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EFICIENCIA Y PARTICIÓN ENERGÉTICA DE DOS LÍNEAS GENÉTICAS HOLANDO BAJO PASTOREO

Daniel Enrique TALMÓN TRAVERS

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Dedico este trabajo a mi familia y amigos

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RESUMEN

El objetivo del trabajo fue evaluar el efecto de dos líneas genéticas Holando (Holando neozelandés *vs.* Holando norteamericano; HNZ *vs.* HNA) sobre la partición de la energía metabolizable consumida (CEM) entre la producción de calor (PC) y la energía retenida (ER) de vacas lecheras en pastoreo. Se realizaron dos experimentos; en el experimento 1, las vacas fueron alimentadas mediante pastoreo y suplementadas con 1/3 de la dieta con concentrado mientras que en el experimento 2 las vacas se alimentaron exclusivamente con pastura mediante pastoreo. La PC se midió utilizando la técnica del pulso de O₂ y la ER en leche se calculó en base a la producción de leche y su composición mientras que la ER en tejido se estimó a través de los cambios en peso vivo (PV) y condición corporal. En el experimento 1, las vacas HNA presentaron mayor PC y PC residual que se asoció con mayores requerimientos de energía metabolizable de mantenimiento (EMm) que las vacas HNZ. Sin embargo, a pesar de las diferencias en PC, la retención de la energía metabolizable consumida (ER/CEM) no fue afectada por la línea genética Holando. Por otro lado, en el experimento 2, las vacas HNZ presentaron un mayor consumo de pastura en relación a su PV que determinó un mayor CEM (kJ/kgPV^{0.75}/d) que en las vacas HNA. El mayor CEM permitió una mayor dilución de los requerimientos de mantenimiento en las vacas HNZ resultando una mayor eficiencia alimenticia y ER/CEM. Los resultados de estos experimentos indicarían que la EMm (kJ/kgPV^{0.75}/d) fue 10% mayor en las vacas HNA que HNZ, lo que probablemente pueda asociarse a un mayor tamaño relativo de órganos internos y/o una mayor proporción de proteína en su composición corporal como consecuencia de su selección genética. Se puede concluir que las vacas HNZ tendrían una mayor partición energética hacia la producción de leche que las vacas HNA cuando son alimentadas exclusivamente bajo pastoreo sin suplementación, mientras que estas diferencias no se expresarían bajo un sistema pastoril con alta suplementación con concentrado que permita levantar, al menos parcialmente, las restricciones en el CEM que impone el pastoreo en las vacas de alta producción (HNA).

Palabras claves: gasto energético, ganado lechero, calorimetría indirecta

ENERGY PARTITIONING AND EFFICIENCY OF TWO HOLSTEIN STRAINS IN GRAZING CONDITIONS

SUMMARY

The aim of this work was to evaluate the effect of two Holstein strains (New Zealand Holstein vs. North American Holstein; NZH vs. NAH) on the partitioning of the metabolizable energy intake (MEI) between heat production (HP) and retained energy (RE) in grazing dairy cows. Two experiments were carried out; in experiment 1, dairy cows grazed pasture and were supplemented with 1/3 of the diet as concentrate while in experiment 2, dairy cows only grazed pasture without supplementation. The HP was measured using the O₂ pulse technique and RE in milk was calculated based on milk production and its composition while RE in tissue was estimated through changes in body weight (BW) and body condition score. In experiment 1, NAH cows had greater HP and residual HP, which were associated with a greater metabolizable energy requirements for maintenance (ME_m), than NZH cows. However, despite the differences in HP, the energy partitioning of the MEI towards milk production and tissue (RE/MEI) did not differ between Holstein strains. On the other hand, in experiment 2, NZH cows had a greater pasture intake related to their BW and therefore, a greater MEI (kJ/kgBW^{0.75}/d) than NAH cows. The greater MEI led to a greater dilution of the maintenance energy requirements for NZH than NAH cows which increased feed efficiency and RE/MEI in the former ones. The results of these experiments would indicate that ME_m (kJ/kgBW^{0.75}/d) was 10% greater for NAH than NZH cows which could probably be associated with a greater relative size of the internal organs and a greater proportion of body protein as consequence of the genetic selection. Moreover, we concluded that NZH cows could have a greater energy partitioning towards milk production than NAH cows when they are managed under a grazing system without supplementation. However, these differences are not expected when they are managed under a grazing system with supplementation of concentrate which allows to partially reduce MEI restrictions imposed by grazing conditions especially challenging for high-producing dairy cows (NAH).

Keywords: energy expenditure, dairy cattle, indirect calorimetry

1. INTRODUCCIÓN

1.1. PLANTEO DEL PROBLEMA

El aumento de la población genera un desafío sin precedentes al momento de asegurar la soberanía alimenticia del mundo. Recientes proyecciones indican que la población mundial continuaría con un crecimiento sostenido alcanzando 9,7 billones de personas para 2050 (United Nations, 2019) que incrementaría notoriamente la demanda por alimentos. En esta línea, el sector ganadero juega un rol crucial aportando a través de alimentos de origen animal el 18 y 34% de la energía y proteína consumida mundialmente, respectivamente (FAO, 2016). Sin embargo, el rápido aumento de la demanda por alimentos sumado también a un incremento en la presión de los consumidores sobre el cuidado y uso responsable de los recursos naturales (UNEP, 2015) exige necesariamente una optimización en la eficiencia de los sistemas de producción.

Los sistemas de producción de leche uruguayos no son ajenos a esta realidad que exige una mejora continua y sustentable de su productividad. Durante los últimos 30 años la producción de leche en Uruguay ha crecido linealmente a una tasa de 3,2% promedio anual (DIEA, 2020) que lo ha posicionado como el 7^{mo} país exportador mundial de leche exportando un 70% de su producción a más de 60 mercados (INALE, 2014). Esta necesidad de comercializar la mayor parte de su producción en el mercado exterior lo expone a variaciones de oferta y demanda mundial que repercuten en una alta volatilidad del precio de la leche que recibe el productor y por lo tanto, el control de los costos de producción se vuelve un factor clave al momento de mantener la competitividad internacional.

Los sistemas de producción de leche nacionales se caracterizan por ser sistemas de producción a cielo abierto con un fuerte componente pastoril en la dieta de sus animales, alcanzando la pastura cosechada directamente por el animal un 55% de la dieta anual y hasta un 75% la suma de pastura y reservas forrajeras que usualmente se producen dentro del propio sistema de producción (Fariña y Chilibroste, 2019). Debido al menor costo de los alimentos fibrosos frente a los alimentos concentrados, es que

esta alta proporción de forraje en la dieta de los animales permite a los sistemas de producción uruguayos mantener un bajo costo por unidad del litro de leche producido frente a otros sistemas con un mayor suministro de alimentos concentrados (Alqaisi et al., 2011).

Sin embargo, ha sido reportado que la producción de vacas lecheras de alta producción manejada bajo condiciones de pastoreo es inferior a la de sus pares alimentadas en condiciones de estabulación consumiendo una dieta totalmente mezclada (DTM; Kolver y Muller, 1998; Bargo et al., 2002). La menor producción alcanzada en estas situaciones se explica por un menor consumo de materia seca (MS) que trae aparejado un menor consumo de energía metabolizable (EM), además de un aumento de los requerimientos energéticos de mantenimiento de los animales asociado con la caminata, búsqueda y cosecha del alimento (Agnew y Yan, 2000), así como también, por costos energéticos extras asociados al contenido de fibra y desbalance de energía: proteína en la dieta (Bruinenberg et al., 2002). Es así como, tanto el menor consumo de EM como los requerimientos energéticos de mantenimiento incrementados, llevan a una menor dilución de los últimos y por consiguiente una caída en la eficiencia alimenticia de estos animales (VandeHaar et al., 2016).

Por otro lado, reportes de la interacción genotipo por ambiente dentro de la raza Holando (Kolver et al., 2002; McCarthy et al., 2007, Macdonald et al., 2008) demuestran la existencia de líneas genéticas dentro la raza que son más adaptadas para ser manejadas bajo condiciones pastoriles. En este sentido, vacas Holando de origen neozelandés (HNZ) presentan una menor respuesta a la suplementación que las vacas Holando de origen norteamericano (HNA) (Horan et al., 2005) indicando que las primeras tienen una mayor capacidad de cubrir sus requerimientos energéticos en base al consumo de pastura y por lo tanto, serían más adecuadas para ser utilizadas en sistemas pastoriles.

En base a lo anterior y proyectando que durante los próximos años nuestros sistemas de producción lecheros van a continuar siendo predominantemente pastoriles, un punto clave para aumentar su productividad y la eficiencia es seleccionar una vaca capaz de satisfacer sus requerimientos energéticos maximizando el consumo de pastura mediante pastoreo (Dillon, 2006). En este contexto, este trabajo pretende

evaluar el efecto de la línea genética Holando sobre la partición energética entre producción y mantenimiento, y desde este punto contribuir a la identificación de una línea genética superior para ser utilizada en los sistemas de producción de leche de Uruguay.

1.2. ANTECEDENTES BIBLIOGRÁFICOS

1.2.1. Partición y utilización de la energía consumida en rumiantes

El término “*Energía*” tiene múltiples definiciones entre las que se puede asociar una de ellas a la capacidad de realizar trabajo. Fisiológicamente hablando, el trabajo es todo proceso realizado por un ser vivo con el objetivo de crear y mantener su organización esencial. Para el caso de los organismos heterótrofos la energía proviene de la digestión de los alimentos consumidos que por medio de los procesos adecuados utilizarán la energía química que éstos proveen para vivir, crecer y reproducirse.

Como se mencionó anteriormente, la energía se almacena en los alimentos mediante compuestos químicos. La cantidad de energía química de un alimento se puede estimar mediante la oxidación completa del mismo en una bomba calorimétrica que permite determinar la producción de calor durante el proceso. La cantidad de calor liberado de la oxidación completa de una unidad de peso de determinado alimento es conocido como su valor de energía bruta (EB) o calor de combustión. Una vez que el alimento es consumido no toda la EB está disponible para su uso por parte del animal, sino que a través de diferentes procesos digestivos-metabólicos parte de esta se pierde bajo forma de las heces, orina, metano y calor como se ilustra en la siguiente imagen (Fig. 1).

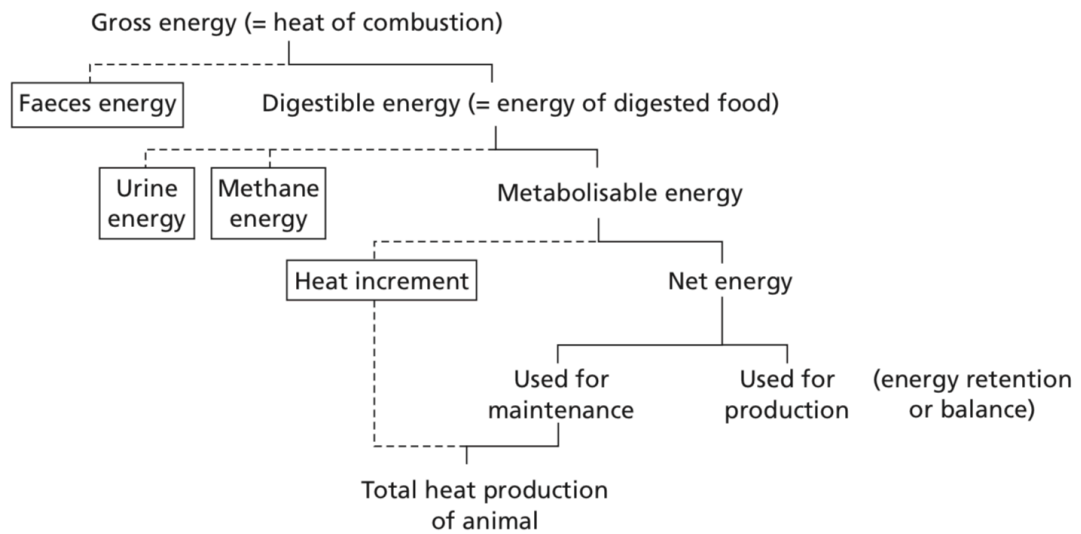


Fig. 1. Partición de la energía consumida en rumiantes. Las pérdidas de energía se muestran dentro de cuadros sobre la izquierda. Fuente: McDonald et al. (2011).

La energía digestible (ED) representa la energía de los alimentos que es potencialmente absorbida por el animal y se calcula como EB consumida menos la EB contenida en las heces. Luego, además de las pérdidas de energía en las heces, también existen pérdidas bajo la forma de compuestos químicos en orina (urea principalmente) o metano producido como consecuencia de la fermentación microbiana en el rumen y el intestino grueso. Al descontar estas pérdidas al contenido de ED se obtiene la energía metabolizable (EM). Las pérdidas de energía en orina van a estar directamente relacionadas con el consumo de proteína cruda del individuo, el balance energía: proteína de la dieta, el balance de aminoácidos y su relación entre ellos, mientras que, para el caso del metano, las pérdidas están asociadas al nivel y tipo de fibra en la dieta y todos los factores que afecten su digestibilidad.

Además de las pérdidas de energía en heces, orina y metano la ingestión de alimento por parte del animal desencadenará también pérdidas bajo la forma de calor. Si a un animal en ayuno se le suministra alimento, luego de unas horas su producción de calor comenzará a incrementarse por encima del nivel representado por el metabolismo basal (calor liberado en un animal en ayuno que representa la mínima energía requerida para mantener su vida). Las causas de este incremento en la producción de calor se deben a los procesos asociados a la digestión de los alimentos

y el metabolismo de los nutrientes derivados de ellos. Finalmente, al sustraer el incremento calórico (IC) de la EM se obtiene la energía neta (EN) que representa la cantidad de energía que está disponible para ser utilizada en funciones de mantenimiento y/o producción por parte del animal.

La EN utilizada para funciones de mantenimiento (EN_m) es usada para realizar trabajo dentro del organismo y dejará el animal como forma de calor mientras que aquella EN utilizada para crecer, engordar o producir leche será almacenada o excretada bajo la forma de energía química y será denominada energía neta de producción (EN_p). Es importante entender que el calor liberado resultado de la EN_m no es parte del IC, sino que fue efectivamente utilizada para un trabajo fisiológico (mantenimiento de la integridad celular y funciones vitales).

A continuación, se muestra la relación entre el consumo de energía metabolizable (CEM) de un animal y su energía retenida (ER; Fig. 2). Cuando el CEM es cero, o sea el animal se encuentra en ayuno, la retención de energía es negativa (① en Fig. 2) por lo que el animal está bajo una situación catabólica de sus reservas corporales con el objetivo de obtener energía para mantenimiento de sus funciones vitales y que es perdida como calor. A medida que el CEM aumenta, el balance energético se vuelve menos negativo hasta alcanzar un balance energético neutro (② en Fig. 2). El CEM que se corresponde con un balance energético neutro (③ en Fig. 2) representa el nivel a partir del cual el animal es capaz de cubrir la totalidad de sus requerimientos de mantenimiento y, por lo tanto, si el CEM es superior a este nivel, parte de esa energía será retenida en tejido corporal y/o leche. Sin embargo, si los requerimientos energéticos de mantenimiento se incrementan por alguna razón como por ejemplo la actividad en animales en pastoreo, los animales necesitarán incrementar su CEM para cubrir sus requerimientos de EM_m para recién luego de este nivel retener energía en tejido y/o leche (④ en Fig. 2).

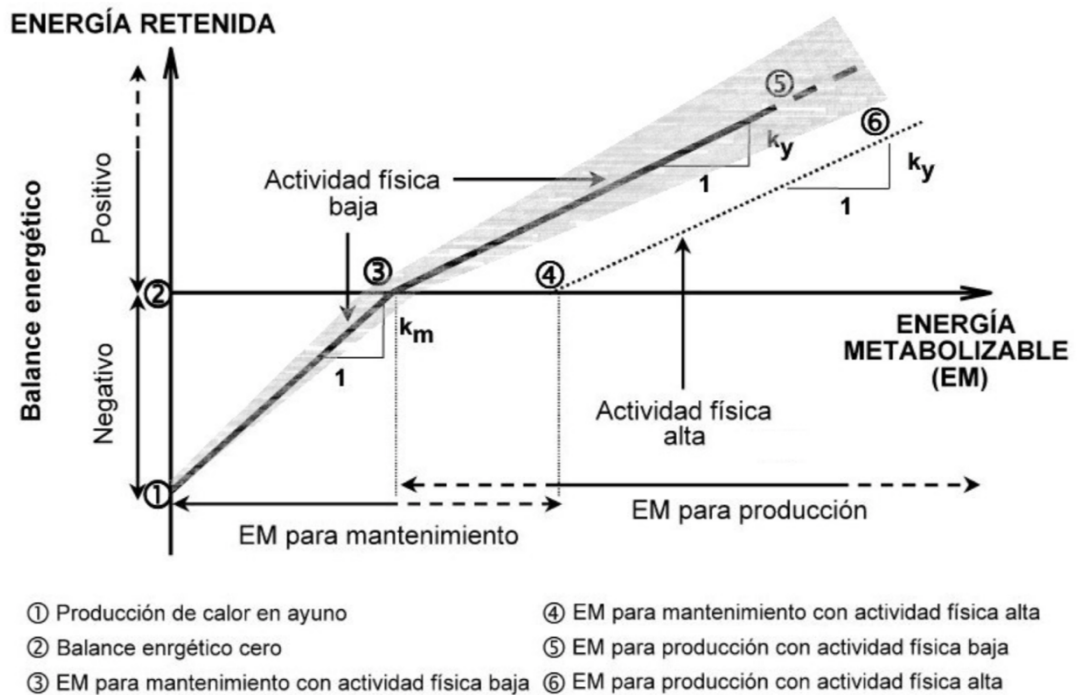


Fig. 2. Eficiencia en la utilización de la energía metabolizable (Adaptado de McDonald et al., 2011).

La pendiente de la relación entre el CEM y la ER corresponde a la eficiencia en la utilización de la EM consumida y su opuesto al IC. Estos valores de eficiencia en el uso de la EM son conocidos como factores k seguido de un subíndice que indica la función fisiológica para la cual se está utilizando la EM. Estas eficiencias se ven afectadas por la metabolibilidad del alimento consumido ($q = EM/EB$) y el proceso fisiológico para el cual es destinada la EM. Para funciones de mantenimiento y producción de leche las eficiencias son similares y elevadas (k_m y $k_l = 0,58 - 0,68$) con respecto a funciones de deposición de tejido o producto de gestación ($k_g = 0,20 - 0,60$ y $k_c = 0,13 - 0,15$; respectivamente) (McDonald et al., 2011)

1.2.2. El costo de mantenimiento y su impacto en la eficiencia energética de vacas lecheras en pastoreo

Los mayores componentes que afectan la eficiencia energética y alimenticia de los animales son aquellos que alteran el mantenimiento y la dilución de los costos de mantenimiento, o, dicho de otra manera, la proporción de la EN que es capturada en leche y/o tejido corporal y que por lo tanto, no es usada para mantenimiento y perdida como calor (VandeHaar et al., 2016). Los costos energéticos de mantenimiento están afectados por tres componentes principales: el costo energético asociado al metabolismo basal (ENmb) de los animales, funciones de termorregulación y actividad (ENact) (CSIRO, 2007).

La ENmb refiere a aquella energía necesaria para mantener funciones vitales, como la circulación y respiración, incluso cuando la vaca no está creciendo o produciendo en una zona termoneutral y sin movimiento. La ENmb fue dividida por Baldwin et al. (1980) en tres grandes clases: actividad de trabajo de órganos vitales (hígado, corazón, riñones, nervios, pulmones) representando el 40 – 50%; síntesis de componentes celulares (síntesis proteica principalmente y membrana lipídica) 10 – 20% y transporte de iones a través de la membrana celular (mantenimiento del potencial de membrana y Na^+ , K^+ -ATPasa) 30 – 40%. Para vacas lecheras, NRC (2001) estima ENmb (Mcal/d) a través de la fórmula $0,08 \times \text{PV}^{0,75}$ (peso metabólico). Sin embargo, evidencia reciente sugiere que la ENmb por unidad de peso metabólico se ha incrementado a lo largo del tiempo como consecuencia indirecta de la selección animal alcanzando valores $0,086 \text{ Mcal/kg PV}^{0,75}/\text{d}$ o incluso superiores (Moraes et al., 2015). Las razones de la mayor ENmb de las vacas actuales podrían ser una mayor proporción de proteína en su estructura corporal (Nour et al., 1983) y un mayor peso relativo de los órganos internos (Agnew y Yan, 2000). De todas formas, McNamara (2015) reportó que la ENmb podría variar cerca de un 20% entre vacas con similar nivel de producción y por lo tanto, sería un aspecto relevante a tener en cuenta al momento de seleccionar animales más eficientes.

La ENmb no solo está condicionada por factores propios del animal, sino que también está afectada por el tipo y composición de la dieta que éste consume. Animales

alimentados con una gran proporción de pastura y/o forrajes en su dieta generalmente presentan una ENmb mayor que otros alimentados con una mayor proporción de alimentos concentrados. En esta línea, Bruinenberg et al. (2002) comprobaron que la performance productiva de las vacas lecheras en pastoreo es usualmente menor a la esperada según la oferta energética. Estos autores estiman que los requerimientos de mantenimiento son 10% superiores a los que se asumen actualmente, debido principalmente al costo asociado al metabolismo y excreción de excesos de nitrógeno. A su vez, resultados de un meta-análisis de datos colectados de 32 cámaras calorimétricas, indicaron que los requerimientos de energía para mantenimiento (Mcal/kg PV^{0,75}) no son constantes, como tienen adoptados diferentes sistemas de alimentación a nivel mundial, sino que se encuentran positivamente relacionados con el consumo de EM/kg PV^{0,75} (Dong et al., 2015a) y la relación forraje: concentrado de la dieta (Dong et al., 2015b), pero ninguno de estos factores afectó la eficiencia de uso de la EM para lactación (*kl*).

Por otro lado, la ENact depende del sistema de producción; animales bajo sistemas de producción pastoriles usualmente caminan distancias más largas e ingieren forraje de menor contenido de MS que lleva a destinar más tiempo consumiendo para alcanzar similar consumo de MS que animales bajo confinamiento (Osuji, 1974). Este mayor trabajo muscular asociado a la caminata desde la pastura a la sala de ordeño, búsqueda, selección y cosecha del alimento genera un incremento significativo en la producción de calor de estos animales frente a sus pares estabulados consumiendo una DTM. Kaufmann et al. (2011) evaluaron el gasto energético durante 6 horas por día de vacas lecheras Holando en lactancia temprana y reportaron que vacas en pastoreo tuvieron un gasto energético 21% mayor al de las vacas consumiendo la misma pastura, pero en estabulación. Además, estos autores reportaron correlaciones positivas entre el gasto energético y la caminata o el tiempo comiendo, lo cual indica que el mayor requerimiento de energía de vacas en pastoreo podría deberse en parte a la mayor actividad física de estos animales.

Como se mencionó anteriormente a medida que una vaca aumenta el consumo de alimento, la proporción del alimento consumido que es utilizada para mantenimiento disminuye; esta “dilución del mantenimiento” incrementa la eficiencia

(Fig. 3). Durante las últimas décadas, la eficiencia alimenticia en la lechería norteamericana se ha incrementado notoriamente como consecuencia de la selección de animales con mayor potencial de producción acompañado de mejoras en las dietas y estrategias de alimentación que aumentaron la producción individual (Capper y Bauman, 2013) mientras que sistemas pastoriles como el neozelandés, también se incrementó la producción individual pero aplicando una fuerte presión de selección a través de un valor económico negativo para mantener y/o disminuir el peso vivo (PV) de las vacas asociado a un control de los costos energéticos de mantenimiento (Miglior et al., 2005).

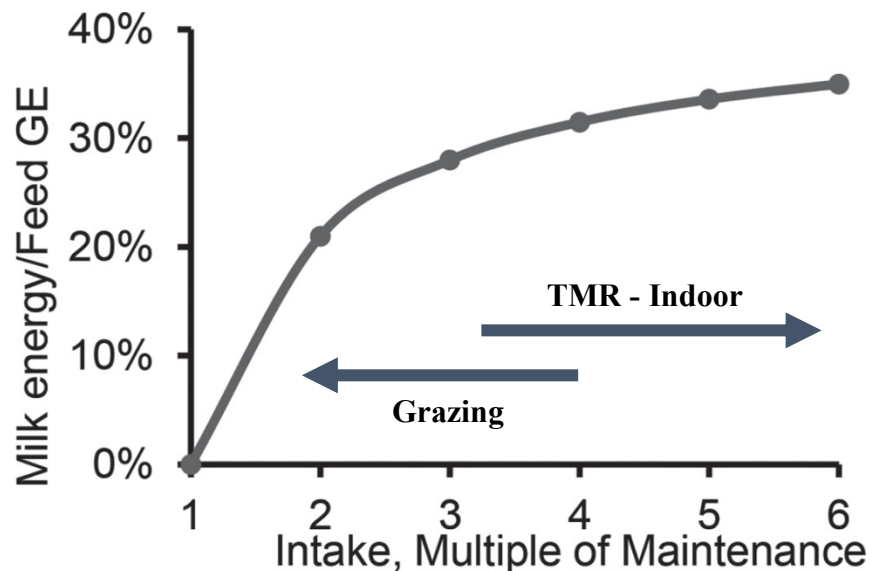


Fig. 3. Eficiencia bruta esperada según nivel de consumo. (Fuente: Adaptado de VandeHaar et al., 2016).

Vacas lecheras en pastoreo consumen menos energía que vacas estabuladas consumiendo una DTM (Kolver y Muller, 1998) y a su vez, incrementan sus costos energéticos de mantenimiento a causa de la actividad y la composición de la dieta. Ambos aspectos atentan contra la dilución de los costos de mantenimiento y por lo tanto la eficiencia energética y alimenticia (Fig. 3). Por lo tanto, la mejora en la eficiencia productiva de los sistemas de base pastoril requiere de vacas lecheras con capacidad de consumir grandes cantidades de pastura en relación a su potencial de

producción de leche y de esta manera poder cubrir la mayor parte de sus requerimientos a través del pastoreo (Dillon, 2006).

1.2.3. Líneas genéticas Holando divergentes

Se ha identificado como uno de los principales problemas de los sistemas pastoriles, la incapacidad de las vacas de alto mérito genético para cubrir sus requerimientos energéticos cuando se las alimenta en mayor o menor medida mediante el pastoreo (Kolver y Muller, 1998; Bargo et al., 2002). A su vez, estudios recientes han demostrado una marcada interacción genotipo \times ambiente (Horan et al., 2005; Dillon et al., 2006; Macdonald et al., 2008), indicando que el tipo de vaca más apropiado será función del sistema en el cual será manejada. Por lo tanto, entender la relación existente entre los diferentes genotipos Holando y el ambiente en el cual se desempeñan se ha vuelto cada vez más importante debido a que las vacas son manejadas en un diverso rango de ambientes a lo largo del mundo (Veerkamp et al., 1994).

En esta línea, se han observado interacciones entre el genotipo y la estrategia de alimentación para la producción de leche (Veerkamp et al., 1994; Fulkerson et al., 2001; Kolver et al., 2002; Kennedy et al., 2003), eficiencia de conversión (Wang et al., 1992), PV y condición corporal (CC) (Berry et al., 2003), y fertilidad (Kolver et al., 2002). La constatación de que estos otros factores pueden afectar la rentabilidad de las explotaciones agrícolas ha conducido a un cambio de dirección hacia objetivos de mejoramiento genéticos más balanceados y sustentables a nivel mundial (Miglior et al., 2017).

La selección genética generalmente se aplica al ganado lechero con el fin de mejorar la rentabilidad, y los índices de selección en los Estados Unidos han tenido un gran peso para la producción de leche (Shook, 2006). Esta selección causó un rápido aumento en la producción individual pero dando como resultado animales que tenían una menor CC durante la lactancia (Hansen, 2000). La menor CC está explicada por partición diferencial de nutrientes durante la lactación temprana, que sustenta un mayor pico de producción de leche (Drackley et al., 2006) y la incapacidad de estas

vacas para direccionar nutrientes a la recuperación de CC (Roche et al., 2006). Esta partición de nutrientes se asocia con una baja performance reproductiva (Chagas et al., 2007; Roche et al., 2007). En esta línea, Veerkamp et al. (1994) discutieron la posibilidad de que las vacas lecheras de alto mérito genético no puedan mantener su ventaja genética bajo un sistema de bajo nivel de insumos ya que el aumento en la eficiencia energética bruta de estas no es debido a una mejor utilización del alimento, sino a un mayor grado de catabolismo del tejido corporal y a una simple dilución del costo de mantenimiento. Por lo tanto, de alcanzar el límite en la tasa de movilización de tejido o en la cantidad de tejido movilizable, determinaría la interacción genotipo \times ambiente.

Por otro lado, la selección en los sistemas pastoriles estacionales incluye rasgos relacionados con la rentabilidad del sistema y la longevidad de la vaca dentro del mismo (Harris y Kolver, 2001). Kolver et al. (2002) compararon la performance productiva de vacas HNZ vs. HNA en un experimento factorial 2×2 donde a cada genotipo se alimentó bajo pastoreo o DTM. Los autores reportaron una mayor producción de leche con un menor contenido de grasa y proteína para las HNA, así como también, un mayor PV y menor CC durante la lactancia en relación a las HNZ. En este trabajo se observó interacción genotipo \times dieta para producción de leche, sólidos, eficiencia de producción y ganancia de PV durante la lactancia, siendo estas variables mayores para HNA en DTM y mayores para HNZ en pastoreo. Sin embargo, en un experimento llevado a cabo en Irlanda, Dillon y Buckley (1998) comparando vacas HNA de alto mérito genético vs. Holando irlandés de medio mérito genético, no encontraron interacción genotipo \times ambiente, indicando que las vacas de mayor mérito genético producen más tanto en sistemas pastoriles como confinados. Para Kolver et al. (2002) las vacas HNA tienen dificultades para consumir suficiente pastura extra para cubrir sus mayores requerimientos de mantenimiento como consecuencia de un mayor PV y por lo tanto, producen similar cantidad de sólidos que las HNZ. Los autores sugieren que las vacas HNZ se encuentran mejor adaptadas a sistemas de alimentación pastoriles. Esto es coincidente con lo reportado por Baudracco et al. (2010) con respecto a que la selección genética centrada en la producción individual ha producido una vaca que ha incrementado su respuesta a la suplementación, reducido

su CC y fertilidad, y es incapaz de cubrir sus requerimientos sin la oferta de suplementos de alta calidad. Consecuentemente, este tipo de vaca tiene una limitada sustentabilidad en los sistemas pastoriles, particularmente aquellos de alta carga y de parición estacional.

Roche et al. (2006) analizaron el efecto del genotipo Holando y el nivel de suplementación sobre la performance productiva, variación de PV y CC usando 113 lactancias de 76 vacas en pastoreo. Los autores no reportaron interacción genotipo \times nivel de suplementación para los parámetros estudiados. Las vacas HNA suplementadas tuvieron un mayor pico y producción de leche corregida a 270 días y la suplementación con concentrado tendió a acelerar la tasa de incremento al pico de producción. La persistencia de la lactancia no se vio afectada por el genotipo ni por el nivel de suplementación. Las vacas HNZ alcanzaron el nadir de CC 14 días antes, ganaron más CC post-nadir y perdieron menos PV postparto que las HNA; además, la tasa de ganancia de CC se incrementó linealmente con la suplementación. A nivel nacional Pereira et al. (2010) reportaron que vacas cruza HNA \times HNZ vs. HNA no presentaron diferencias en producción de leche o sólidos a lactancias corregidas a 305 días, pero si reportaron diferencias a favor de las cruza cuando se expresó la producción en sólidos producidos por unidad de peso metabólico ($PV^{0,75}$).

Escasa es la bibliografía a nivel mundial realizando comparaciones entre los genotipos Holstein enfocadas en el gasto y eficiencia energética. Vacas con alto potencial de producción son incapaces de lograr una buena performance productiva-reproductiva bajo sistemas pastoriles como consecuencia de un balance energético negativo acentuado, por lo tanto, es de gran interés identificar genotipos que sean capaces de cubrir sus requerimientos energéticos en estos sistemas. Thanner et al. (2014) midieron el gasto energético bajo pastoreo en vacas HNZ vs. Holstein suizo en lactancia avanzada y no reportaron diferencias en producción ni gasto energético por kg $PV^{0,75}$. Coincidiendo con este último autor, Xue et al. (2011) no encontraron efecto del genotipo en la eficiencia de uso de la EM para lactación (*kl*) y la partición de la energía entre leche y tejido para vacas primíparas Holando vs. Holando \times Jersey. Además, ambos genotipos presentaron similar EMm (0,69 MJ/kg $PV^{0,75}$). Dong et al. (2015a) tampoco reportaron diferencias en el gasto energético o la eficiencia de

utilización de la energía para vacas Holstein, Norwegian o la cruce de Holstein × Jersey. Por otro lado, Aharoni et al. (2006) reportaron similar PC para vacas Holstein vs. cruce Montbeliarde × Holstein, pero la mayor producción de las HNA determinó una mayor eficiencia bruta y disminuyó un 23% los requerimientos de EM por unidad de energía en leche en relación con las cruces Montbeliarde.

En este sentido, se puede concluir que no está claro el efecto de la línea genética Holando sobre el costo de mantenimiento ni la eficiencia energética de vacas lecheras bajo sistemas pastoriles con o sin suplementación y por lo tanto, generar información con el objetivo de identificar el genotipo que mejor se adapte al pastoreo es necesario para maximizar la eficiencia de producción de estos sistemas.

1.3. HIPÓTESIS Y OBJETIVOS DEL TRABAJO

1.3.1. Hipótesis

Cuando ambas líneas genéticas Holando son alimentadas mediante estrategias que determinen altos consumos de pastura mediante pastoreo, las vacas HNZ presentan una mayor partición energética hacia productos (leche y tejido) como consecuencia de una mayor dilución de los requerimientos energéticos de mantenimiento que las vacas HNA.

1.3.2. Objetivo general

Evaluar y cuantificar los componentes del balance energético, así como también la partición de la energía consumida de vacas lecheras de dos líneas genéticas Holando divergentes (HNZ vs. HNA) manejadas bajo estrategias de alimentación pastoriles.

1.3.3. Objetivos específicos

- Cuantificar la producción de calor (PC) y la energía retenida (ER) en leche y tejido, así como también la eficiencia de uso de la energía consumida de vacas lecheras multíparas Holando de diferente línea genética bajo una dieta de base pastoril con suplementación durante lactancia media y tardía.
- Evaluar la partición de la energía consumida entre la producción de calor (PC) y la energía retenida (ER) en leche de vacas lecheras multíparas Holando de diferente línea genética alimentadas bajo una dieta exclusivamente pastoreo durante lactancia media-tardía.
- Comparar las estimaciones del requerimiento de EMm frente a los valores propuestos por el modelo NRC (2001).

1.4. ESTRUCTURA DE LA TESIS

La estructura central de la tesis consiste en dos artículos científicos. El primero titulado “*Energy partitioning and energy efficiency of two Holstein genotypes under a mixed pasture-based system during mid and late lactation*” constituye el Segundo capítulo de esta tesis. Este artículo se encuentra publicado en *Livestock Science* **239**, 104166 (doi:10.1016/j.livsci.2020.104166) y tuvo como objetivo cuantificar y evaluar la PC, la partición energética entre mantenimiento y producción (leche y tejido) y la eficiencia energética de dos líneas genéticas Holando (HNZ vs. HNA) en un sistema de base pastoril durante lactancia media y tardía (Objetivo específico 1). Los resultados indicaron que las vacas HNA presentaron mayores requerimientos de EMm que las vacas HNZ y en ambas líneas genéticas este valor fue mayor al valor de EMm propuesto por el NRC (2001) mientras que *kl* no fue diferente entre las líneas genéticas evaluadas. A pesar de las diferencias en EMm, la eficiencia energética (ER/CEM) no difirió entre las líneas genéticas durante el experimento. Sin embargo, con el avance de la lactancia las vacas HNZ disminuyeron su CEM asociado a una menor producción de leche en comparación a las vacas HNA; a pesar del menor CEM durante la lactancia

tardía de las vacas HNZ, su eficiencia energética fue similar a las vacas HNA debido a sus menores requerimientos de EMm.

El tercer capítulo de la tesis se compone de un segundo artículo científico que fue enviado a *Animal Production Science* y se titula “***Holstein strain affected energy and feed efficiency in a grazing dairy system***”. El objetivo de este trabajo fue evaluar y cuantificar la partición energética entre mantenimiento y producción de leche de dos líneas genéticas Holando divergentes manejadas bajo un sistema pastoril sin suplementación (Objetivo específico 2). Los resultados demostraron que las vacas HNZ presentaron una mayor eficiencia alimenticia y energética que las vacas HNA bajo pastoreo sin suplementación. La mayor eficiencia en las vacas HNZ estuvo asociada a una mayor dilución de los requerimientos de mantenimiento que las vacas HNA que se explicó por dos factores centrales: mayor CEM (kJ/kg PV^{0,75}/d) en las vacas HNZ como consecuencia de un mayor consumo de pastura relativo a su PV; y menor requerimientos de EMm.

El cuarto capítulo de la tesis se compone de una discusión general y conclusiones globales sobre el problema abordado.

2. ENERGY PARTITIONING AND ENERGY EFFICIENCY OF TWO HOLSTEIN GENOTYPES UNDER A MIXED PASTURE-BASED SYSTEM DURING MID AND LATE LACTATION

Daniel Talmón^{a,*}, Mercedes Garcia-Roche^a, Alejandro Mendoza^b, Diego A
Mattiauda^a, Mariana Carriquiry^a

^a Departamento de Producción Animal y Pasturas, Facultad de Agronomía,
Universidad de la República, 12900 Montevideo, Uruguay

^b Instituto Nacional de Investigación Agropecuaria, Route 50 km 11, 70000 Semillero,
Uruguay

* Corresponding author. E-mail address: danieltalmon94@gmail.com

Highlights:

- Heat production was greater in North American than New Zealand Holstein cows
- Adjusted energy efficiency was not different between Holstein genotypes
- Fasting heat production was greater in North American than New Zealand Holstein
- Grazing activity increased 20% metabolizable energy maintenance requirements
- Residual heat production was greater in North American than New Zealand Holstein



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



Daniel Talmón^{a,*}, Mercedes Garcia-Roche^a, Alejandro Mendoza^b, Diego A Mattiauda^a, Mariana Carriquiry^a

^a Departamento de Producción Animal y Pasturas, Facultad de Agronomía, Universidad de la República, 12900 Montevideo, Uruguay

^b Instituto Nacional de Investigación Agropecuaria, Route 50 km 11, 70000 Semillero, Uruguay

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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_b 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

* Corresponding author.

E-mail address: danieltalmon94@gmail.com (D. Talmón).

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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.

Item	Stage of lactation			
	115 DIM		192 DIM	
	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.

Item	Pasture				SEM	P-value		
	115 DIM		192 DIM			G	SL	G × SL
	NZH	NAH	NZH	NAH				
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, Hillerød, 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) – O₂ pulse (O₂P) 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-O₂P technique is based on the indirect estimation of HP through O₂ consumption measurement and it was calculated assuming 20.47 kJ/L O₂ consumed (Nicol and Young, 1990). Oxygen consumption (VO₂) was calculated as VO₂ = HR × O₂P where O₂P is the amount of O₂ 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 O₂P was estimated as the ratio between O₂ 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 (N₂ recovery) into the facemask (McLean and Tobin, 1990). The N₂ recovery at 115 DIM was 101 ± 2% and at 192 DIM was 103 ± 5%. The O₂P measurements were made once at each measurement period no more than 15 d before or after the 4 d-HR measurement.

During the VO₂ 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 O₂ concentration was measured by a paramagnetic O₂ 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 ($\text{kJ}/\text{BW}^{0.75}/\text{d}$) = HR (beats/min) \times O_2P ($\text{mL } O_2/\text{kg } \text{BW}^{0.75}/\text{beat}$) \times 20.47 ($\text{kJ}/\text{mL } O_2$) \times 60 min/h \times 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 (RE_{milk}) and retained energy in tissue (RE_{tissue}) were estimated by the equations reported by the NRC model for Dairy Cattle (NRC, 2001) using individual cow records. Retained energy in milk (RE_{milk}) 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]:

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

Retained energy in tissue (RE_{tissue}) 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]:

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

where

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

and

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

where

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

and

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

Total retained energy (RE) was calculated by the sum of RE_{milk} + RE_{tissue} and MEI was estimated as total RE + HP. Predicted HP was calculated from BW and total RE using the coefficients of 335 $\text{kJ}/\text{kg } \text{BW}^{0.75}/\text{d}$ 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]:

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

or

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

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 RE_{milk} 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).

Item	Genotype				SEM	P-value		
	115 DIM		192 DIM			G	SL	G × SL
	NZH	NAH	NZH	NAH				
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 ^a	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).

Item	Genotype				SEM	P-value		
	115 DIM		192 DIM			G	SL	G × SL
	NZH	NAH	NZH	NAH				
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 ₂ P (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; O₂P = O₂ Pulse; BW = Body weight

¹ MEI = Total RE + HP.

² Total RE = REmilk + RETissue.

³ According to NRC (2001).

⁴ HP estimated by HR-O₂P 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 NZH 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 ($P = 0.030$) O₂P (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 O₂P ($P = 0.087$) as O₂P tended to be increased ($P = 0.098$) 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_t 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

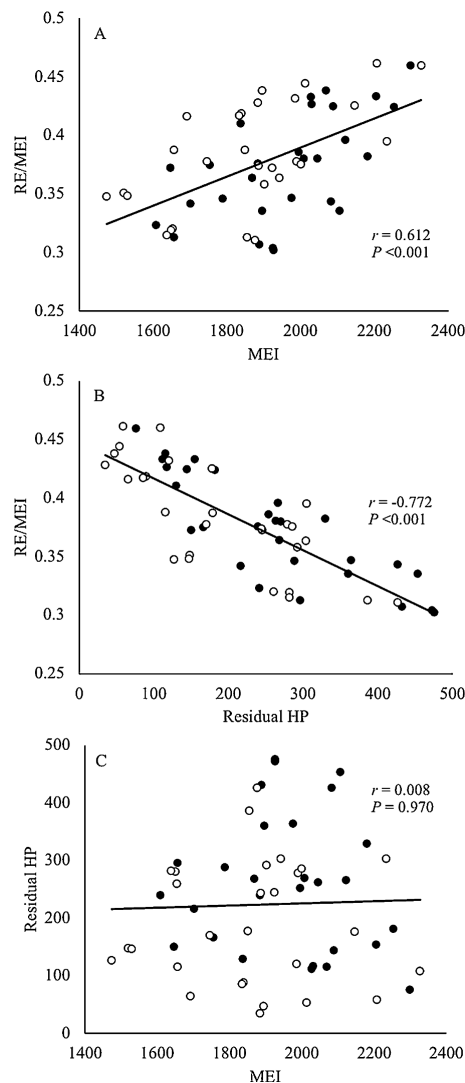


Fig. 1. (A) Relationship between RE/MEI (unitless) and Metabolizable energy intake (MEI; kJ/BW^{0.75}/d); (B) Relationship between RE/MEI and residual heat production (residual HP; kJ/BW^{0.75}/d); (C) Relationship between residual HP and MEI. Black circles (●) represent North American Holstein cows ($n=14$) 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 ¹³C bicarbonate dilution technique used for HP estimation. Estimation of HP

from VO₂ are more accurate than those solely from CO₂ production ([McLean, 1972](#)) as according to [Brouwer equation \(1965\)](#) the latter contributes approximately to 25% of HP whereas VO₂ 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/kgBW^{0.75}/d), neither RE_{milk} nor RE_{tissue} 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 O₂P 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 O₂P in NAH than NZH 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 O₂P averaged 450 μ L O₂/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 O₂P have been reported as consequence of greater energy requirements in lactating vs. non-lactating or grazing vs. confined beef cows ([Brosh, 2007](#)). Thus, the O₂P 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 (HP_m), production heat production (HP_p) 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 HP_p but to increased HP_m. 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

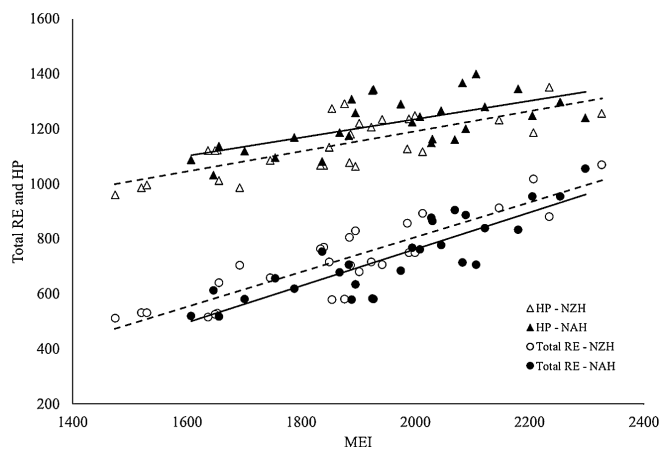


Fig. 2. Relationship between Heat production (HP; kJ/BW^{0.75}/d) and total Retained Energy (Total RE; kJ/BW^{0.75}/d) with Metabolizable Energy Intake (MEI; kJ/BW^{0.75}/d) in New Zealand Holstein (NZH, $n=14$) and North American Holstein (NAH, $n=14$). Solid lines represent the linear regression for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

(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_t values for both genotypes (0.67 vs. 0.63 for NAH and NZH, respectively) were close of k_t values reported by Moe and Tyrrell (1972) ($k_t=0.64$) and used in NRC (2001), Xue et al. (2011) for Holstein dairy cows fed with 30% of concentrate ($k_t=0.60$) and Dong et al. (2015a; 2015b) through a meta-analysis for high-producing Holstein dairy cows ($k_t=0.64$) or dairy cows consuming diets with >60% forage ($k_t=0.63$). Indeed, the negligible difference of 5% between genotypes on k_t was expected because it has been reported that cow genotype or milk yield would have a limited effect on k_t 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_t) varies with diet composition because it is dependent on stoichiometric 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 O₂P 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_t 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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References

- Agnew, R.E., Yan, T., 2000. Impact of recent research on energy feeding systems for dairy cattle. *Livest. Prod. Sci.* 66, 197–215. [https://doi.org/10.1016/S0301-6226\(00\)00161-5](https://doi.org/10.1016/S0301-6226(00)00161-5).
- Aharoni, Y., Brosh, A., Kafchuk, E., 2006. The efficiency of utilization of metabolizable energy for milk production: a comparison of Holstein with F1 Montbelliarde × Holstein cows. *Anim. Sci.* 82, 101–109. <https://doi.org/10.1079/ASC200515>.
- Asher, A., Shabtay, A., Cohen-Zinder, M., Aharoni, Y., Miron, J., Agmon, R., Halachmi, I., Orlov, A., Haim, A., Tedeschi, O., Carstens, G.E., Johnson, K.A., Brosh, A., 2018. Consistency of feed efficiency ranking and mechanism associated with inter-animal variation among growing calves. *J. Anim. Sci.* 96, 990–1009. <https://doi.org/10.1093/jas/skx045>.
- AOAC International, 1990. *Official Methods of Analysis*, 15th ed. AOAC International, Washington, DC, USA.
- Baldwin, R.L., 1995. *Modeling Ruminant Digestion and Metabolism*. Chapman and Hall, London, UK.
- Bargo, F., Muller, L.D., Delahoy, J.E., Cassidy, T.W., 2002. Performance of high producing dairy cows with three different feeding systems combining pasture and total mixed rations. *J. Dairy. Sci.* 85, 2948–2963. [https://doi.org/10.3168/jds.S0022-0302\(02\)74381-6](https://doi.org/10.3168/jds.S0022-0302(02)74381-6).
- Brosh, A., 2007. Heart rate measurements as an index of energy expenditure and energy balance in ruminants: a review. *J. Anim. Sci.* 85, 1213–1227. <https://doi.org/10.2527/jas.2006-298>.
- Brosh, A., Aharoni, Y., Degen, A.A., Wright, D., Young, B.A., 1998. Effects of solar radiation, dietary energy, and time of feeding on thermoregulatory responses and energy balance in cattle in a hot environment. *J. Anim. Sci.* 76, 2671–2677. <https://doi.org/10.2527/1998.76102671x>.
- Brouwer, E., 1965. Report of sub-committee on constants and factors. Symposium of Energy Metabolism. European Association for Animal Production. EAAP Academic, London, pp. 441–443.
- Bruinenberg, M.H., Van Der Honing, Y., Agnew, R.E., Yan, T., Van Vuuren, A.M., Valk, H., 2002. Energy metabolism of dairy cows fed on grass. *Livest. Prod. Sci.* 75, 117–128. [https://doi.org/10.1016/S0301-6226\(01\)00306-2](https://doi.org/10.1016/S0301-6226(01)00306-2).
- Connor, E.E., Hutchison, J.L., Norman, H.D., Olson, K.M., van Tassel, C.P., Leith, J.M., Baldwin, R.L., 2013. Use of residual feed intake in Holstein during early lactation shows potential to improve feed efficiency through genetic selection. *J. Anim. Sci.* 91, 3978–3988. <https://doi.org/10.2527/jas.2012-5977>.
- Dillon, P., Buckley, F., O'Connor, P., Hegarty, D., Rath, M., 2003. A comparison of different dairy cow breeds on a seasonal grass-based system of milk production. 1. Milk production, live weight, body condition score and DM intake. *Livest. Prod. Sci.* 83, 21–33. [https://doi.org/10.1016/S0301-6226\(03\)00041-1](https://doi.org/10.1016/S0301-6226(03)00041-1).
- Dillon, P., 2006. Achieving high dry-matter intake from pasture with grazing dairy cows. In: Elgersma, A., Dijkstra, J., Tamminga, S. (Eds.), *Fresh Herbage for Dairy Cattle, the Key to a Sustainable Food Chain* 18. Springer, Dordrecht, the Netherlands, pp. 1–26.
- Dohme-Meier, F., Kaufmann, L.D., Görs, S., Junghans, P., Metges, C.C., van Dorland, H.A., Bruckmaier, R.M., Münger, A., 2014. Comparison of energy expenditure, eating pattern and physical activity of grazing and zero-grazing dairy cows at different time points during lactation. *Livest. Sci.* 162, 86–96. <https://doi.org/10.1016/j.livsci.2014.01.006>.
- Dong, L.F., Yan, T., Ferris, C.P., McDowell, D.A., 2015a. Comparison of maintenance energy requirement and energetic efficiency between lactating Holstein-Friesian and other groups of dairy cows. *J. Dairy Sci.* 98, 1136–1144. <https://doi.org/10.3168/jds.2014-8629>.
- Dong, L.F., Ferris, C.P., McDowell, D.A., Yan, T., 2015b. Effects of diet forage proportion on maintenance energy requirement and the efficiency of metabolizable energy use for lactation by lactating dairy cows. *J. Dairy Sci.* 98, 8846–8855. <https://doi.org/10.3168/jds.2015-9465>.
- Edmonson, A.J., Lean, L.J., Weaver, L.D., Farver, T., Webster, G., 1989. A body condition scoring chart for Holstein dairy cows. *J. Dairy Sci.* 72, 68–78. [https://doi.org/10.3168/jds.S0022-0302\(89\)79081-0](https://doi.org/10.3168/jds.S0022-0302(89)79081-0).
- Fedak, M.A., Rome, L., Sheeherman, H.J., 1981. One-step N₂ dilution technique for calibrating open-circuit VO₂ measuring systems. *J. Appl. Physiol.* 51, 772–776. <https://doi.org/10.1152/jappl.1981.51.3.772>.
- Horan, B., Dillon, P., Favardin, P., Delaby, L., Buckley, F., Rath, M., 2005. Strain of Holstein-Friesian by pasture-based feed system interaction for milk production, bodyweight and body condition score. *J. Dairy Sci.* 88, 1231–1243. [https://doi.org/10.3168/jds.S0022-0302\(05\)72790-9](https://doi.org/10.3168/jds.S0022-0302(05)72790-9).
- Jasinsky, A., Mattiauda, D.A., Ceriani, M., Casal, A., Carriquiry, M., 2019. Heat production and body composition of primiparous Holstein cows with or without grazing pastures in early lactation. *Livest. Sci.* 225, 1–7. <https://doi.org/10.1016/j.livsci.2019.04.017>.
- Kaufmann, L.D., Münger, A., Rérat, M., Junghans, P., Görs, S., Metges, C.C., Dohme-Meier, F., 2011. Energy expenditure of grazing cows and cows fed grass indoors as determined by the 13C bicarbonate dilution technique using an automatic blood sampling system. *J. Dairy Sci.* 94, 1989–2000. <https://doi.org/10.3168/jds.2010-3658>.
- Kolver, E.S., Muller, L.D., 1998. Performance and nutrient intake of high producing Holstein cows consuming pasture or a total mixed ration. *J. Dairy Sci.* 81, 1403–1411. [https://doi.org/10.3168/jds.S0022-0302\(98\)75704-2](https://doi.org/10.3168/jds.S0022-0302(98)75704-2).
- Lucy, M.C., Verkerk, G.A., Whyte, B.E., Macdonald, K.A., Burton, L., Cursors, R.T., Roche, J.R., Holmes, C.W., 2009. Somatotropic axis components and nutrient partitioning in genetically diverse dairy cows managed under different feed allowances in a pasture system. *J. Dairy Sci.* 92, 526–539. <https://doi.org/10.3168/jds.2008-1421>.
- Macdonald, K.A., Verkerk, G.A., Thorrold, B.S., Pryce, J.E., Penno, J.E., McNaughton, L.R., Burton, L.J., Lancaster, J.A.S., Williamson, J.H., Holmes, C.W., 2008. A comparison of three strains of Holstein-Friesian grazed on pasture and managed under different feed allowances. *J. Dairy Sci.* 91, 1693–1707. <https://doi.org/10.3168/jds.2007-0441>.
- McCarthy, S., Horan, B., Rath, M., Linnane, M., O'Connor, P., Dillon, D., 2007. The influence of strain of Holstein-Friesian dairy cow and pasture-based feeding system on grazing behavior, intake and milk production. *Grass Forage Sci.* 62, 13–26. <https://doi.org/10.1111/j.1365-2494.2007.00557.x>.
- McLean, J.A., 1972. On the calculation of heat production from open-circuit calorimetric measurements. *Brit. J. Nutr.* 27, 597–600. <https://doi.org/10.1079/BJN19720130>.
- McLean, J.A., Tobin, G., 1990. *Animal and Human Calorimetry*. Cambridge University Press, Cambridge, UK.
- Mertens, D.R., 1987. Predicting intake and digestibility using mathematical models of ruminal function. *J. Anim. Sci.* 64, 1548–1558. <https://doi.org/10.2527/jas1987.6451548x>.
- Miron, J., Adin, G., Solomon, R., Nikbachat, M., Zenou, A., Shamay, A., Brosh, A., Mabeesh, S.Y., 2008. Heat production and retained energy in lactating cows held under hot summer conditions with evaporative cooling and fed two rations differing in roughage content and in vitro digestibility. *Animal* 2, 843–848. <https://doi.org/10.1017/S1751731108001900>.
- Moe, P.W., Tyrrell, H.F., 1972. The net energy value of feeds for lactation. *J. Dairy Sci.* 55, 945–958. [https://doi.org/10.3168/jds.S0022-0302\(72\)85601-7](https://doi.org/10.3168/jds.S0022-0302(72)85601-7).
- Moraes, L.E., Kebreab, E., Strathe, A.B., Dijkstra, J., France, J., Casper, D.P., Fadel, J.G., 2015. Multivariate and univariate analysis of energy balance data from lactating dairy cows. *J. Dairy Sci.* 98, 4012–4029. <https://doi.org/10.3168/jds.2014-8995>.
- NRC (National Research Council), 2001. *Nutrient Requirements of Dairy Cattle*, 7th revised ed. National Academy Press, Washington, DC, USA.
- Nicol, A.M., Young, B.A., 1990. Short-term thermal and metabolic responses of sheep to ruminal cooling: Effects of level of cooling and physiological state. *Can. J. Anim. Sci.* 70, 833–843. <https://doi.org/10.4141/cjas90-102>.
- Oldham, J.D., Emmans, G.C., 1990. Animal performance as the criterion for feed evaluation. In: Wiseman, J., Cole, D.J.A. (Eds.), *Feedstuff Evaluation*. Butterworths, London, pp. 73–90.
- Oss, D.B., Marcondes, M.I., Machado, F.S., Tomich, T.R., Chizzotti, M.L., Campos, M.M., Pereira, L.G.R., 2016. Technical note: assessment of the oxygen pulse and heart rate method using respiration chambers and comparative slaughter for measuring heat production of cattle. *J. Dairy Sci.* 99, 8885–8890. <https://doi.org/10.3168/jds.2016-11157>.
- Phillips, C.J.C., Rind, M.I., 2002. The effect of social dominance on the production and behavior of grazing dairy cows offered forage supplements. *J. Dairy Sci.* 85, 51–59. [https://doi.org/10.3168/jds.S0022-0302\(02\)74052-6](https://doi.org/10.3168/jds.S0022-0302(02)74052-6).
- Potts, S.B., Boerman, J.P., Lock, A.L., Allen, M.S., VandeHaar, J.M., 2015. Residual feed intake is repeatable for lactating Holstein dairy cows fed high and low starch diets. *J. Dairy Sci.* 98, 4735–4747. <https://doi.org/10.3168/jds.2014-9019>.
- Roche, J.R., Berry, D.P., Kolver, E.S., 2006. Holstein-Friesian strain and feed effects on milk production, body weight, and body condition score profiles in grazing dairy cows. *J. Dairy Sci.* 89, 3532–3543. [https://doi.org/10.3168/jds.S0022-0302\(06\)00161-5](https://doi.org/10.3168/jds.S0022-0302(06)00161-5).

- 72393-1.
- Tempelman, R.J., Spurlock, D.M., Coffey, M., Veerkamp, R.F., Armentano, L.E., Weigel, K.A., de Haas, Y., Staples, C.R., Connor, E.E., Lu, Y., VandeHaar, M.J., 2015. Heterogeneity in genetic and nongenetic variation and energy sink relationships for residual feed intake across research stations and countries. *J. Dairy Sci.* 98, 2013–2026. <https://doi.org/10.3168/jds.2014.8510>.
- Thanner, S., Dohme-Meier, F., Görs, S., Metges, C.C., Bruckmaier, R.M., Schori, F., 2014. The energy expenditure of 2 Holstein cow strains in an organic grazing system. *J. Dairy Sci.* 97, 2789–2799. <https://doi.org/10.3168/jds.2013-7394>.
- Valtorta, S., Gallardo, M., 1996. El estrés por calor en producción lechera. 'Miscelánea 81'. Instituto Nacional de Tecnología Agropecuaria, Argentina.
- VandeHaar, M.J., Armentano, L.E., Weigel, K., Spurlock, D.M., Tempelman, R.J., Veerkamp, R., 2016. Harnessing the genetics of the modern dairy cow to continue improvements in feed efficiency. *J. Dairy Sci.* 99, 4941–4954. <https://doi.org/10.3168/jds.2015-10352>.
- Waller, A., Martínez, R., Fariña, S. 2017. Comparación de dos métodos de estimación de biomasa de pasturas en Uruguay. Resultados preliminares. In: Congreso de la Asociación Argentina de Producción Animal – RAPA. Vol. Xy. Supl. 1.
- Xue, B., Yan, T., Ferris, C.F., Mayne, C.S., 2011. Milk production and energy efficiency of Holstein and Jersey-Holstein cross-bred dairy cows offered diets containing grass silage. *J. Dairy Sci.* 94, 1455–1464. <https://doi.org/10.3168/jds.2010-3663>.

3. HOLSTEIN STRAIN AFFECTED ENERGY AND FEED EFFICIENCY IN A GRAZING DAIRY SYSTEM

Daniel Talmón^{A,*}, Alejandro Mendoza^B, Mariana Carriquiry^A

^A Departamento de Producción Animal y Pasturas, Facultad de Agronomía, Universidad de la República, 12900 Montevideo, Uruguay.

^B Instituto Nacional de Investigación Agropecuaria, Programa Nacional de Producción de Leche, Estación Experimental “INIA La Estanzuela”, Ruta 50 km 11, 39173 Colonia, Uruguay.

* Corresponding author. Email: danieltalmon94@gmail.com

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The interest in grazing dairy systems has increased during recent years associated with benefits related with their production cost, product quality and animal welfare. However, not all dairy cows are equally suitable to be managed under grazing systems, and for the Holstein breed, energy efficiency, a key factor in the sustainability of the grazing systems, was greater for New Zealand Holstein than North American Holstein cows.

3.1. ABSTRACT

Context. Improving the partitioning of the energy consumed towards milk solid production is a priority in grazing dairy systems as energy efficiency has been associated to their sustainability. Different selection criteria in the Holstein breed have led to divergent Holstein strains (New Zealand Holstein; NZH and North American Holstein; NAH) 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 in a grazing system without supplementation.

Methods. Nine NZH and nine NAH in late mid-lactation (183 ± 37 days in milk) allocated in a randomized block design were evaluated in grazing conditions. Cows were managed under a daily strip grazing system and grazed perennial ryegrass without supplementation. After an adaptation period (14 days), during a measurement period of seven days, heat production, retained energy in milk and metabolizable energy intake were measured and simultaneously, animal behavior was recorded.

Key results. Milk yield did not differ between Holstein strains, but fat and protein content were greater for NZH than NAH cows and therefore, retained energy in milk was 13% greater for the former ones. Heat production did not differ between Holstein strains but metabolizable energy intake ($\text{kJ}/\text{body weight}^{0.75} \cdot \text{d}$) was greater for NZH than NAH cows which was associated with a greater pasture dry matter intake relative to their body weight. Both, feed and energy efficiency were greater for NZH than NAH cows.

Conclusions. Results supported that NZH strain have a greater energy and feed efficiency which would indicate that it could be a more suitable strain to be managed under a grazing dairy system without supplementation than the NAH strain.

Implications. Selection of a dairy cow with the capacity of fulfilling their energy requirements from pasture is a key factor to improve production efficiency of grazing dairy systems.

Additional keywords: Holstein-Friesian, indirect calorimetry, pasture-based system, energy expenditure.

3.2. 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 as well as their potential for accessing high-value markets due to perceived animal welfare benefits (Roche et al., 2017) and healthier characteristics in the product for the consumers (Croissant et al., 2007). However, despite these advantages, grazing systems account for approximately 10% of the world's milk production (Steinfeld and Mäki-Hokkonen, 1995) and therefore, most of the research, technology developments or animal genetic selection criteria have not been focused on these systems.

Nowadays, it is well-documented the existence of interaction between animal genotype and the production system where they are managed (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 of achieve a high herbage intake to maximize 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 world-wide dairy breeds, 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 in a dairy cow with a low body weight (BW) and maintenance requirements, medium milk yield but with high milk-solid contents. On the other hand, 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, NZH cows had greater dry matter intake (DMI) and efficiency at producing a kilogram of milk-solid per unit of metabolic BW ($BW^{0.75}$), without differences in the total milk-solid yield per cow in the lactation, when compared with NAH cows.

Recently, we reported (Talmón et al., 2020) that when cows were supplemented with one third of their DMI as concentrate, maintenance energy requirement 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 metabolizable energy intake (MEI) during late mid-lactation. This diet could have favored the NAH cow due to its greater response to concentrate supplementation (McCarthy et al., 2007) which would have not allowed us to find differences in energy efficiency between Holstein strains although they were managed in a pasture-based system. In this context, we hypothesized that when both Holstein strains were managed in a grazing system without supplementation, the NZH cows would achieve a greater DM and energy intake per kg of 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 two divergent Holstein strains (NZH vs. NAH) in a grazing system without supplementation.

3.3. MATERIALS AND METHODS

3.3.1. Animals and experimental design

The experiment was carried out during spring 2019 at the Experimental Station of the Instituto Nacional de Investigación Agropecuaria – “La Estanzuela” (INIA; Colonia, Uruguay; latitude: 34° 21' 14" S, longitude: 57° 41' 43" W). All 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 conducted as a randomized block design and lasted 35 days with three successive periods: a transition period of 14 days and an experimental period comprising a 14-d adaptation period and a 7-d measurement period. Eighteen Holstein, nine NAH and nine NZH cows, selected from the experimental station dairy herd were blocked in three groups according to lactation number (3.0 ± 1.6 and 3.2 ± 1.5 for NAH and NZH, respectively; mean \pm s.d.), days in milk (DIM) and milk yield and assigned to three replicates per genetic strain (three cows per replicate). Experimental cows had more than 87.5% of their genes belonging to their corresponding strain and their economic and productive breeding index was on average 106 ± 11 and 122 ± 6 (mean \pm s.d.) for NAH and NZH cows. North American Holstein cows had a 305-days expected progeny difference of $+ 90 \pm 132$ kg for milk yield, $+ 4.7 \pm 7.6$ kg and $+ 0.02 \pm 0.12\%$ for fat yield and content and $+ 4.8 \pm 3.6$ kg and $+ 0.03 \pm 0.07\%$ for protein yield and content, respectively. New Zealand Holstein cows had a 305-days expected progeny difference of $- 77 \pm 180$ kg for milk yield, $+ 4.8 \pm 5.1$ kg and $+ 0.11 \pm 0.08\%$ for fat yield and content and $+ 5.8 \pm 5.8$ kg and $+ 0.12 \pm 0.05\%$ for protein yield and content, respectively (mean \pm s.d.) (Mejoramiento y Control Lechero Uruguayo; <https://www.mu.org.uy>). Cows calved in fall 2019 (5 May 2019 \pm 37 days; mean \pm s.d.) and were managed, as a contemporary group, under a grazing system with individual and variable concentrate supplementation until the beginning of the experiment.

At the start of the transition period, NAH and NZH cows were producing 36.7 ± 8.6 kg and 30.2 ± 9.1 (mean \pm s.d.) of milk/d and were supplemented with 6.0 ± 1.2 and 5.3 ± 1.7 kg DM (mean \pm s.d.) of concentrate/d, respectively. During the transition period cows' supplementation was gradually decreased (by 20% every three days) until the end of the period when cows were fed only with grazing pasture (without supplementation). During the adaptation period cows were offered a similar diet (only grazing pasture) and were managed in the same conditions than during the measurement period. At the end of the adaptation period, NAH cows had on average 571 ± 79 kg of BW, 3.0 ± 0.34 units of body condition score (BCS) using a 1-5 scale (Edmonson et al., 1989) and 179 ± 38 DIM while NZH cows had 526 ± 64 kg of BW, 3.1 ± 0.37 units of BCS and 186 ± 36 DIM (mean \pm s.d.).

3.3.2. Experimental period: daily routine, grazing management and weather conditions

Cows were milked twice a day at 0630 and 1600 h and had access day and night to a pasture paddock (1930 h; from 1730 to 0600 h and from 0845 to 1545 h), with free access to fresh water, which was located 450 m from the milking parlor. The pasture was perennial tetraploid ryegrass of first year (cv. Halo, PGG Wrightson Seeds, Uruguay, **Table 1**) with an herbage mass of 3673 ± 194 kg of DM/ha and a herbage allowance of 31 ± 4 kg of DM/cow.d above of 5 cm of the ground level (mean \pm s.e.m. (standard error of the mean)), which was considered non-restrictive to maximize pasture DM intake (Pérez-Prieto and Delagarde, 2013). The paddock was divided into six sub-paddocks, two sub-paddocks per block (one replicate of strain within block), in which herbage mass was measured every day by cutting five pasture samples of 50×50 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 fertilized with 70 kg of N/ha to reach a good-quality vegetative structure of the pasture during the experiment.

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

Item	Perennial Ryegrass
Dry matter (DM; g/kg)	149
Chemical composition (g/kg of DM)	
Crude protein	130
Neutral detergent insoluble crude protein	42
Acid detergent insoluble crude protein	16
Ether extract	40
Non-fiber carbohydrates ^A	211
Neutral detergent fiber	522
Acid detergent fiber	327
Lignin	39
Ash	139
Gross energy (kJ/kg of DM)	16.0

Daily pasture samples were collected above 5 cm above ground level.

^A Calculated as 1000 – Crude protein – Ether extract – Neutral detergent fiber – Ash.

Weather conditions were registered by an automatic meteorological station (Campbell Scientific, Logan, Utah, USA) placed at 1500 meters from the milking parlor. During the experimental period, the mean temperature was $19.4 \pm 0.7^{\circ}\text{C}$ (25.3 ± 2.0 and $14.8 \pm 1.4^{\circ}\text{C}$ of maximum and minimum temperature; mean \pm s.d.) while the mean relative humidity was $73 \pm 10\%$ (91 ± 8 and $51 \pm 16\%$ of maximum and minimum relative humidity; mean \pm s.d.). The average temperature humidity index (Valtorta and Gallardo, 1996) was 66 ± 1 which did not indicate the presence of heat stress conditions.

3.3.3. Data recording, sample collection and laboratory analysis

Daily milk yield was measured individually using automatic milk meters synchronized to Dairy Plan software (Dairy Plan; GEA Farm Technologies, Düsseldorf, Germany). Samples for milk composition were collected for three days during the measurement period (days 2, 4 and 6) from both milkings and preserved with potassium dichromate 5% (Lactopol[®], Grupo Benzo, Uruguay). Milk fat, protein and lactose were analyzed using a milk analyzer (Combi FOSS FT+, Foss Electric, Hillerød, Denmark). Cow BW was recorded at start and the end of the measurement period using an animal scale model ID3000 (Tru-Test, Auckland, New Zealand) immediately after the am 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 (O₂P) as described by Talmón et al. (2020). Briefly, cow HR was recorded for six consecutively days (from day 1 to 6 of the measurement period) every 5 seconds interval using Polar[®] devices (Polar Electro Oy, Kempele, Finland), with a model H10 HR transmitter and a RCX3 data logger watch model, mounted on the animal using an elastic belt fitted around the thorax and behind the forelegs. On days -1 and 7, cow O₂P was measured through the simultaneously measurement of the HR and the oxygen consumption for 12 min using a facemask open-circuit respiratory system (Fedak et al. 1981). The N₂ recovery was 0.98 ± 0.02 (mean \pm s.d.).

In order to estimate organic matter digestibility (OMD; Comerón and Peyraud, 1993), fecal samples were collected in the grazing paddock (two samples per cow; am and pm) 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 until reached a constant weight and then, were ground using a 2 mm sieve. Ground fecal samples were composited in a unique sample per cow to be analyzed for fecal N and acid detergent fiber (ADFom) (AOAC, 2000).

Ingestive (grazing, ruminating) and postural (lying, standing) behaviors were registered for five consecutive days (from days 2 to 6 of the experimental period) by visual observation through scan sampling every 10 min since cows entered to a new paddock until the sunset (for 0930 h). Thus, a total of 57 behavioral recordings were performed per day and per 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 with the four members supported in the station. Time spent per activity (min) was calculated assuming that the activity recorded was maintained during the time until the next observation. Length of the first am and pm 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 (NZH = 5 and NAH = 4) were mounted with an activity collar (Moonitor®, Tel Aviv, Israel) to record the animal activity (eating or resting) every 5 minutes 24 h a day.

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

3.3.4. Calculations and statical analysis

Heat production was estimated based on HR and O₂P [Eq. 1]; retained energy in milk (RE_{milk}) was calculated based on the individual records of daily milk yield and composition [Eq. 2] while retained energy in tissue was assumed zero as not changes in BCS and BW were detected, and MEI was estimated as the sum of RE_{milk} plus HP.

$$\text{HP (kJ/kg BW}^{0.75}\text{.d)} = \text{HR (beats/min)} \times \text{O}_2\text{P (mL O}_2\text{/kg BW}^{0.75}\text{.beat)} \times 20.47 \text{ (J/mL O}_2\text{)} / 1000 \text{ (J/kJ)} \times 60 \text{ (min/h)} \times 24 \text{ (h/d)} \text{ [Eq.1];}$$

$$\text{REmilk (MJ/d)} = 38.8 \times \text{kg of fat/d} + 22.8 \times \text{kg of crude protein/d} + 16.5 \times \text{kg lactose/d} \text{ [Eq. 2];}$$

Residual HP was calculated as the difference between measured and predicted HP which was calculated using the coefficients of 335 kJ/kg BW^{0.75}.d for maintenance energy requirement and 0.62 and 0.64 for the efficiency in the use of ME for maintenance (*km*) and lactation (*kl*), respectively. Therefore, residual HP was calculated according to the following equation [Eq. 3];

$$\text{Residual HP (kJ/kgBW}^{0.75}\text{.d)} = \text{MEI (kJ/kgBW}^{0.75}\text{.d)} - (335 \text{ kJ/kgBW}^{0.75}\text{.d})/0.62 + \text{REmilk (kJ/kgBW}^{0.75}\text{.d})/0.64 \text{ [Eq. 3];}$$

Pasture OMD was estimated based on fecal N and ADFom [Eq. 4] (Comerón and Peyraud, 1993) and pasture DMI was estimated according to the MEI, pasture gross energy and OMD [Eq. 5] using National Research Council (NRC) equation (2001) [Eq. 6] to estimate metabolizable energy (ME) content from digestible energy (DE).

$$\text{OMD (kg digestible organic matter (OM)/kg total OM)} = 0.791 + 0.0334 \times \text{fecal N (\% OM)} - 0.0038 \times \text{fecal ADFom (\% OM)} \text{ [Eq. 4];}$$

$$\text{Pasture DE (MJ/kg DM)} = \text{Gross energy (MJ/kg DM)} / ((100 - \text{Ash (\% DM)})/100) \times \text{OMD (kg digestible OM/kg total OM)} \text{ [Eq. 5];}$$

$$\text{Pasture ME (MJ/kg DM)} = 4.23 \times \text{DE (MJ/kg DM)} - 1.88 \text{ [Eq. 6];}$$

Pasture DMI (kg DM/d) = MEI (kJ/kg BW^{0.75}.d) × BW^{0.75} / 1000 (kJ/MJ) / pasture ME (MJ/kg DM) [Eq. 8].

Energy corrected milk (ECM) was calculated according to the equation reported by Kirchgeßner (1997) [Eq. 9];

ECM (kg/d) = milk yield (kg/d) × ((0.39 × fat% + 0.24 × protein% + 0.17 × lactose%) / 3.17);

and feed efficiency was calculated according to the following equation [Eq. 10];

Feed efficiency = ECM (kg/d) / Pasture DMI (kg/d) [Eq. 10].

Data were analyzed using the SAS software (SAS[®] University Edition, SAS Institute Inc. Cary, NC, USA). Univariate analyses were performed on all variables to check the normality of the residuals and identify outlier data. Productive variables were analyzed with a mixed model which included the Holstein strain (NZH vs. NAH) as fixed effect, the block as a random effect and days in milk as a covariate.

$$Y_{ijk} = \mu + S_i + \beta_j + DIM + \varepsilon_{ijk}$$

where Y_{ikl} is the analyzed variable, μ is the mean of the experiment, S_i is the Holstein strain effect, β_k is the block effect and DIM represents days in milk.

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

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

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

3.4. RESULTS

3.4.1. Milk production and composition

Daily milk yield and percentage of lactose were not different ($P \geq 0.22$) between Holstein strains while 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).

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.

s.e.m., standard error of the mean

Item	NZH	NAH	s.e.m.	p-value
Milk yield (kg/d)	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 (MJ/kg of milk) ^A	3.35	2.97	0.08	<0.01
Energy corrected milk (kg/d) ^B	18.5	15.8	1.30	0.13

^A According to NRC (2001).

^B According to Kirchgeßner (1997).

3.4.2. Organic matter digestibility, pasture intake and energy partitioning

Organic matter digestibility was not different ($P = 0.31$) between Holstein strains and therefore, neither DE nor ME concentration of the pasture (Table 3). Moreover, pasture DMI expressed as kg/d, did not differ ($P = 0.81$) between Holstein strains but, expressed as kg of DM/100 kg of BW or as g of DM/kg BW^{0.75}, was greater

and tended to be greater for NZH than NAH cows ($P = 0.04$ and $P = 0.08$, respectively; Table 3).

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.

BW, body weight; DMI, dry matter intake; ECM, energy corrected milk; O₂P, oxygen pulse; s.e.m., standard error of the mean

Item	NZH	NAH	s.e.m.	p-value
Organic matter digestibility (%) ^A	72.0	71.2	1.0	0.31
Metabolizable energy of pasture (MJ/kg DM) ^B	9.75	9.62	0.16	0.31
Pasture dry matter intake (kg/d)	16.6	16.3	0.8	0.81
Pasture dry matter intake (kg/100 kg BW)	3.18	2.86	0.10	0.04
Pasture dry matter intake (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/kgBW ^{0.75} .d)				
Metabolizable 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 ₂ P (mL O ₂ /kgBW ^{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 O₂P technique (Brosh, 2007).

^E Based on NRC (2001).

^F Calculated as retained energy in milk/metabolizable energy intake.

^G Difference between measured heat production and predicted heat production (NRC, 2001).

Metabolizable energy intake, expressed per unit of $BW^{0.75}$, was 10% greater ($P = 0.05$) while REmilk was 25% greater ($P = 0.01$) for NZH than NAH cows. Despite differences in REmilk, there were not 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 did not differ ($P = 0.75$) between strains (Table 3).

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

3.4.3. Grazing behavior

Grazing time during daylight hours did not differ ($P \geq 0.11$) between strains neither considering visual observations (Table 4) nor with behavior recorders (data not shown) but during the night NZH cows grazed 23 min more than NAH cows ($P = 0.05$). However, total grazing time did not differ ($P = 0.13$) between strains and averaged 8 h/d (478 ± 25 min/d; mean \pm s.e.m.; Table 4).

According to the visual observation method, there were no differences ($P \geq 0.11$) in the proportion of time that the cows spent grazing, ruminating, standing or lying down during the daylight hours (Table 4). Holstein strains did not differ in the number of grazing sessions during the daylight hours ($P = 0.33$) neither in the duration of the first grazing session after the AM and PM milking ($P \geq 0.44$) nor in bite rate ($P = 0.12$) (Table 4). In average, the first AM grazing session was longer than the first PM grazing session (140 vs. 124 min, respectively; $P < 0.01$). In addition, both grazing activity and bite rate were affected by the time of measurement ($P < 0.01$) reaching the higher values immediately after cows entered to the paddock after milking and progressively decreased once grazing advanced (Fig. 4).

Table 4. Animal activity and grazing behavior for New Zealand Holstein (NZH) and North American Holstein (NAH) cows during the measurement period.

s.e.m., standard error of the mean

Item	NZH	NAH	s.e.m.	p-value
Total grazing time (min/d)	494	462	25	0.13
Daylight grazing time (min/d) ^A	384	373	8	0.13
Night grazing time (min/d) ^B	115	92	13	0.05
Daylight grazing ^A				
Grazing session (sessions/d)	4.3	4.6	0.3	0.33
Duration 1st AM grazing session (min)	139	142	10	0.71
Duration 1st PM 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®)

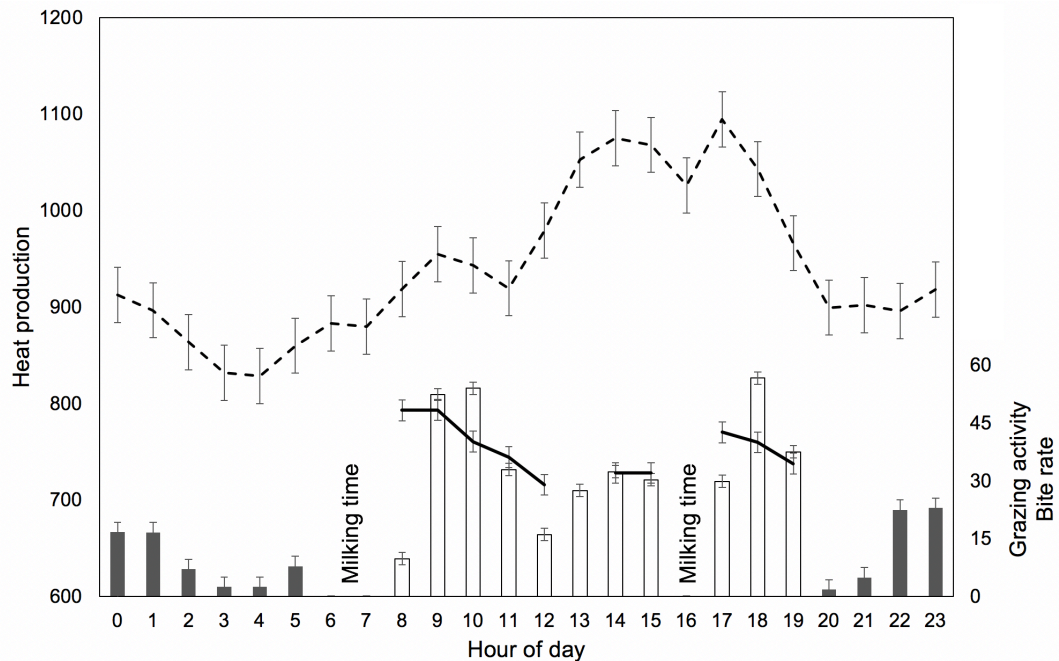


Fig. 4. Heat production and grazing activity along the day. White bars represent daylight grazing activity (min/h) recorded through visual observation and dark bars represent night grazing activity (min/h) recorded by activity collars. Solid lines represent the bite rate (bites/min) and the dashed line represent the heat production (kJ/kgBW^{0.75}.d). There was no interaction between Holstein strain and time of measurement for the analyzed variables.

3.5. DISCUSSION

Our results supported that both Holstein strains during late mid-lactation (183 ± 37 DIM; mean ± s.d.) managed under a grazing system without supplementation had similar milk yield, but NZH cows had a greater milk solid content and therefore, they had also greater REmilk when compared with NAH cows. Moreover, MEI was greater for NZH than NAH cows which allowed them to dilute more the maintenance energy cost which was reflected in a greater energy and feed efficiency. Thus, the greater partitioning of consumed energy towards milk solid production 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), when compared with NAH cows, NZH cows produced milk with a greater fat and protein content which is usually a key factor to define milk price in countries with a strongly exporting profile as New Zealand (Marshall, 1989). In 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 was reported previously (Kolver and Muller, 1998), that NAH cows were limited to express 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 of NAH cows was not enough to supply their energy requirements. The lower MEI, expressed as $\text{kJ/kgBW}^{0.75} \cdot \text{d}$, for NAH than NZH cows was explained by differences in pasture DMI since both strains grazed the same pasture and there were neither differences in chemical composition nor in OMD between Holstein strains.

Although daily pasture DMI did not differ between Holstein strains, when expressed per unit of BW or $\text{BW}^{0.75}$, NZH cows consumed 11 or 9% more pasture than NAH cows, respectively. However, differences between Holstein strains in pasture DMI per unit of BW or $\text{BW}^{0.75}$ were not explained by animal behavior during daylight as neither grazing time nor bite rate differed between NZH and NAH cows. In contrast, McCarthy et al. (2007) reported that daily grazing time (24 h) was longer for NZH than NAH cows which explained how NZH cows reached similar pasture DMI than NAH cows in this experiment despite the difference in BW between strains. Indeed, in our experiment NZH cows grazed 23 min more than NAH cows during the night hours, but night grazing time only represented 23% of the total grazing time for NZH cows and 20% for NAH cows, therefore, it only could partially explain the differences found in pasture DMI per unit of BW or $\text{BW}^{0.75}$.

In the present work, as neither grazing time nor bite rate were different between Holstein strains, it could be expected that bite weight (g/bite) would not differ between NZH than 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 the bite depth which is mainly influenced by the sward

height and the bite area which is dependent of the animal's dental arcade width that have a strong relationship with $BW^{0.36}$ (Gregorini et al., 2013). Hence, dairy cows with less BW, as NZH when 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, duration of first AM and PM 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 report differences in number or duration of the grazing sessions between NZH and Swiss Holstein-Friesian. On the other hand, independently of the Holstein strain, the first AM was 16 min longer than the first PM grazing session which may be related with a greater animal fasting status as consequence of the lower grazing activity during the night (Chilibroste et al., 2007).

The greater MEI of NZH than NAH cows allowed the former ones to have a greater dilution of the maintenance energy requirements than the latter ones and 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 RE_{milk} was 25% greater for NZH than NAH cows, HP did not differ between Holstein strains suggesting maintenance energy requirement was reduced for NZH cows. Total HP is the sum of the HP associated with maintenance functions (HP_m) and the HP associated with production functions (HP_p) (Miron et al., 2008), thus it could be expected that NZH cows would have greater HP_p associated with the greater RE_{milk} and therefore, less HP_m when compared with NAH cows. Indeed, in a recent work (Talmón et al., 2020), we reported that ME requirements for maintenance were 17% greater for NAH than NZH cows which could be associated with increased fasting HP associated to 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 $BW^{0.75}$.d, indicating that the measured HP in this experiment was greater than the predicted HP based on NRC (2001) model. This value represents a 25% increment of the ME requirement for maintenance proposed by NRC (2001) (540 kJ/kg $BW^{0.75}$.d). 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 an increased basal metabolism associated with the high proportion of fiber in the diet (Agnew and Yan, 2000). On the other hand, it is well known that the NRC model (2001) 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 as proposed equations for activity energy requirements are based on many assumptions and very limited data. In contrast, the Egraze model developed by CSIRO (2007), which contemplate the environment in which the animal is managed (distance from pasture to milking parlor, topography, grazing density, green forage availability, pasture digestibility and dry matter intake), 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}.d for NRC (2001) while it was 257 kJ/kg BW^{0.75}.d for CSIRO (2007) which demonstrate that CSIRO (2007) predicted 4-fold greater ME requirements of activity than those proposed by NRC (2001) and 90% greater than the average residual HP (135 kJ/kg BW^{0.75}.d) of both strains. Thus, predicted activity requirements estimated by both systems do not explain the activity energy cost calculated based on the residual HP as they under or overestimate it.

Independently of the Holstein strain, grazing activity and HP varied along the day; grazing activity occurred mainly within daylight hours (approximately 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 walking from pasture to the milking parlor and during the milking time (Chilibroste et al., 2007). During 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 was, in the present study, 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 requires an extra muscular activity that is associated with an increment in HP in comparison when the cow is not grazing. In addition, in this experiment there was a gradual increment of the HP as the daylight hours progressed which is related with the accumulative pasture

DMI during the day that stimulates the heat increment associated with the absorption, digestion and transport of the feed along the gastrointestinal tract (Webster, 1980).

3.6. CONCLUSIONS

Energy and feed efficiency were greater for NZH than NAH cows when they were fed with an only-pasture diet. This greater efficiency was explained by a greater pasture DMI related to their BW which led to a greater MEI expressed as $\text{kJ/kg BW}^{0.75}\cdot\text{d}$ and allowed further dilution of their maintenance energy requirements. Moreover, it was possible to infer that NAH cows had a greater maintenance energy cost because HP was similar but RE_{milk} was lower (less HP_p) for NAH than NZH cows and therefore, the HP_m would be greater for the former ones. Differences between Holstein strains in maintenance energy requirements could not be associated with the grazing activity but probably due to differences in basal metabolism.

3.7. CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

3.8. ACKNOWLEDGEMENTS

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3.9. REFERENCES

- Agnew RE, Yan T (2000) Impact of recent research on energy feeding systems for dairy cattle. *Livestock Production Science* **66**, 197–215. doi:[10.1016/S0301-6226\(00\)00161-5](https://doi.org/10.1016/S0301-6226(00)00161-5)
- AOAC (2000) ‘Official Methods of Analysis (17th edn).’ (The Association of Official Analytical Chemists: Gaithersburg, MD, USA).
- Brosh A (2007) Heart rate measurements as an index of energy expenditure and energy balance in ruminants: a review. *Journal of Animal Science* **85**, 1213–1227. doi:[10.2527/jas.2006-298](https://doi.org/10.2527/jas.2006-298)
- Chilibroste P, Tamminga S, Van Bruchem J, Van der Togt PL (1998) Effect of allowed grazing time, inert rumen bulk and length of starvation before grazing, on the weight, composition and fermentative end-products of the rumen contents of lactating dairy cows. *Grass and Forage Science* **53**, 146–156. doi:[10.1046/j.1365-2494.1998.5320146.x](https://doi.org/10.1046/j.1365-2494.1998.5320146.x)
- Chilibroste P, Soca P, Mattiauda DA, Bentancur O, Robinson PH (2007) Short term fasting as a tool to design effective grazing strategies for lactating dairy cattle: a review. *Australian Journal of Experimental Agriculture* **47**, 1075–1084. doi:[10.1071/ea06130](https://doi.org/10.1071/ea06130)
- Chilibroste P, Mattiauda DA, Bentancur O, Soca P, Meikle A (2012) Effect of herbage allowance on grazing behavior and productive performance of early lactation primiparous Holstein cows. *Animal Feed Science and Technology* **173**, 201–209. doi:[10.1016/j.anifeedsci.2012.02.001](https://doi.org/10.1016/j.anifeedsci.2012.02.001)
- Comerón EA, Peyraud JL (1993) Predicción de la digestibilidad del pasto ingerido por vacas lecheras. *Revista Argentina de Producción Animal* **13**: 23–30.
- Croissant AE, Washburn SP, Dean LL, Drake MA (2007) Chemical properties and consumer perception of fluid milk from conventional and pasture-based production systems. *Journal of Dairy Science* **90**, 4942–4953. doi:[10.3168/jds.2007-0456](https://doi.org/10.3168/jds.2007-0456)

- CSIRO (Commonwealth Scientific and Industrial Research Organisation) (2007) 'Nutrient Requirements of Domesticated Ruminants'. (CSIRO Publishing, Melbourne, AU).
- Dillon P (2006) Achieving high dry-matter intake from pasture with grazing dairy cows. In 'Fresh Herbage for Dairy Cattle, the Key to a Sustainable Food Chain'. (Eds A Elgersma, J Dijkstra, S Tamminga) pp. 1-26. (Springer: Dordrecht, NL)
- Edmonson AJ, Lean IJ, Weaver LD, Farver T, Webster G (1989) A body condition scoring chart for Holstein dairy cows. *Journal of Dairy Science* **72**, 68–78. doi:[10.3168/jds.S0022-0302\(89\)79081-0](https://doi.org/10.3168/jds.S0022-0302(89)79081-0)
- Fedak MA, Rome L, Sheeherman HJ (1981) One-step N₂- dilution technique for calibrating open-circuit VO₂ measuring systems. *Journal of Applied Physiology* **51**, 772–776. doi:[10.1152/jappl.1981.51.3.772](https://doi.org/10.1152/jappl.1981.51.3.772)
- Gregorini P, Beukes PC, Romera AJ, Levy G, Hanigan MD (2013) A model of diurnal grazing patterns and herbage intake of a dairy cow, MINDY: Model description. *Ecological Modelling* **270**, 11-29. doi:[10.1016/j.ecolmodel.2013.09.001](https://doi.org/10.1016/j.ecolmodel.2013.09.001)
- Heublein C, Dohme-Meier F, Südekum KH, Bruckmaier RM, Thanner S, Schori F (2017) Impact of cow strain and concentrate supplementation on grazing behaviour, milk yield and metabolic state of dairy cows in an organic pasture-based feeding system. *Animal* **11**, 1163-1173. doi:[10.1017/S1751731116002639](https://doi.org/10.1017/S1751731116002639)
- Horan B, Dillon P, Faverdin P, Delaby L, Buckley F, Rath M (2005) Strain of Holstein-Friesian by pasture-based feed system interaction for milk production, bodyweight and body condition score. *Journal of Dairy Science* **88**, 1231-1243. doi:[10.3168/jds.S0022-0302\(05\)72790-9](https://doi.org/10.3168/jds.S0022-0302(05)72790-9)
- Kirchgeßner M (1997) Tierernährung, Vol. 10, DLG-Verlag, Frankfurt a. Main, Germany.
- Kolver ES, Muller LD (1998) Performance and nutrient intake of high producing Holstein cows consuming pasture or a total mixed ration. *Journal of Dairy Science* **81**, 1403–1411. doi:[10.3168/jds.S0022-0302\(98\)75704-2](https://doi.org/10.3168/jds.S0022-0302(98)75704-2)

- Kolver ES, Roche JR, de Veth MJ, Thorne PL, Napper AR (2002) Total mixed rations versus pasture diets: Evidence for a genotype x diet interaction in dairy cow performance. *Proceedings of the New Zealand Society of Animal Production* **62**, 246-251.
- Macdonald KA, Verkerk GA, Thorrold BS, Pryce JE, Penno JE, McNaughton LR, Burton LJ, Lancaster JAS, Williamson JH, Holmes CW (2008) A comparison of three strains of Holstein-Friesian grazed on pasture and managed under different feed allowances. *Journal of Dairy Science* **91**, 1693–1707.
doi:[10.3168/jds.2007-0441](https://doi.org/10.3168/jds.2007-0441)
- Marshall KR (1989) The origin and history of the A + B – C payment system. In ‘Milk payment and quality’. (Ed GK Barrell) pp. 9-11. (Lincoln College: Canterbury, NZ)
- McCarthy S, Horan B, Rath M, Linnane M, O'Connor P, Dillon D (2007) The influence of strain of Holstein-Friesian dairy cow and pasture-based feeding system on grazing behavior, intake and milk production. *Grass and Forage Science* **62**, 13–26. doi:[10.1111/j.1365-2494.2007.00557.x](https://doi.org/10.1111/j.1365-2494.2007.00557.x)
- Miglior F, Muir BL, Van Doormaal BJ (2005) Selection indices in Holstein cattle of various countries. *Journal of Dairy Science* **88**, 1255-1263.
doi:[10.3168/jds.S0022-0302\(05\)72792-2](https://doi.org/10.3168/jds.S0022-0302(05)72792-2)
- Miron J, Adin G, Solomon R, Nikbachat M, Zenou A, Shamay A, Brosh A, Mabweesh SY (2008) Heat production and retained energy in lactating cows held under hot summer conditions with evaporative cooling and fed two rations differing in roughage content and in vitro digestibility. *Animal* **2**, 843–848. doi:[10.1017/S1751731108001900](https://doi.org/10.1017/S1751731108001900)
- NRC (National Research Council) (2001) ‘Nutrient Requirements of Dairy Cattle (7th revised edn).’ (National Academy Press, Washington, DC, USA).
- Pérez-Prieto LA, Delagarde R (2013) Meta-analysis of the effect of pasture allowance on pasture intake, milk production, and grazing behavior of dairy cows grazing temperate grasslands. *Journal of Dairy Science* **96**, 6671-6689.
doi:[10.3168/jds.2013-6964](https://doi.org/10.3168/jds.2013-6964)

- Roche JR, Berry DP, Bryant AM, Burke CR, Butler ST, Dillon PG, Donaghy DJ, Horan B, Macdonald KA, Macmillan KL (2017) A 100-Year Review: A century of change in temperate grazing dairy systems. *Journal of Dairy Science* **100**, 10189-10233. doi:[10.3168/jds.2017-13182](https://doi.org/10.3168/jds.2017-13182)
- Steinfeld H, Mäki-Hokkonen J (1995) A classification of livestock production systems. *World Animal Review* **84/85**, 83-94.
- Talmón D, Garcia-Roche M, Mendoza A, Mattiauda DA, Carriquiry M (2020) Energy partitioning and energy efficiency of two Holstein genotypes under a mixed pasture-based system during mid and late lactation. *Livestock Science* **239**, 104166. doi:[10.1016/j.livsci.2020.104166](https://doi.org/10.1016/j.livsci.2020.104166)
- Valtorta S, Gallardo M (1996) El estrés por calor en producción lechera. 'Miscelánea 81'. Instituto Nacional de Tecnología Agropecuaria, Argentina.
- VandeHaar MJ, Armentano LE, Weigel K, Spurlock DM, Tempelman RJ, Veerkamp R (2016) Harnessing the genetics of the modern dairy cow to continue improvements in feed efficiency. *Journal of Dairy Science* **99**, 4941–4954. doi:[10.3168/jds.2015-10352](https://doi.org/10.3168/jds.2015-10352)
- Veerkamp RF, Simm G, Oldham JD (1994) Effects of interaction between genotype and feeding system on milk production, feed intake, efficiency and body tissue mobilization in dairy cows. *Livestock Production Science* **39**, 229-241. doi:[10.1016/0301-6226\(94\)90202-X](https://doi.org/10.1016/0301-6226(94)90202-X)
- Webster AJF (1980) Energy costs of digestion and metabolism in the gut. In: 'Digestive Physiology and Metabolism in Ruminants'. (Eds Y Ruckebusch, P Thivend). (Springer: Dordrecht, NL). doi:[10.1007/978-94-011-8067-2_22](https://doi.org/10.1007/978-94-011-8067-2_22)

4. DISCUSIÓN Y CONCLUSIONES FINALES

4.1. DISCUSIÓN

Los sistemas de producción de leche uruguayos se caracterizan por ser sistemas de producción pastoriles a cielo abierto; en los cuales la dieta anual se compone un 55% como pastura cosechada directamente por los animales y hasta un 75% como pastura + reservas forrajeras que usualmente son producidas dentro del predio. Esta alta relación de alimentos fibrosos con respecto a los alimentos concentrados es la razón del bajo costo de producción y por lo tanto, el sustento de la competitividad internacional de nuestros sistemas de producción de leche (Fariña y Chilibroste, 2019).

Sin embargo, existen trabajos que reportan que la performance productiva de vacas lecheras que integren el pastoreo como parte de su estrategia de alimentación es menor a la de sus pares consumiendo una DTM en condiciones de estabulación como consecuencia de un menor consumo de energía (Kolver y Muller, 1998; Bargo et al., 2002). Estos trabajos fueron pioneros en identificar la energía como el primer nutriente limitante de la producción en los sistemas pastoriles y por lo tanto, el diseño de estrategias de alimentación que permitan lograr mayores consumos de energía o hacer un uso más eficiente de este nutriente en los animales sigue siendo un aspecto relevante para aumentar la productividad de estos sistemas.

Por otro lado, el efecto de la estrategia de alimentación en la productividad del sistema no es independiente del genotipo lechero que se utilice. De hecho, se ha reportado una superioridad del HNZ frente al HNA en cuanto a consumo de MS (%PV), balance energético, performance reproductiva y eficiencia de producción (kg sólidos/kg PV^{0.75}) cuando ambas líneas genéticas son manejadas bajo pastoreo (Kolver et al., 2002; Horan et al., 2005; Macdonald et al., 2008). A pesar de esto, y teniendo en cuenta que nuestros sistemas son esencialmente pastoriles, solamente un 6,3 % del rodeo lechero nacional está compuesto por HNZ mientras que el HNA representa un 83,6 % (INALE, 2014).

Es así como, se llevó adelante este trabajo con el objetivo de generar evidencia sobre la eficiencia y partición de la energía de cada línea genética Holando en un

sistema de producción representativo de la lechería nacional (sistema mixto; pastoreo + suplementación con concentrado; experimento 1). El sistema de producción mixto es predominante en nuestro país (Fariña y Chilibroste, 2019) y representa un entorno productivo muy diferente a lo que es una estrategia de alimentación exclusivamente pastoril o de baja suplementación con concentrado (<15% dieta) y/o confinamiento con suministro de DTM. De hecho, la gran mayoría de los experimentos donde se evaluó el efecto de la línea genética Holando es bajo uno de estos dos sistemas (Kolver et al., 2002; Macdonald et al., 2008; Thanner et al., 2014) y por lo tanto es necesario conocer que línea genética se desempeña mejor bajo una condición de pastoreo con alta suplementación con concentrado (1/3 de la dieta). Las vacas HNA bajo pastoreo pueden alcanzar respuestas lineales a la suplementación hasta 10 kg MS/d de suplemento consumido (Bargo et al., 2002) dejando en clara evidencia el desacople entre los requerimientos y el consumo de energía que presenta esta línea genética de alta producción bajo condiciones de pastoreo (Baudracco et al., 2010), y posicionando a la suplementación energética como la alternativa de manejo que ayudaría a explotar el potencial genético de las vacas HNA en pastoreo.

Los resultados productivos encontrados en el experimento 1 fueron los esperados en base al criterio de selección que originó cada línea genética. Las vacas HNA produjeron $4,7 \pm 1,9$ kg/d más de leche que las vacas HNZ, pero con menores porcentajes de grasa y proteína. Esta diferencia en el contenido de sólidos fue la razón por la cual ambas líneas genéticas tuvieron similar producción de grasa y proteína. En países netamente exportadores como es el caso de Uruguay, la industria láctea fija el precio del litro de leche en base a un sistema de pago denominado “A + B – C” donde paga por cada kg de grasa y proteína y penaliza por cada litro remitido (Marshall, 1989) con el objetivo que los productores prioricen la producción de sólidos lácteos frente a la producción de leche. Desde este punto de vista, manejando ambas líneas genéticas bajo un sistema mixto, las vacas HNZ generarían un mayor ingreso bruto ya que produjeron la misma cantidad de grasa y proteína, pero en un menor volumen de leche que las vacas HNA a pesar de ser 60 ± 15 kg más livianas.

Por otro lado, los resultados obtenidos en el experimento 1 indicaron que las vacas HNA presentaron un mayor requerimiento energético de mantenimiento,

evidenciado a través de una mayor PC residual y ENmb, que las vacas HNZ. El mayor costo de mantenimiento que presentaron las vacas HNA podría estar explicado por una mayor tasa metabólica como consecuencia de su selección genética focalizada en la producción de leche. Es esperable que vacas de alta producción presenten un mayor costo energético de mantenimiento como consecuencia de un mayor tamaño relativo de sus órganos internos (corazón, hígado, vísceras) y una mayor proporción de proteína en su composición corporal que impacta en un alto turnover proteico (Agnew y Yan, 2000). En este experimento la EMm fue un 17% mayor en las vacas HNA que en las vacas HNZ (853 vs. 729 kJ/kgPV^{0.75}/d) y en promedio fue 46% mayor que el valor de 540 kJ/kg PV^{0.75}/d propuesto por el NRC (2001). Esto indica que el costo energético asociado a la actividad de pastoreo tiene un peso importante en los requerimientos de EMm, así como también deja en evidencia que los requerimientos ENmb propuestos por el NRC (2001) están subestimados frente a los que se proponen actualmente para las vacas modernas (Moraes et al., 2015).

A pesar de las diferencias en la EMm, la proporción de energía consumida que fue retenida en leche y tejido (ER/CEM) no fue diferente entre las líneas genéticas Holando evaluadas, lo cual indica que, desde el punto de la eficiencia energética, tendrían un comportamiento similar cuando son manejadas en un sistema mixto con alta suplementación. La suplementación con concentrado incrementa el CEM permitiendo una mayor dilución de los costos energéticos de mantenimiento que repercute en una mayor eficiencia energética (VandeHaar et al., 2016). Si bien este efecto es independiente de la línea genética es esperable que las vacas HNA aumenten en mayor medida el CEM que las vacas HNZ en base a la mayor respuesta a la suplementación reportada (Horan et al., 2005). Sin embargo, parece evidente que la suplementación con 1/3 de la dieta en base a concentrado no fue suficiente para explotar el potencial genético de las vacas HNA ya que no pudieron superar a las vacas HNZ en lo que respecta a la eficiencia alimenticia (1,41 vs. 1,37 kg de leche corregida por energía/kg de MS consumida para HNZ y HNA, respectivamente).

En el experimento 2 ambas líneas genéticas se manejaron bajo un sistema exclusivamente pastoril sin suplementación. En estas condiciones el CEM de las vacas fue 21% inferior al obtenido en el experimento 1 con suplementación. Esto llevó a que

las vacas HNA logren una menor dilución de sus altos requerimientos de EMm y por lo tanto la ER/CEM fue menor en comparación a las vacas HNZ. Este experimento reafirma lo reportado por Kolver y Muller (1998) sobre las restricciones que impone una dieta exclusivamente pastoril en las vacas de alta producción (HNA) para explotar su potencial genético. A diferencia del experimento 1, en esta situación sin suplementación, la producción de leche (kg/d) no fue diferente entre las líneas genéticas a pesar del mayor PV de las vacas HNA frente a las vacas HNZ. Al no ser suplementadas, las vacas HNZ presentaron un mayor CEM, expresado como $\text{kJ/kgPV}^{0,75}/\text{d}$, que sumado a una menor EMm permitió una mayor retención en leche de la energía consumida (ER/CEM) y repercutió en una eficiencia alimenticia 14% mayor en las vacas HNZ que las vacas HNA. Las diferencias en CEM ($\text{kJ/kgPV}^{0,75}/\text{d}$) observadas entre las líneas genéticas bajo condiciones exclusivamente de pastoreo sin suplemento responden a diferencias en el consumo de MS de pastura (3,18 vs. 2,86 kg MS/100 kg PV para HNZ y HNA, respectivamente), indicando que, bajo estas condiciones, las vacas HNZ tendrían una mayor capacidad de satisfacer sus requerimientos energéticos a través del consumo de pastura que las vacas HNA.

Por otro lado, este trabajo demuestra el potencial que presenta la técnica del pulso de O_2 (Brosh, 2007) para la estimación del gasto energético de animales en pastoreo. Sin embargo, Oss et al. (2016) reportaron que la técnica del pulso de O_2 tiene una gran exactitud que proporciona buenas estimaciones de la PC, pero con una precisión moderada debido al alto coeficiente de variación entre animales que repercute en pérdida de potencia estadística y por lo tanto un mayor número de animales experimentales (n) serían necesarios para identificar diferencias. A pesar de esto, Tedeschi (2006) argumentó que la utilización de un método de estimación exacto es más importante que un método preciso ya que el valor promedio “real” puede detectarse utilizando un método impreciso, pero promediando un gran número de datos. Por lo tanto, se compuso una base de datos mayor en base a los resultados obtenidos en ambos experimentos con el objetivo de aumentar el número de observaciones experimentales y mediante el análisis de la regresión lineal entre el CEM y la PC para estimar la EMm (Brosh, 2007) para cada línea genética Holando.

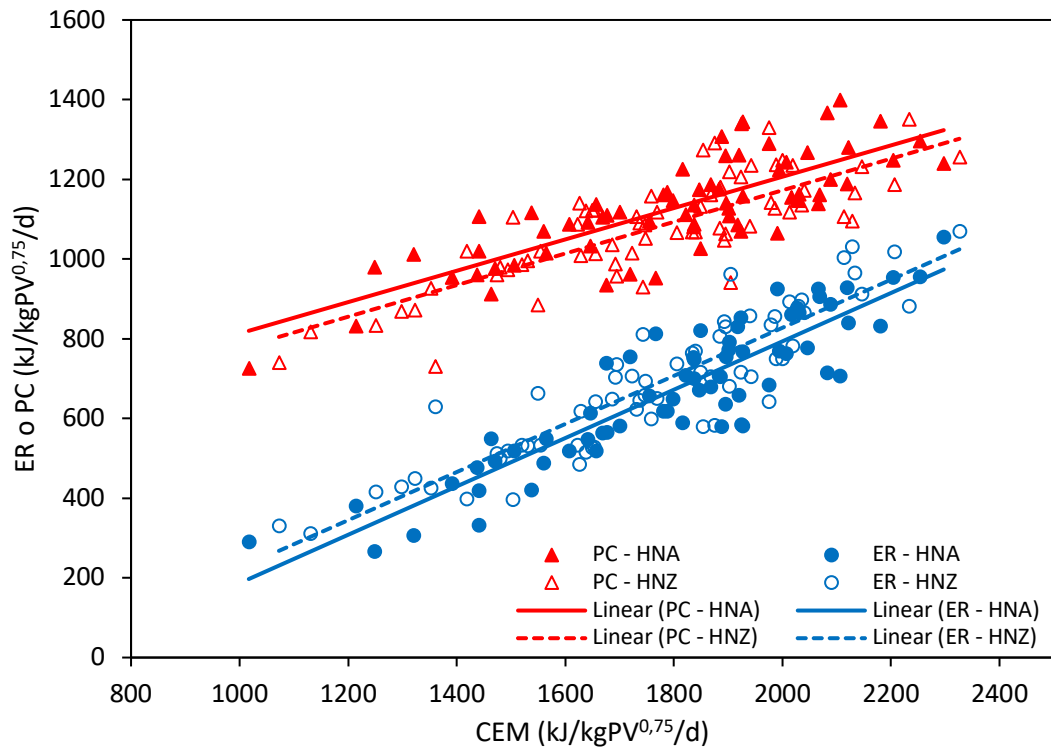


Fig. 5. Relación entre el consumo de energía metabolizable (CEM) y la producción de calor (PC) o la energía retenida (ER). PC-HNA = $420 + 0,393 \text{ CEM}$; PC-HNZ = $379 + 0,396 \text{ CEM}$; ER-HNA = $-420 + 0,607 \text{ CEM}$; ER-HNZ = $-379 + 0,604 \text{ CEM}$.

Utilizando la regresión lineal entre la PC y el CEM se puede estimar indirectamente los requerimientos energéticos de mantenimiento. El intercepto de la regresión entre el CEM y la PC representa el requerimiento de energía neta de mantenimiento (ENm) mientras que la pendiente de la regresión entre la ER y el CEM representa la eficiencia en el uso de la energía metabolizable (kl). El requerimiento de energía metabolizable de mantenimiento (EMm) se puede estimar como ENm / kl .

En base a la Fig. 5. se puede concluir que el kl no fue diferente entre las líneas genéticas Holando y fue en promedio 0,61. Este trabajo está en línea con lo reportado por Gordon et al. (1995) y Ferris et al. (1999) quienes no reportaron diferencias en kl entre vacas Holando de diferente mérito genético indicando que el kl no se afectaría por el genotipo lechero y/o la producción de leche. Además, el valor de 0,61 es muy cercano al 0,62 y 0,64 utilizado por el NRC (2001) para mantenimiento y lactación respectivamente, así como también al 0,63 reportado por Dong et al. (2015b) para

vacas consumiendo > 60 % de forraje en la dieta o 0,60 reportado por Xue et al. (2011) para vacas consumiendo 30% de concentrado.

Comparando los interceptos de las regresiones lineales entre el CEM y la PC (con una pendiente en común) para cada línea genética, se observa una ENmb 11% mayor ($P = 0,010$) para las vacas HNA que las HNZ, lo cual representa 65 kJ/kgPV^{0,75}/d de EMm (692 vs. 627 kJ/kgPV^{0,75}/d para las vacas HNA y HNZ, respectivamente). La mayor EMm de las vacas HNA podría asociarse a la selección genética en base a la producción de leche que ha generado una vaca que necesita más energía por kg de PV^{0,75} para vivir (Moraes et al., 2015) como consecuencia de una mayor proporción de proteína en su composición corporal (Nour et al., 1983) y un mayor tamaño relativo de órganos internos (Agnew y Yan, 2000) que las vacas HNZ. Además, en este trabajo, el comportamiento de las vacas en pastoreo (tiempo de pastoreo y tasa de bocado) no fue diferente entre las líneas genéticas lo que indicaría que las diferencias observadas en el costo energético de mantenimiento no estarían principalmente asociadas a diferencias en la actividad de pastoreo entre las líneas genéticas Holando.

Por otro lado, el valor promedio de EMm de este experimento fue 660 kJ/kgPV^{0,75}/d, siendo muy similar al reportado por Dong et al. (2015b) de 675 kJ/kgPV^{0,75}/d para vacas lecheras consumiendo >60% de su dieta como forraje. Sin embargo, este valor se encuentra 22% por encima del valor reportado por el NRC (2001) de 540 kJ/kgPV^{0,75}/d, lo cual estaría explicado por mayores gastos de energía asociados a la actividad de pastoreo (Dohme-Meier et al., 2014), desbalances de energía:proteína de la pastura (Bruinenberg et al., 2002) y trabajo del tracto gastrointestinal y otros órganos (Dong et al., 2015b).

Este trabajo está en línea con una serie de estudios que demuestran la superioridad de las vacas HNZ frente a las HNA cuando son manejadas en sistemas pastoriles (Kolver et al., 2002; Horan et al., 2005; Macdonald et al., 2008), y además, plantea la suplementación energética con concentrados como una alternativa de manejo que permite mejorar la eficiencia energética de vacas HNA en pastoreo, aunque se sabe que altos niveles de suplementación incrementan los costos de producción y por lo tanto atentan contra la competitividad internacional de nuestros

sistemas lecheros pastoriles (Alqaisi et al., 2011). Finalmente, es importante destacar que este trabajo solo aborda aspectos referidos a la partición y eficiencia energética durante la lactancia media – tardía, sin contemplar los múltiples efectos que tiene el período de transición y la lactancia temprana sobre la salud y la performance reproductiva de las vacas lecheras (Kolver et al., 2002; Lucy et al., 2009; Baudracco et al., 2010; White et al. 2012), por lo tanto, es necesario integrar todos estos aspectos al momento de identificar la línea genética Holando que mejor se adapte a cada sistema de producción.

4.2. CONCLUSIONES FINALES

Las vacas HNA presentaron un mayor requerimiento de mantenimiento que las vacas HNZ probablemente asociados a diferencias en la composición corporal y el peso relativo de sus órganos internos. Además, bajo un sistema mixto con suplementación, ambas líneas genéticas presentaron similar eficiencia energética pero cuando fueron alimentadas exclusivamente mediante pastoreo las vacas HNZ fueron 12% más eficiente energéticamente que las vacas HNA como consecuencia de un mayor consumo de pastura en relación a su PV que permitió una mayor dilución de sus requerimientos energéticos de mantenimiento. Los resultados indican que las vacas HNZ presentan mayor eficiencia alimenticia que las HNA cuando son manejadas en sistemas pastoriles resultando en una reducción de los costos de producción por unidad de sólido lácteo, así como también en una disminución de la huella ambiental.

5. BIBLIOGRAFÍA

- Agnew RE, Yan T. 2000. Impact of recent research on energy feeding systems for dairy cattle. *Livestock Production Science*. 66 (3): 197-215. doi: 10.1016/S0301-6226(00)00161-5.
- Aharoni Y, Brosh A, Kafchuk E. 2006. The efficiency of utilization of metabolizable energy for milk production: a comparison of Holstein with F1 Montbeliarde × Holstein cows. *Animal Science*. 82 (1): 101-109. doi: 10.1079/ASC200515.
- Alqaisi O, Asaah O, Hemme T. 2011. Global view on feed cost and feed efficiency on dairy farms. *All About Feed*. 2: 2-5.
- Baldwin RL, Smith NE, Taylor J, Sharp M. 1980. Manipulating metabolic parameters to improve growth rate and milk secretion. *Journal of Animal Science*. 51 (6): 1416-1428. doi: 10.2527/jas1981.5161416x.
- Bargo F, Muller LD, Delahoy JE, Cassidy TW. 2002. Performance of high producing dairy cows with three different feeding systems combining pasture and total mixed rations. *Journal of Dairy Science*. 85 (11): 2948-2963. doi: 10.3168/jds.S0022-0302(02)74381-6.
- Baudracco J, Lopez-Villalobos N, Holmes CW, Macdonald KA. 2010. Effects of stocking rate, supplementation, genotype and their interactions on grazing dairy systems: a review. *New Zealand Journal of Agricultural Research*. 53 (2): 109-133. doi: 10.1080/00288231003777665.
- Berry DP, Buckley F, Dillon P, Evans RD, Rath M, Veerkamp RF. 2003. Genetic relationships among body condition score, body weight, milk yield, and fertility in dairy cows. *Journal of Dairy Science*. 86 (6): 2193-2204. doi: 10.3168/jds.S0022-0302(03)73809-0.
- Brosh A. 2007. Heart rate measurements as an index of energy expenditure and energy balance in ruminants: a review. *Journal of Animal Science*. 85 (5): 1213-1227. doi: 10.2527/jas.2006-298.
- Brosh A, Aharoni Y, Degen AA, Wright D, Young BA. 1998. Effects of solar radiation, dietary energy, and time of feeding on thermoregulatory responses

- and energy balance in cattle in a hot environment. *Journal of Animal Science*. 76 (10): 2671-2677. doi: 10.2527/1998.76102671x.
- Bruinenberg MH, Van Der Honing Y, Agnew RE, Yan T, Van Vuuren AM, Valk H. 2002. Energy metabolism of dairy cows fed on grass. *Livestock Production Science*. 75 (2): 117-128. doi: 10.1016/S0301-6226(01)00306-2.
- Capper JL, Bauman DE. 2013. The role of productivity in improving the environmental sustainability of ruminant production systems. *Annual Review of Animal Bioscience*. 1: 469-489. doi: 10.1146/annurev-animal-031412-103727.
- Chagas LM, Bass JJ, Blache D, Burke CR, Kay JK, Lindsay DR, Lucy MC, Martin GB, Meier S, Rhodes FM, Roche JR, Thatcher WW, Webb R. 2007. Invited Review: New perspectives on the roles of nutrition and metabolic priorities in the subfertility of high-producing dairy cows. *Journal of Dairy Science*. 90 (9): 4022-4032. doi: 10.3168/jds.2006-852.
- CSIRO (Commonwealth Scientific and Industrial Research Organisation). 2007. *Nutrient Requirements of Domesticated Ruminants*. Melbourne, Australia: CSIRO Publishing. 296 p.
- DIEA (Dirección de Estadísticas Agropecuarias). 2020. *Anuario estadístico agropecuario*. Montevideo: MGAP (Ministerio de Ganadería, Agricultura y Pesca). Disponible en: <https://www.gub.uy/ministerio-ganaderia-agricultura-pesca/datos-y-estadisticas/estadisticas/anuario-estadistico-agropecuario-2020>.
- Dillon P. 2006. Achieving high dry-matter intake from pasture with grazing dairy cows. En: Elgersma A, Dijkstra J, Tamminga S ed. *Fresh herbage for dairy cattle, the key to a sustainable food chain*. Dordrecht, the Netherlands: Springer. 1-26.
- Dillon P, Berry DP, Evans RD, Buckley F, Horan B. 2006. Consequences of genetic selection for increased milk production in European seasonal pasture based systems of milk production. *Livestock Science*. 99 (2-3): 141-158. doi: 10.1016/j.livprodsci.2005.06.011.

- Dillon P, Buckley F. 1998: Effects of genetic merit and feeding on spring calving dairy heifers. En: Ruakura dairy farmers' conference (50th, 1998, Hamilton, New Zealand). Proceedings. 50: 50-56.
- Dong LF, Yan T, Ferris CP, McDowell DA. 2015a. Comparison of maintenance energy requirement and energetic efficiency between lactating Holstein-Friesian and other groups of dairy cows. *Journal of Dairy Science*. 98 (2): 1136-1144. doi: 10.3168/jds.2014-8629.
- Dong LF, Ferris CP, McDowell DA, Yan T. 2015b. Effects of diet forage proportion on maintenance energy requirement and the efficiency of metabolizable energy use for lactation by lactating dairy cows. *Journal of Dairy Science*. 98 (12): 8846-8855. doi: 10.3168/jds.2015-9465.
- Drackley JK, Donkin SS, Reynolds CK. 2006. Major advances in fundamental dairy cattle nutrition. *Journal of Dairy Science*. 89 (4): 1324-1336. doi: 10.3168/jds.S0022-0302(06)72200-7.
- FAO (Food and Agriculture Organization of the United Nations). 2016. Nutrition and Livestock: Technical guidance to harness the potential of livestock for improved nutrition of vulnerable populations in programme planning. Rome: FAO. 47 p. doi: 10.4060/ca7348en.
- Fariña SR, Chilibróste P. 2019. Opportunities and challenges for the growth of milk production from pasture: The case of systems in Uruguay. *Agricultural Systems*. 176: 102631. doi: 10.1016/j.agsy.2019.05.001.
- Fedak MA, Rome L, Sheeherman HJ. 1981. One-step N₂ - dilution technique for calibrating open-circuit VO₂ measuring systems. *Journal of Applied Physiology*. 51 (3): 772-776. doi: 10.1152/jappl.1981.51.3.772.
- Fulkerson WJ, Wilkins J, Dobos RC, Hough GM, Goddard ME, Davidson T. 2001. Reproductive performance in Holstein-Friesian cows in relation to genetic merit and level of feeding when grazing pasture. *Journal of Animal Science*. 73 (3): 397-406. doi: 10.1017/S1357729800058367.
- Harris BL, Kolver ES. 2001. Review of Holsteinization on intensive pastoral dairy farming in New Zealand. *Journal of Dairy Science*. 84 (E. Suppl.): E56-E61. doi: 10.3168/jds.S0022-0302(01)70197-X.

- Hansen LB. 2000. Consequences of selection for milk yield from a geneticist's viewpoint. *Journal of Dairy Science*. 83 (5): 1145–1150. doi: 10.3168/jds.S0022-0302(00)74980-0.
- Horan B, Dillon P, Faverdin P, Delaby L, Buckley F, Rath M. 2005. Strain of Holstein-Friesian by pasture-based feed system interaction for milk production, bodyweight and body condition score. *Journal of Dairy Science*. 88 (3): 1231-1243. doi: 10.3168/jds.S0022-0302(05)72790-9.
- INALE (Instituto Nacional de la Leche). 2014. Encuesta lechera INALE 2014. Montevideo: INALE. Disponible en: <https://www.inale.org/estadisticas/encuesta-2014-produccion-de-leche/>.
- Kaufmann LD, Münger A, Rérat M, Junghans P, Görs S, Metges CC, Dohme-Meier F. 2011. Energy expenditure of grazing cows and cows fed grass indoors as determined by the ¹³C bicarbonate dilution technique using an automatic blood sampling system. *Journal of Dairy Science*. 94 (4): 1989-2000. doi: 10.3168/jds.2010-3658.
- Kennedy J, Dillon P, Delaby L, Faverdin P, Stakelum G, Rath M. 2003. Effect of genetic merit and concentrate supplementation on grass intake and milk production with Holstein-Friesian dairy cows. *Journal of Dairy Science*. 86 (2): 610-621. doi: 10.3168/jds.S0022-0302(03)73639-X.
- Kolver ES, Roche JR, de Veth MJ, Thorne P, Napper AR. 2002. Total mixed ration versus pasture diets: Evidence of a genotype × diet interaction. *Proceedings of the New Zealand Society of Animal Production*. 62: 246-251.
- Kolver ES, Muller LD. 1998. Performance and nutrient intake of high producing Holstein cows consuming pasture or a total mixed ration. *Journal of Dairy Science*. 81: 1403-1411. doi: 10.3168/jds.S0022-0302(98)75704-2.
- Lucy MC, Verkerk GA, Whyte BE, Macdonald KA, Burton L, Cursons RT, Roche JR, Holmes CW. 2009. Somatotropic axis components and nutrient partitioning in genetically diverse dairy cows managed under different feed allowances in a pasture system. *Journal of Dairy Science*. 92 (2): 526-539. doi: 10.3168/jds.2008-1421.

- Macdonald KA, Verkerk GA, Thorrold BS, Pryce JE, Penno JE, McNaughton LR, Burton LJ, Lancaster JAS, Williamson JH, Holmes CW. 2008. A comparison of three strains of Holstein-Friesian grazed on pasture and managed under different feed allowances. *Journal of Dairy Science*. 91 (4): 1693-1707. doi: 10.3168/jds.2007-0441.
- Marshall KR. 1989. The origin and history of the A + B – C payment system. En: Barrell GK ed. *Milk payment and quality*. Canterbury, New Zealand: Lincoln College. 9-11.
- McCarthy S, Horan B, Rath M, Linnane M, O'Connor P, Dillon D. 2007. The influence of strain of Holstein-Friesian dairy cow and pasture-based feeding system on grazing behavior, intake and milk production. *Grass and Forage Science*. 62 (1):13-26. doi: 10.1111/j.1365-2494.2007.00557.x.
- McDonald P, Edwards RA, Greenhalgh JFD, Morgan CA, Sinclair LA, Wilkinson RG. 2011. *Animal Nutrition*. 7th ed. Harlow, United Kingdom: Pearson Education Limited. 712 p.
- McLean JA, Tobin G. 1988. *Animal and Human Calorimetry*. Cambridge, United Kingdom: Cambridge University Press. 352 p.
- McNamara, J.P. 2015. Triennial Lactation Symposium: Systems biology of regulatory mechanisms of nutrient metabolism in lactation. *Journal of Animal Science*. 93 (12): 5575-5585. doi: 10.2527/jas.2015-9010.
- Miglior F, Fleming A, Malchiodi F, Brito LF, Martin P, Baes CF. 2017. A 100-Year Review: Identification and genetic selection of economically important traits in dairy cattle. *Journal of Dairy Science*. 100 (12): 10251-10271. doi: 10.3168/jds.2017-12968.
- Miglior F, Muir BL, Van Doormaal BJ. 2005. Selection indices in Holstein cattle of various countries. *Journal of Dairy Science*. 88 (3): 1255-1263. doi: 10.3168/jds.S0022-0302(05)72792-2.
- Moraes LE, Kebreab E, Strathe AB, Dijkstra J, France J, Casper DP, Fadel JG. 2015. Multivariate and univariate analysis of energy balance data from lactating dairy cows. *Journal of Dairy Science*. 98 (6): 4012-4029. doi: 10.3168/jds.2014-8995.

- Nicol AM, Young BA. 1990. Short-term thermal and metabolic responses of sheep to ruminal cooling: Effects of level of cooling and physiological state. *Canadian Journal of Animal Sciences*. 70 (3): 833-843. doi: 10.4141/cjas90-102.
- Nour AYM, Thonney ML, Stouffer JR, White WRC. 1983. Changes in carcass weight and characteristics with increasing weight of large and small cattle. *Journal of Animal Science*. 57 (5): 1154-1165. doi: 10.2527/jas1983.5751154x.
- NRC (National Research Council). 2001. *Nutrient Requirements of Dairy Cattle*, 7th revised ed. Washington, DC, USA: National Academy Press. 450 p.
- Osuji PO. 1974. The physiology of eating and the energy expenditure of the ruminant at pasture. *Journal of Range Management*. 27 (6): 437-443.
- Pereira I, Laborde D, Carriquiry M, Lopez-Villalobos N, Meikle A. 2010. Productive and reproductive performance of Uruguayan Holstein and Uruguayan Holstein × New Zealand Holstein Friesian cows in a predominantly pasture-based system. *Proceedings of the New Zealand Society of Animal Production*. 70: 306-310.
- Roche JR, Macdonald KA, Burke CR, Lee JM, Berry DP. 2007. Associations among body condition score, body weight, and reproductive performance in seasonal-calving dairy cattle. *Journal of Dairy Science*. 90 (1): 376-391. doi: 10.3168/jds.S0022-0302(07)72639-5.
- Roche JR, Berry DP, Kolver ES. 2006. Holstein-Friesian strain and feed effects on milk production, body weight, and body condition score profiles in grazing dairy cows. *Journal of Dairy Science*. 89 (9): 3532-3543. doi: 10.3168/jds.S0022-0302(06)72393-1.
- Shook GE. 2006. Major advances in determining appropriate selection goals. *Journal of Dairy Science*. 89 (4): 1349-1361. doi: 10.3168/jds.S0022-0302(06)72202-0.
- Thanner S, Dohme-Meier F, Görs S, Metges CC, Bruckmaier RM, Schori F. 2014. The energy expenditure of 2 Holstein cow strains in an organic grazing system. *Journal of Dairy Science*. 97 (5): 2789-2799. doi: 10.3168/jds.2013-7394.
- UNEP (United Nations Environment Programme). 2015. *Sustainable Consumption and Production: A Handbook for Policymakers*. Global edition. 212 p.

- United Nations - Department of Economic and Social Affairs - Population Division. 2019. World Population Prospects 2019: Highlights. New York, USA: United Nations. 39 p.
- VandeHaar MJ, Armentano LE, Weigel K, Spurlock DM, Tempelman RJ, Veerkamp R. 2016. Harnessing the genetics of the modern dairy cow to continue improvements in feed efficiency. *Journal of Dairy Science*. 99 (6): 4941-4954. doi: 10.3168/jds.2015-10352.
- Veerkamp RF, Simm G, Oldham JD. 1994. Effects of interaction between genotype and feeding system on milk production feed intake, efficiency and body tissue mobilization in dairy cows. *Livestock Production Science*. 39 (3): 229-241. doi: 10.1016/0301-6226(94)90202-X.
- Wang S, Roy GL, Lee AJ, McAllister AJ, Batra TR, Lin CY, Vesely JA, Wauthy JM, Winter KA. 1992. Evaluation of various measures of and factors influencing feed efficiency of dairy cattle. *Journal of Dairy Science*. 75 (5): 1273-1280. doi: 10.3168/jds.S0022-0302(92)77877-1.
- White HM, Donkin SS, Lucy MC, Grala TM, Roche JR. 2012. Short communication: Genetic differences between New Zealand and North American dairy cow alter milk production and gluconeogenic enzyme expression. *Journal of Dairy Science*. 95 (1): 455-459. doi: 10.3168/jds.2011-4598.
- Xue B, Yan T, Ferris CF, Mayne CS. 2011. Milk production and energy efficiency of Holstein and Jersey-Holstein cross-bred dairy cows offered diets containing grass silage. *Journal of Dairy Science*. 94 (3): 1455-1464. doi: 10.3168/jds.2010-3663.

6. ANEXOS

6.1. CALORIMETRÍA INDIRECTA

El término calorimetría hace referencia a la medición del calor. El calor puede ser medido directamente a través de métodos físicos (calorimetría directa) o puede ser inferido a partir de la medición cuantitativa de algunos de los productos químicos del metabolismo (calorimetría indirecta). La calorimetría indirecta es posible debido a las limitaciones naturales impuestas a la transformación de energía por las leyes de la termodinámica. De fundamental importancia son la Ley de Conservación de la Energía (la energía no puede ser creada o destruida, solo se transforma) y la Ley de Hess conocida como la Ley de Sumatoria de Calor Constante (el calor liberado por una cadena de reacciones es independiente de la ruta metabólica, y únicamente es dependiente de los productos finales). En efecto, estas leyes establecen que el calor involucrado en el complejo ciclo de reacciones bioquímicas que ocurre en un organismo es exactamente el mismo que fue medido cuando el mismo alimento fue convertido en los mismos productos finales mediante simple combustión en una bomba calorimétrica (McLean y Tobin, 1988).

6.1.1. Técnica de Frecuencia cardíaca – Pulso de O₂ (FC-O₂P)

La técnica de FC-O₂P reportada en primera instancia por Brosh et al. (1998) y posteriormente validada a través de una revisión por Brosh (2007) consiste en la estimación indirecta de la producción de calor (PC) de un rumiante mediante la medición de su consumo de oxígeno. La técnica tiene el potencial de ser utilizada para la medición del gasto energético de animales en pastoreo ya que estima el consumo de O₂ (VO₂) del rumiante a través de la relación existente entre el VO₂ y la frecuencia cardíaca (FC). Esta justificación se basa en que, para el caso de los mamíferos, la mayor parte del O₂ es transportado hacia los tejidos a través de la acción del corazón, y por consecuencia la relación calibrada entre FC y PC tiene gran potencial para ser utilizada en mediciones del gasto energético de animales fuera de cámaras

calorimétricas (Brosh, 2007). La calibración entre la FC y la PC se realiza mediante un coeficiente denominado O_2P que representa la cantidad de O_2 consumido por latido cardíaco y que es propio de cada individuo con determinada dieta y condiciones fisiológicas y ambientales específicas, por lo tanto, la técnica requiere de esta calibración para cada vez que vaya a ser utilizada.

Por lo tanto, la técnica consiste en dos set de mediciones; una medición de corto plazo (10 – 12 min) en donde se mide en simultáneo la FC (mediante pulsímetros) y el consumo de oxígeno (mediante máscaras conectadas a un sistema de circuito abierto; Fedak (1981) de un animal inmovilizado sin evidencia de estrés con el objetivo de estimar su O_2P ; y una medición de largo plazo en donde se mide la FC del rumiante durante al menos 4 días consecutivos cada intervalos de 5 segundos en su rutina diaria. En base a esta información se estima el consumo de O_2 que es convertido a calor asumiendo 20,47 kJ/L O_2 consumido (Nicol y Young, 1990).