0	4.1	0.56

[A] Calculated as heat production + retained energy in milk.
[B] Measured using O_2P technique (Brosh 2007).
[C] Based on NRC (2001).
[D] Difference between measured and predicted heat production without activity requirements (NRC 2001).
s.e.m., standard error of the mean.

Otherwise, time of measurement markedly affected ($P < 0.01$) HP, but there was no interaction between Holstein strain and time of measurement (Fig. 1).

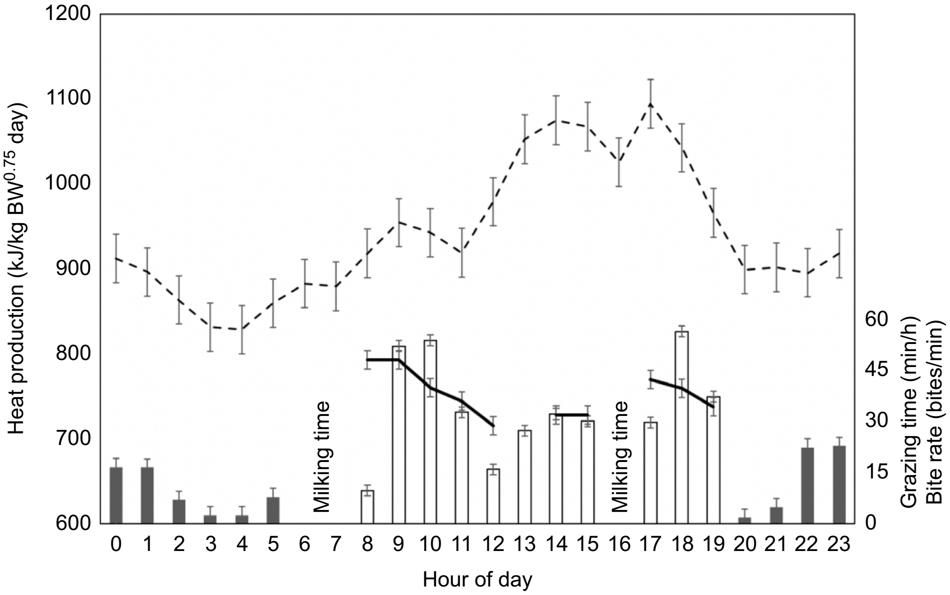

Fig. 1. Heat production, grazing time and bite rate throughout the day. Open bars represent daylight grazing time recorded thought visual observation, and filled bars represent night grazing time recorded by activity collars. Solid lines represent the bite rate and the dashed line represents heat production. There was no interaction between Holstein strain and time of measurement for the analysed variables.

Grazing behaviour

Grazing time during daylight hours did not differ ($P \geq 0.11$) between strains, considering either visual observations (Table 5) or with behaviour recorders (data not shown). During the night, NZH cows grazed for longer (by 23 min; $P = 0.05$) than NAH cows. However, total grazing time did not differ ($P = 0.13$) between strains and averaged 8 h/day (478 ± 25 min/day, mean ± s.e.m.; Table 5).

According to the visual observation method, there were no differences ($P \geq 0.11$) in the proportion of time that cows spent grazing, ruminating, standing or lying down during daylight hours (Table 5). Holstein strains did not differ in the number of grazing sessions during daylight hours ($P = 0.33$) or in the duration of the first grazing session after the morning and afternoon milking ($P \geq 0.44$) or in bite rate ($P = 0.12$) (Table 5). On average, the first morning grazing session was longer than the first afternoon grazing session (140 vs 124 min, $P < 0.01$). In addition, both grazing activity and bite rate were affected by the time of measurement ($P < 0.01$), reaching higher values immediately after cows entered the paddock after milking and decreased once grazing advanced (Fig. 1).

Table 5. Animal activity and grazing behaviour for New Zealand Holstein (NZH) and North American Holstein (NAH) cows during the measurement period.

	NZH	NAH	s.e.m.	*P*-value
Total grazing time (min/day)	494	462	25	0.13
Daylight grazing time^{A} (min/day)	384	373	8	0.13
Night grazing time^{B} (min/day)	115	92	13	0.05
Daylight grazing^{A}				
Grazing session (no. of sessions/day)	4.3	4.6	0.3	0.33
Duration first morning grazing session (min)	139	142	10	0.71
Duration first afternoon grazing session (min)	127	123	5	0.44
Bite rate (bites/min)	38	40	2	0.12
Animal activity (% visual observed time)				
Grazing	68	66	2	0.11
Ruminating	17	18	3	0.32
Standing	82	84	2	0.22
Lying down	18	16	2	0.18

Animal activity and bite rate were affected by the time of measurement but there was no interaction between Holstein strain and time of measurement.
^{A}Measured by visual observation.
^{B}Measured using activity recorder collars (Moonitor).
s.e.m., standard error of the mean.

Discussion

Our results supported that both Holstein strains during mid-lactation (183 ± 37 DIM, mean ± s.d.) managed under a grazing system without supplementation had similar milk yield, but NZH cows had greater milk energy content than NAH cows. Thus, although REmilk expressed as MJ/cow.day did not differ between Holstein strains, REmilk was greater for NZH than NAH cows when it was expressed per unit $BW^{0.75}$. Moreover, MEI per unit $BW^{0.75}$ was greater for NZH than NAH cows, which allowed them to dilute the maintenance energy cost more, which was reflected in greater energy and feed efficiency. Thus, the greater partitioning of consumed energy towards production of milk solids observed for NZH cows would indicate that this Holstein strain is more suitable to be managed on pasture-based dairy systems than the NAH strain.

According to the different selection criteria in each strain (Miglior *et al.* 2005), NZH cows produce milk with a greater fat and protein content, which is usually a key factor to define milk price in countries with a strong exporting profile, such as New Zealand (Marshall 1989). By contrast, despite the greater milk yield potential of NAH than NZH cows (Miglior *et al.* 2005), milk yield was similar between Holstein strains, which indicated, as reported previously (Kolver and Muller 1998), that NAH cows were limited in expressing their high milk production potential when they were managed in a grazing-only dairy system. Indeed, as observed by Kolver and Muller (1998), the MEI from the pasture by NAH cows was not enough to supply their energy requirements. The lower MEI, expressed as kJ/kg $BW^{0.75}$.day, for NAH than NZH cows was explained by differences in pasture DMI because both strains grazed the same pasture and there were no differences in chemical composition or in OMD between Holstein strains.

Although daily pasture DMI did not differ between Holstein strains, when expressed per unit BW or $BW^{0.75}$, NZH cows consumed 11% or 9% more pasture than NAH cows, respectively. However, differences between Holstein strains in pasture DMI per unit BW or $BW^{0.75}$ were not evident from animal behaviour during daylight, with neither grazing time nor bite rate differing between NZH and NAH cows. By contrast, McCarthy *et al.* (2007) reported that daily (24 h) grazing time was longer for NZH than NAH cows, which explained how NZH cows reached similar pasture DMI to NAH cows in this experiment despite the difference in BW between strains. Indeed, in our experiment NZH cows grazed for 23 min more than NAH cows during the night hours (mostly from 22:00 to 01:00 hours), although night grazing time represented only 23% of the total grazing time for NZH cows and 20% for NAH cows. In addition to the low proportion that night grazing represented in total grazing time, there was greater variation in grazing time among animals during the night than during daylights hours. This greater variation could be associated with how grazing time was recorded; activity collars were used during the night, whereas during daylight hours grazing time was recorded through visual observation. Therefore, the longer grazing time during the night for NZH than NAH cows could not fully explain the differences found in pasture DMI per unit BW or $BW^{0.75}$ between Holstein strains.

In the present work, because neither grazing time nor bite rate differed between Holstein strains, it could be expected that bite weight (g/bite) would not differ between NZH and NAH cows. Bite weight is a function of pasture density and bite volume (Gregorini *et al.* 2013); thus, as all cows were grazing the same pasture and therefore similar pasture density, differences in bite volume between strains could be expected. Bite volume is a function of bite depth, which is mainly influenced by sward height and bite area, the latter being dependent on the animal's dental arcade width, which has a strong relationship with $BW^{0.36}$ (Gregorini *et al.* 2013). Hence, dairy cows with lower BW, such as NZH compared with NAH cows, would have a greater bite area in relation to their BW and therefore, a greater relative bite weight (g/bite.kg BW).

In addition, the durations of first morning and afternoon grazing sessions as well as the number of grazing sessions during daylight hours were similar between Holstein strains, which was in agreement with Heublein *et al.* (2017) who did not find differences in number or duration of grazing sessions between NZH and Swiss Holstein–Friesian. In contrast, independent of Holstein strain, the first morning session was 16 min longer than the first afternoon grazing session, which may be related to greater fasting status as a consequence of the lower grazing activity during the night (Chilibroste *et al.* 2007).

The higher MEI per unit $BW^{0.75}$ of NZH than NAH cows allowed the former group to have a greater dilution of the maintenance energy requirements; therefore, they were able to partition a greater proportion of their MEI to milk-solid production (VandeHaar *et al.* 2016), which was clearly reflected in both energy and feed efficiency. Although REmilk per unit $BW^{0.75}$ was 25% greater for NZH than NAH cows, HP per unit $BW^{0.75}$ did not differ between Holstein strains, suggesting that maintenance energy requirement was reduced for NZH cows. On the other hand, the efficiency in the use of ME for milk production (*kl*) could explain part of the difference in HP between Holstein strains. Nevertheless, previous work reported that genotype did not affect *kl* (Ferris *et al.* 1999; Yan *et al.* 2006; Xue *et al.* 2011), which reinforces the hypothesis that differences in HP would be associated with differences in maintenance energy requirements.

Total HP is the sum of the HP associated with maintenance functions (HPm) and the HP associated with production functions (HPp) (Miron *et al.* 2008); thus, it could be expected that NZH cows would have greater HPp associated with the greater REmilk, and therefore less HPm compared with NAH cows. Indeed, we recently reported that ME requirements for maintenance expressed per unit $BW^{0.75}$ were 17% greater for NAH than NZH cows (Talmón *et al.* 2020), which could be associated with increased fasting HP associated with a higher proportion of body protein mass and higher relative mass of the internal organs.

However, residual HP was not different between Holstein strains and averaged 135 kJ/kg $BW^{0.75}$.day, indicating that the measured HP in this experiment was greater than the predicted HP based on NRC (2001) model. The average residual HP represented an increment of 25% with respect to the 540 kJ/kg $BW^{0.75}$.day proposed by NRC (2001) as ME requirement for maintenance. Although it could be considered entirely as an increment of the energy cost as consequence of the grazing activity cost, it is more likely that the residual HP includes part of the maintenance energy costs associated with walking and grazing activity, as well as increased basal metabolism associated with the high proportion of fibre in the diet (Agnew and Yan 2000). On the other hand, it is well known that the NRC (2001) model was not developed with focus on grazing dairy systems, so it would be expected that prediction of performance of grazing dairy cows could be limited because proposed equations for activity energy requirements are based on many assumptions and very limited data. By contrast, the Egraze model developed by CSIRO (2007) which considers the environment in which the animal is managed (distance from pasture to milking parlour, topography, grazing density, green forage availability, pasture digestibility and DMI), could be more suitable to predict the activity energy requirement of a grazing animal in a wide range of grazing conditions. The predicted ME cost of activity for the grazing conditions of this experiment was 63 kJ/kg $BW^{0.75}$.day for NRC (2001), whereas it was 257 kJ/kg $BW^{0.75}$.day for CSIRO (2007), which demonstrates that the latter predicted 4-fold greater ME requirements of activity than those proposed by NRC (2001) and 90% higher than the average residual HP (135 kJ/kg $BW^{0.75}$.day) of both strains. Thus, predicted activity requirements estimated by both feeding systems (NRC and CSIRO) do not explain the activity energy cost calculated based on the residual HP because they under- or overestimate it.

Independent of the Holstein strain, grazing activity and HP varied through the day; grazing activity occurred mainly within daylight hours (~80% of the total grazing time), and the most important grazing bouts, in terms of grazing time and bite rate, were the first ones immediately after milking. This could be associated with a fasting period during the walk from pasture to the milking parlour and during the milking time (Chilibroste *et al.* 2007). In the first half of these grazing sessions, a high proportion of the removable pasture is consumed as consequence of a high instantaneous intake rate (Chilibroste *et al.* 1998), which, in the present study, was reflected not only in grazing time but also in high bite rate at this time. The high pasture intake rates reached by cows in the first grazing sessions after milking require extra muscular activity that is associated with an increment in HP compared with when the cow is not grazing. In addition, in this experiment there was a gradual increment of the HP as the daylight hours progressed, related to the accumulated pasture DMI during the day, which stimulates the heat increment associated with the absorption, digestion and transport of the feed along the gastrointestinal tract as well as with the synthesis of milk production (NRC 1981).

In the present study, grazing conditions determined most of the variables involved in energy partitioning, which were measured indirectly, implying a certain level of error intrinsically associated with the moderate precision, but there was great accuracy of the HP measurement through the HR-O_2P technique (Oss *et al.* 2016). Indeed, those authors reported a correlation and concordance coefficient of 0.70 between the HP of non-grazing 10-month-old bulls measured using the HR-O_2P technique and respiration chamber method, indicating that the reproducibility of the results between those methodologies is moderate. Nevertheless, to our knowledge, this coefficient has not been confirmed in other studies. Despite this, the present work provides valuable information about cow energy performance of two Holstein strains under grazing conditions that cannot be obtained in a respiration chamber, reinforcing the concept that the HR-O_2P technique appears to be a useful methodology for the study of energy metabolism of grazing cattle (Brosh 2007).

Conclusions

Energy and feed efficiency were greater for NZH than NAH cows when they were fed with a pasture-only diet. This greater efficiency was explained by a greater pasture DMI related to BW, which led to a greater MEI expressed as kJ/kg $BW^{0.75}$.day and allowed further dilution of their maintenance energy requirements.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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