Evaluación de la eficiencia de uso de la energía de vaquillonas Hereford en pastoreo

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Dedico este trabajo a todos los que me acompañaron en este camino

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TABLA DE CONTENIDO

RESUMEN

El objetivo del trabajo fue evaluar y cuantificar la eficiencia en el uso de la energía de vaquillonas Hereford en pastoreo mediante la cuantificación de la producción de calor residual (RHP) y su relación con el consumo residual de alimento (RFI) paterno. Para ello se realizaron dos trabajos en los que se evaluaron vaquillonas Hereford nacidas en 2017 y 2018 (n = 145) progenie de diez toros con valor de cría estimado (EBV) para RFI. Estas se evaluaron durante dos años en tres períodos de 70 d (dos en primavera a los 24-25 meses de edad, previo al servicio, y uno en otoño a los 18 meses de edad). La producción de calor (HP) se midió utilizando la técnica de tasa cardíaca y pulso de oxígeno, la energía retenida (ER) se determinó con las variaciones PV y el consumo de energía metabolizable (EM) como la suma de HP + ER. En el experimento 1, se utilizaron datos de las dos generaciones evaluadas en primavera y los resultados mostraron que las vaquillonas progenie de toros de alta eficiencia (PHE**,** bajo RFI), fueron más eficientes (menor RHP) en condiciones de pastoreo que las hijas de toros de baja eficiencia (PLE**,** alto RFI). A su vez, se observó una mayor ER sin diferencias en HP, EM o consumo de MS expresadas como unidades de $PV^{0,75}$, así como una mayor eficiencia energética, lo que sugiere una reducción en los costos de energía de mantenimiento (ENM) y/o un aumento en la eficiencia parcial de crecimiento (k). En el experimento 2, se utilizaron vaquillonas de una única generación medidas en otoño y primavera. Se determinó que la RHP fue una característica repetible, aunque, en otoño, la disponibilidad de pastura y, por lo tanto, la nutrición fueron más restrictivas que en primavera. Las vaquillonas eficientes mostraron menores HP, consumo de EM y MS sin diferencias en ER que sus pares ineficientes. Más aún, se estimaron menores requerimientos de ENM y EMM así como una mayor eficiencia parcial del uso de la EM consumida (*k*) para las vaquillonas más eficientes (bajo RHP; HH). Las hembras eficientes mostraron una actividad luteal más precoz, así como un menor intervalo servicio- concepción a la vez que un parto más temprano en la estación que sus pares de baja eficiencia.

Palabras clave: eficiencia energética, calorimetría indirecta, reproducción

ENERGY EFFICIENCY OF GRAZING HEREFORD HEIFERS

SUMMARY

The objective of this work was to evaluate and quantify the efficiency of use of energy of grazing Hereford heifers trough residual heat production (RHP) and its relationship to paternal residual feed intake (RFI). For this purpose, two studies were conducted in which Hereford heifers born in 2017 and 2018 (n = 145), progeny of ten bulls with estimated breeding value (EBV) for RFI where heifers were evaluated for two years in three periods of 70 d (two in spring at 24-25 months of age, prior to service, and one in autumn at 18 months of age). Heat production (HP was measured using the heart rate and oxygen pulse technique, retained energy (RE) was determined with PV variations and metabolizable energy (ME) intake as the sum of HP + RE. In experiment 1, data from the two generations evaluated in spring were used and the results showed that heifers' progeny of high efficiency bulls (pHE, low RFI) were more efficient (lower RHP) under grazing conditions than daughters of low efficiency bulls (pLE, high RFI). In turn, higher RE was observed with no differences in HP, ME or DM intake expressed as units of $PV^{0.75}$ as well as higher energy and feed efficiency in the progeny of pHE than pLE, suggesting a reduction in maintenance energy costs (ENm) and/or an increase in partial growth efficiency (*k*). In experiment 2, a single generation of heifers measured in autumn and spring were used. The RHP was found to be a repeatable trait, although, in the fall, pasture availability and, therefore, nutrition were more restrictive than in the spring. Efficient heifers showed lower HP, ME and DM intake with no differences in RE than their inefficient peers. Moreover, lower ENm and EMm requirements as well as higher partial use efficiency of consumed ME (k) were estimated for the most efficient heifers (low RHP; HH). Efficient females showed earlier luteal activity, as well as a shorter service-conception interval and earlier calving in the season than their low efficiency counterparts, probably associated with earlier adipose tissue development.

Keywords energy efficiency, indirect calorimetry, reproduction

1. INTRODUCCIÓN

1.1. PLANTEO DEL PROBLEMA

El sector ganadero ha sido históricamente un rubro de suma importancia para Uruguay. Reflejo de esto es que, para el año 2021, las exportaciones de carne y ganado en pie significaron ingresos de algo más de 2800 millones de dólares (29 % del total de ingresos producto de exportaciones), lo que convirtió a la ganadería en el rubro que más ingresos generó al país (DIEA, 2022).

Sin embargo, la producción de carne ha enfrentado en los últimos años una fuerte competencia por el uso de la tierra con la forestación y la agricultura, y el costo de la renta por hectárea ha tenido un crecimiento promedio de 12 % anual entre 2000 y 2021. Tal es así, que, para el período 2000-2018, la cantidad de kilos de carne necesarios para cubrir los costos de arrendamiento experimentó un crecimiento en el orden del 30 %. A su vez, a partir del año 2011 se ha registrado una consistente caída del ingreso de capital por hectárea por parte de las empresas ganaderas equivalente al 8 % anual. Esta problemática se ve especialmente acentuada en las empresas criadoras que históricamente han percibido menores ingresos de capital que los registrados por empresas de ciclo completo o invernadoras (FUCREA, 2017). En este contexto de elevados costos, reducidos o nulos márgenes económicos e incertidumbre en lo que respecta a mercado, los sistemas criadores se ven particularmente obligados a conducirse hacia una producción más eficiente.

Por otra parte, para satisfacer la demanda creciente de alimentos en el ámbito mundial, es necesario un aumento de la producción agrícola, para lo cual se ha demostrado que el aumento de la productividad es más ventajoso, en términos ambientales, que el aumento del área destinada a producción (Tilman et al., 2011). Más aún, bajo el contexto del cambio climático y el creciente interés de los consumidores por productos que generen menor impacto ambiental, los sistemas ganaderos se han visto bajo escrutinio. Esta situación ha llevado a que se haya desarrollado un creciente interés por la eficiencia animal y, en particular, en el sector ganadero como una manera de satisfacer la demanda de carne, ahorrar insumos y reducir costos e impactos al medioambiente, de manera de mejorar resultado económico y la sostenibilidad ambiental de los sistemas de producción de carne (Kenny et al., 2018).

El proceso de la cría está calificado como biológicamente ineficiente debido a las bajas y lentas tasas reproductivas y los altos costos energéticos del rodeo: entre el 70 y el 75 % del costo total de energía de la dieta es destinado a mantenimiento (Ferrell y Jenkins, 1985). A pesar de ello, los sistemas criadores poseen la capacidad de transformar forrajes «toscos» en producto animal de alta calidad para la nutrición humana (Jenkins y Ferrell, 1994). En los países templados, como Uruguay, la ganadería se lleva a cabo esencialmente sobre pasturas, lo que hace que esta esté sujeta a las variaciones estacionales y anuales de cantidad y calidad del forraje (Soca et al., 2007). En particular, los sistemas criadores están caracterizados por desarrollarse sobre campos con bajos índices productivos y proporción de mejoramientos y por haber sido históricamente manejados con altas cargas animales, lo que ha resultado en bajas tasas reproductivas, bajo peso de venta del ganado y baja productividad de las pasturas naturales (Aguerre et al., 2015). Particularmente en estos sistemas, la principal limitante productiva continúa siendo el consumo de energía por la vaca (Soca et al., 2007) que afecta negativamente las tasas de reproducción (Hess et al., 2005).

En este marco, es lógico pensar que la eficiencia de cada animal tendrá una gran influencia en los costos unitarios de producción y, por consiguiente, en la competitividad de los productos cárnicos tanto en mercados locales como internacionales (Basarab et al., 2003). En este sentido, en el ámbito nacional se ha generado y/o evaluado tecnologías de manejo relacionadas, entre otros aspectos, con la asignación de forraje (Carriquiry et al., 2012, Do Carmo et al., 2019), el genotipo animal (Espasandín et al., 2006), la interacción de asignación de forraje con genotipo (Do Carmo et al., 2018), el efecto del destete y la condición corporal (Quintans et al., 2010) o el efecto de suplementaciones cortas (Pérez-Clariget et al., 2007, Astessiano et al., 2011) con el fin de mejorar la eficiencia productiva-reproductiva de los sistemas ganaderos.

Por otra parte, se ha propuesto la mejora de la eficiencia individual como otra vía para mejorar la eficiencia global del sistema. En este sentido, en las últimas décadas, el consumo residual de alimento (*residual feed intake*; RFI), definido como la diferencia entre el consumo real y el esperado para cubrir los requerimientos de mantenimiento y crecimiento, se ha convertido en el índice de referencia en cuanto a eficiencia alimenticia (Berry, 2009, Moore et al., 2009). En el ámbito nacional, las evaluaciones de la eficiencia de conversión a través de pruebas estándar de RFI realizadas en toros y novillos Hereford (Navajas, 2017) han desarrollado y validado un estimador del valor de cría para eficiencia de conversión. A su vez, se investigó la asociación de RFI con el desempeño durante la invernada y calidad de carne y se demostró que se puede seleccionar animales con menor RFI (más eficientes) sin comprometer el desempeño productivo en la invernada o la calidad del producto (Navajas et al., 2018). Asimismo, resultados preliminares han indicado una alta asociación entre la eficiencia de conversión de los animales en la fase de recría e invernada (Navajas y Silveira, 2019).

Sin embargo, a pesar de que la mayoría de la producción de carne del mundo, y en particular en Uruguay, está basada en sistemas pastoriles, las investigaciones nacionales e internacionales en torno a RFI han sido básicamente desarrolladas sobre machos en engorde o crecimiento en condiciones de confinamiento. La información sobre la relación del RFI y desempeño productivo en animales a pastoreo es escasa, y la evidencia indicaría la existencia de interacción genotipo x ambiente para esta característica de eficiencia (Kenny et al., 2018). Esta situación puede generar una cierta incertidumbre, ya que se evalúa una variable asociada a características deseables en cuanto a crecimiento y productividad de machos, pero aún no se ha reportado la incidencia de esta en las hembras que se desarrollan en un sistema productivo muy diferente al de evaluación y con un destino productivo generalmente distinto al de los machos.

Los escasos y contrastantes resultados de las evaluaciones de RFI en condiciones de pastoreo (Manafiazar et al., 2015, Wiley et al., 2016) están probablemente asociadas a la gran dificultad que supone obtener medidas precisas de consumo de materia seca (MS) en animales en pastoreo (Lawrence et al., 2012), así como las características del proceso de pastoreo (Lahart et al., 2020) que también explicarían la variación detectada entre estudios. En este sentido, la técnica de tasa cardíaca-pulso de O_2 (HR-O_2P; Brosh, 2007) sería útil para determinar el gasto energético en animales en pastoreo y podría ser usada como una alternativa para identificar animales eficientes sin la necesidad de determinar el consumo, ya que la mayoría de la energía metabolizable (EM) consumida se pierde como calor. Así, la producción residual de calor (*residual heat production*; RHP), estimada como la diferencia entre la producción de calor (HP) real y la esperada para cierto nivel de producción y peso, podría permitir identificar animales más eficientes: individuos con menor RHP serán energéticamente más eficientes, ya que producirán menor calor del esperado.

1.2. ANTECEDENTES BIBLIOGRÁFICOS

1.2.1. Eficiencia energética y alimenticia

En los predios, uno de los principales factores económicos que afectan la rentabilidad de los sistemas ganaderos es el suministro de alimento, que puede llegar a representar hasta tres cuartas partes del total de los costos directos (Nielsen et al., 2013). En el rodeo de cría, la mayor parte del costo de alimentación está adjudicado a cubrir los requerimientos de mantenimiento de los animales, que pueden representar de 60 a 75 % de los requerimientos totales, con una variación considerable entre individuos independientemente del tamaño corporal (Ferrell y Jenkins, 1985, Montaño-Bermudez et al., 1990). En los animales, existen múltiples definiciones de eficiencia alimenticia; las más utilizadas tradicionalmente fueron la eficiencia o conversión alimenticia, que se calculan como la ganancia media diaria (GMD) sobre el consumo de MS o su inverso matemático, respectivamente (Berry y Crowley, 2013, Kenny et al., 2018). Sin embargo, ninguno de estos parámetros toma en cuenta las diferencias existentes entre animales en cuanto a la eficiencia de mantenimiento, definida para animales en crecimiento como la relación entre el peso vivo (PV) o energía retenida (ER) y el consumo de MS o EM cuando no existen cambios en los primeros (Archer et al., 1999).

Como se mencionó anteriormente, el RFI, definido como la diferencia entre el consumo de alimento observado y el estimado para cubrir tanto los requerimientos de mantenimiento como de crecimiento, o, alternativamente, como el residual de la regresión del consumo de MS respecto al peso metabólico ($PV^{0.75}$) y GMD (Koch et al., 1963), se ha convertido en una medida ampliamente difundida de la eficiencia alimentaria animal (Berry, 2009, Moore et al., 2009). Por definición, el RFI es independiente del nivel de producción, lo que lo convierte en un índice útil para explorar los mecanismos asociados con la variación en la eficiencia entre animales (Arthur y Herd, 2008, Crowley et al., 2010, Berry y Crowley, 2013). Sin embargo, Berry y Crowley (2012) citan la falta de correlación entre RFI y la GMD como una posible explicación para la baja aceptación por parte de la industria respecto al RFI, ya que animales con bajas tasas de crecimiento pueden, a la vez, estar bien categorizados respecto a RFI. Las tasas de ganancia altas son tradicionalmente deseables en el ámbito comercial, mientras que la eficiencia alimentaria es un concepto relativamente novedoso y a veces poco tangible en el ámbito productivo.

A la vez, se ha demostrado que esta característica es moderadamente heredable (Arthur et al., 2001, Robinson y Oddy, 2004, Schenkel et al., 2004): Berry and Crowley (2013), compendiando un extenso número de trabajos con variedad de razas y poblaciones de animales en crecimiento, determinaron que esta variaba entre 0,07 y 0,62 con una media de 0,33 ± 0,013. Más aún, se ha determinado que una única generación de selección a favor de valores de RFI posdestete negativos mejoraron la eficiencia en evaluaciones posdestete para RFI de toros jóvenes y vaquillonas (Herd et al., 1997) y novillos alimentados en confinamiento (Richardson et al., 1998). A su vez, se han encontrado correlaciones moderadas entre dos períodos de medición consecutivos de RFI para novillos alimentados con la misma (r = 0,42-0,44) o diferente dieta (dieta de crecimiento vs. finalización; r = 0,33; Durunna et al., 2011), o para vaquillonas de reemplazo alimentados con la misma dieta (r = 0,50; Durunna et al., 2012). De manera similar, Archer et al. (2002) y Hafla et al. (2013) reportaron correlaciones moderadas (r = 0,40-0,42) entre el RFI medido como vaquillonas posdestete y como vacas adultas a las que se les ofrecieron dietas concentradas o dietas con diferente proporción de forraje. Sin embargo, Kelly et al. (2010) reportan una correlación alta (r = 0,62) entre el RFI medido en vaquillonas alimentadas con dietas de crecimiento y finalización, mientras que Lahart et al. (2020) reportaron correlaciones débiles (r < 0,25) para vaquillonas y novillos alimentados con diferentes dietas y Black et al. (2013) no encontraron ninguna relación entre el RFI medido como vaquillonas en crecimiento y vacas lactantes, ambas con una dieta basada en forrajes.

La investigación en RFI en animales en pastoreo es escasa y muchas veces contradictoria. Wiley et al. (2016), trabajando con toros clasificados por RFI en confinamiento, reportaron que 47 ± 13 % de los animales mantuvieron su ranking en condiciones de pastoreo y Trujillo et al. (2013) reportaron una correlación moderada (r = 0,50) entre el RFI de vaquillonas medidas consecutivamente en confinamiento. Por su parte, Manafiazar et al. (2015) reportaron una correlación menor (r = 0,30) entre el RFI medido en vaquillonas en crecimiento en condiciones de *dry-lot* y con los mismos animales preñados en pastoreo. Además, a pesar de que, en condiciones de confinamiento, el RFI ha sido positivamente correlacionado con el consumo de MS, con animales más eficientes consumiendo menos MS (Cantalapiedra-Hijar et al., 2018), el consumo de pastura de vaquillonas o novillos previamente clasificados como alto o bajo RFI no ha sido diferente evaluado en condiciones de pastoreo (Herd et al., 1998, Herd et al., 2002, Meyer et al., 2008, Lawrence et al., 2012, Oliveira et al., 2016). En contraste, otros estudios han reportado un menor consumo de pastura para animales de bajo RFI cuando fueron evaluados consecutivamente (Trujillo et al., 2013) o como vacas preñadas en pastoreo (Knight et al., 2015).

Sin embargo, dado que tanto el RFI como los demás índices mencionados están expresados en unidades de peso y no en unidades energéticas, la selección por estos parámetros de eficiencia no necesariamente implica una selección por eficiencia de utilización de la energía consumida. La EM consumida comprende la ER en producto (*i. e.,* tejido) y la HP, incluyendo esta última la energía destinada mantenimiento y el incremento calórico. El incremento calórico, que se considera una pérdida de energía, representa el incremento en calor por aumento del consumo de alimento, y es originado debido a la fermentación, digestión, metabolismo y excreción de los nutrientes. El mantenimiento es el estado fisiológico cuando no hay cambio neto en la energía corporal o, alternativamente, cuando el balance de energía es cero (Baldwin et al., 1980) y está comprendido por los gastos de energía necesaria para el metabolismo basal (funciones de servicio y mantenimiento celular; Baldwin et al., 1980), la actividad (comer/pastorear, rumiar, caminar, etc.) y la termorregulación. El costo de mantenimiento no está solo determinado por factores asociados al animal, sino que también estará afectado por el consumo y el tipo y composición de la dieta: el aumento en la ingesta de EM y dietas con mayor inclusión de forraje tendrán mayores costos de mantenimiento (Dong et al., 2015a, Dong et al., 2015b).

Una disminución en la HP y en el costo energético de mantenimiento han sido factores mencionados como la base de la variación en la eficiencia alimenticia medida como RFI (Richardson y Herd, 2004, Cantalpiedra-Hijar et al., 2018). Asher et al. (2018), trabajando con terneros enteros Holstein, reportaron relaciones positivas entre RFI y consumo de EM, ER y HP. Esto indica que terneros de alto RFI tuvieron un mayor consumo de EM, retuvieron más energía y produjeron más calor que los terneros de bajo RFI. Esta relación positiva entre HP diaria y RFI indica que terneros más eficientes mostraron una HP menor a la esperada, resultados que concuerdan con lo determinado por Richardson et al. (2001) y Basarab et al. (2003). En esta línea, Nkrumah et al. (2006), trabajando con animales cruza Aberdeen Angus x Charolais, alimentados 2,5 veces por sobre sus requerimientos de mantenimiento, reportaron una HP diaria de 149,0 ± 19,72 kcal/kg $PV^{0.75}$, lo que representó aproximadamente un 59 % del consumo de EM diario. A su vez, la asociación de HP y ER con RFI fue altamente significativa. Los animales de bajo RFI tuvieron una HP 21 y 10 % menor a los animales de alto y medio RFI, respectivamente. De manera consistente, la ER fue menor para los animales de alto y medio RFI (44 y 23%, respectivamente) comparados con los de bajo RFI. Este estudio entonces concluye una correlación de 0,68 entre el RFI y la HP. Más aún, Chaves et al. (2015) encontró una tendencia positiva entre HP y RFI y Menezes et al. (2020) reportó una menor HP y consumo de EM para toros de bajo RFI respecto a alto RFI sin diferencias en ER. Si consideramos que la HP total es una función de la HP de mantenimiento (HPm) y la de producción (HPp; Miron et al., 2008), entonces en animales con una menor HP e igual RE sería esperable una similar HPp y menor HPm. Herd y Bishop (2000), trabajando con toros jóvenes Hereford, encontraron una alta correlación genética (r_g = 0,93) entre el requerimiento de energía para mantenimiento por unidad de $PV^{0,75}$ y el RFI y Menezes et al. (2020) determinaron una menor energía neta (EN) de mantenimiento (63.4 vs. 78.1 kcal/kg $PV^{0,75}$/d) para toros de bajo RFI respecto a alto RFI.

Por otra parte, el tamaño, la tasa y la composición de la ganancia, así como la composición corporal influenciarán los costos de mantenimiento. Varios estudios han descrito una relación directa entre los requerimientos de mantenimiento y la composición corporal (Moe et al., 1971, Noblet et al., 1999, Kirkland et al., 2002) debido a la gran diferencia que existe entre el mantenimiento del tejido graso y el proteico. En esta línea, Ball y Thompson (1995), trabajando con ovinos, reportaron menores requerimientos de mantenimiento para animales que poseían un mayor engrasamiento que otros animales más magros a un mismo PV y Di Costanzo et al. (1990), trabajando con vacas de carne, estimaron que son necesarios 804 kJ de energía para mantener un kg de proteína y 86,7 kJ para mantener un kg de grasa; es decir que, según estos datos, el costo de mantenimiento del kilo de proteína es 9,3 veces más caro que el de grasa. Estas diferencias se deben a que la proteína está continuamente siendo degradada y resintetizada (el llamado *turnover* proteico) mientras que el *turnover* graso es mínimo o inexistente (Kirkland et al., 2002). Reforzando estos hallazgos, Richardson et al. (2004) encontraron una correlación positiva entre la concentración de urea en plasma al destete y el RFI en la progenie de toros seleccionados por bajo RFI, es decir que los animales más eficientes tuvieron una menor concentración de urea en plasma. Siendo la urea un subproducto de la degradación proteica, estos resultados implicarían que los RFI menores se asociaron positivamente a la menor degradación proteica. Sin embargo, estos hallazgos no son consistentes y no siempre son detectadas diferencias (Lawrence et al., 2011, Broleze et al., 2020), pero esto podría estar explicado por la dieta suministrada (Guarnido-Lopez et al., 2021).

Sin embargo, la relación entre las diferencias en composición corporal y la eficiencia alimenticia no es clara. Kenny et al. (2018), realizando un metaanálisis de estudios de ganado en crecimiento bajo dietas altamente concentradas, no encontraron diferencias en deposición muscular ni en espesor de grasa subcutánea tanto en animales vivos como faenados de alto y bajo RFI. Estos hallazgos se contraponen a lo determinado por Berry y Crowley (2013) que, realizando también un metaanálisis, reportaron que el RFI se encontraba negativamente asociado a la muscularidad (r_g = -0,18; n = 14) y positivamente asociado al contenido graso (r_g = 0,20; n = 12) tanto en animales vivos como faenados. Estas inconsistencias en la información reportada pueden estar dadas por las diferencias en las razas, el sexo y el estado fisiológico de los animales entre los estudios, así como por las diferencias en las metodologías usadas para el reporte de los resultados.

Otro factor que tiene influencia sobre el mantenimiento es la actividad asociada al consumo, especialmente en dietas de base pastoril (Fitzsimons et al., 2014). El consumo es una función de la cantidad de alimento ingerido por comida y la frecuencia de alimentación, en el que la importancia relativa de estos procesos es dependiente de las características de la dieta (Fitzsimons et al., 2017). Las actividades clave asociadas al consumo incluyen la frecuencia y duración de cada evento de consumo individual que conjuntamente constituyen la longitud del consumo (min/día) así como la tasa de consumo (g/min). Kenny et al. (2018), mediante un metaanálisis de datos de 9 estudios de animales de carne en crecimiento alimentados con dietas altamente concentradas y energéticas, encontraron que el ganado de alto RFI estuvo 12 % más tiempo (10,3 min dentro de un promedio de 93 min/día) más alimentándose que sus pares de bajo RFI. A su vez, estos animales tuvieron un consumo de MS 17 % mayor, lo que indica también que tuvieron una tasa de consumo más alta que los animales de bajo RFI. Datos similares han sido reportados para hembras preñadas de varias razas carniceras con dietas con alta proporción de forraje (Basarab et al., 2007, Hafla et al., 2013, Fitzsimons et al., 2014). La literatura disponible respecto a la relación RFI y eventos de consumo diarios es equívoca debido parcialmente a la diversidad de dietas, así como a la definición de un evento de consumo entre los estudios (Kenny et al., 2018). Sin embargo, la limitada literatura que ha cuantificado tasa de consumo de novillos de bajo RFI en crecimiento (Robinson y Oddy, 2004, Montanholi et al., 2009), vaquillonas (Robinson y Oddy, 2004) y vacas preñadas (Hafla et al., 2013, Fitzsimons et al., 2014) ha determinado que poseen una tasa de consumo más lenta que sus pares de alto RFI. Por otro lado, Richardson et al. (2000), trabajando con toros en confinamiento, utilizando podómetros, sugirieron que aproximadamente el 10 % de la variación observada en RFI era producto de diferencias en la actividad entre animales.

Es necesario remarcar que la gran mayoría de estos trabajos fueron realizados en condiciones de confinamiento, a pesar de que la mayoría de los sistemas ganaderos en el mundo se desarrollan en base pastoril (Lawrence et al., 2012, Manafiazar et al., 2015, Oliveira et al., 2016). No es algo fortuito, sino que esto está ocasionado por la gran dificultad que conlleva obtener medidas precisas de consumo en pastoreo, lo que también explica las grandes discrepancias entre estudios (Lawrence et al., 2012). Es claro que, en pastoreo, tanto la disponibilidad de nutrientes como la composición de la pastura cambian entre parcelas, lo que genera diferencias en el gasto energético asociado con el proceso de cosecha del forraje, por lo que el comportamiento ingestivo-digestivo se torna sumamente importante (Gregorini et al., 2008). En conjunto, estos estudios muestran que, en confinamiento, las diferencias en comportamiento entre animales de bajo y alto RFI son mayormente un reflejo de diferencias en el consumo; pero, en condiciones pastoriles, la influencia de estos parámetros en las diferencias entre animales en cuanto a eficiencia es aún desconocida. Debido a esto, la interacción entre genotipo y ambiente se vuelve particularmente importante si es que las estimaciones de mérito genético para eficiencia del consumo están asociadas a condiciones de manejo muy distintas a aquellas de producción.

Más allá del consumo, la digestión del alimento determinará la eficiencia con la que se capturará la energía de la dieta. Es así que Richardson y Herd (2004), utilizando variedad de razas de carne, concluyeron que las diferencias entre animales en su habilidad digestiva explicaban un 10 % de la variación del RFI, a la vez que detectaron una correlación moderada negativa entre digestibilidad y RFI en confinamiento; es decir que los animales más eficientes tuvieron asociadas mayores digestibilidades. Similarmente, Bonilha et al. (2017), trabajando con toros Nelore alimentados con una relación de forraje:concentrado de 20:80, encontraron que los animales de bajo RFI mostraron una digestibilidad de la MS superior a favor de los animales con bajo RFI (52,7 % vs. 42,8 %). Kenny et al. (2018), realizando una revisión de estudios asociando digestibilidad de la MS con RFI, detectaron una correlación negativa entre la digestibilidad de la dieta y RFI, aunque no es claro si esta mayor digestibilidad está asociada a características inherentes a los animales más eficientes o es solamente una consecuencia de una menor tasa de pasaje por un menor consumo MS. Cantalapiedra et al. (2018), realizando un metaanálisis de 15 trabajos relacionando digestibilidad y consumo de MS en líneas de selección divergentes para

RFI, encontraron que, en promedio, existía una correlación negativa entre estas variables.

Como se mencionó anteriormente, la principal limitante en el uso de la mayoría de las medidas de eficiencia alimenticia es la disponibilidad de información precisa sobre el consumo (Berry, 2009), especialmente en condiciones de pastoreo, siendo la RHP una alternativa para la identificación de animales eficientes alimenticiamente sin necesidad de determinar el consumo individual. De la misma manera que el RFI, este índice está basado en la hipótesis de que existe variación entre animales en el costo de mantenimiento y en la eficiencia del uso de energía para mantenimiento y para producción. Sin embargo, pocos estudios han explorado la RHP y su asociación con RFI (Richardson et al., 2001, Asher et al., 2018); Richardson et al. (2001), calculando el RHP de novillos Angus (n = 33) progenie de líneas divergentes de RFI usados para determinar la HP esperada, la proporción de grasa y proteína depositada y el incremento calórico, reportaron que la progenie de toros con alto RFI tenía mayor RHP por unidad de ganancia de proteína que la progenie de toros con bajo RFI, mientras que Asher et al. (2018), midiendo la HP con la técnica de HR-O_2P y usando un esquema de mediciones similar al de nuestros experimentos, encontraron una asociación positiva entre RFI y RHP individuales en toros jóvenes alimentados con una dieta de alta calidad, aunque esta relación no fue evidente cuando los animales eran terneros. Estos resultados indicarían que el RHP puede ser un parámetro de evaluación de la eficiencia en animales en crecimiento, pero medidas de composición de la ganancia deben ser incluidas para aumentar su efectividad en esta etapa. Por otra parte, la RHP ha sido utilizada como una medida de eficiencia individual en ganado Holstein puro o cruza (Aharoni et al., 2006, Talmón et al., 2020). La estimación de RHP en la literatura es diversa, por lo que sería importante determinar la RHP utilizando un protocolo experimental adecuado y un procedimiento matemático similar a la estimación usada para el RFI.

1.2.2. Eficiencia alimenticia y reproducción

Relativamente hay pocos estudios que hayan intentado cuantificar el impacto de la selección por eficiencia alimentaria en el desempeño reproductivo. Crowley et al. (2011), trabajando con una base de datos (312.167 animales de 22.866 padres), reportaron correlaciones genéticas negativas entre medidas de eficiencia (*feed convertion ratio*, RFI) en los toros respecto a la edad al primer parto en las hembras ($r_g = -0{,}55 \pm 0{,}14$; $r_g = -0{,}29 \pm 0{,}14$, respectivamente), mientras que la correlación con intervalo interparto no difirió de cero.

Por otra parte, existen reportes contradictorios respecto a las tasas de preñez, parto y destete en relación con el RFI. Basarab et al. (2007), trabajando con animales de varias razas carniceras, y Morris et al. (2014) y Jones et al. (2016) con hembras Aberdeen Angus, no encontraron diferencias para ninguno de los tres parámetros entre los animales de alto y bajo RFI. Sin embargo, otros estudios reportan menores tasas de preñez (76,84 vs. 86,32 %, $P < 0{,}09$), parto (72,63 vs. 84,21 %, $P = 0{,}05$; Basarab et al., 2011) y destete (81,5 % vs. 93,3 %, $P < 0{,}05$) para las hembras de bajo RFI (Copping et al., 2016) cuando el RFI no tuvo en cuenta la composición corporal.

Más aún, numerosos trabajos han reportado que las hembras de bajo RFI tienden a parir entre 4 y 8 días después que las de alto RFI (Arthur et al., 2005, Basarab et al., 2007, Crowley et al., 2011, Donoghue et al., 2011, Hebart et al., 2016). El retraso en el parto registrado en las hembras de bajo RFI podría estar asociado a un retraso en la entrada en la pubertad (Shaffer et al., 2011) que, a su vez, tiene relación con el contenido graso de los animales (Diskin y Kenny, 2014). Los animales más magros han demostrado tener una entrada más tardía en la pubertad, lo que puede conllevar, además de retrasos en la fecha de primer parto y partos consecutivos, una reducción en la longevidad de la vaca, así como menores pesos al destete de los terneros (Friggens, 2003, Jones et al., 2016, Walmsley et al., 2016). En esta línea, Basarab et al. (2011) destacaron que muchos de los estudios en eficiencia en machos ocurren en torno al período donde los animales están alcanzando la madurez sexual. No tener en cuenta este hecho puede resultar en la tendencia a seleccionar animales de madurez sexual más tardía, hecho sumamente contraproducente si pensamos en la importancia de la edad de pubertad en las hembras. En un principio, estos autores no reportaron asociación entre RFI en vaquillonas con su edad de pubertad, peso a la pubertad o la tasa a la que esta se alcanzaba a pesar de que animales de bajo RFI alcanzaron la pubertad a una edad numéricamente mayor (353 vs. 347 días). Sin embargo, las diferencias fueron significativas cuando el espesor de grasa subcutánea fue incluido en el modelo utilizado para derivar el RFI, lo que corroboró una relación negativa (r = -0,16, P = 0,06) entre este y la edad a pubertad.

Finalmente, existe relativamente poco conocimiento sobre el impacto de la selección en eficiencia alimenticia sobre la producción de leche del rodeo de carne. Arthur et al. (2005), trabajando con vacas Aberdeen Angus seleccionadas divergentemente por 1,5 generaciones por RFI posdestete, no reportaron diferencias en la producción de leche 60 días posparto. Las variables de eficiencia evalúan la eficiencia en crecimiento o engorde de los animales; sin embargo, parecería importante la inclusión de medidas reproductivas en dichas evaluaciones. La relación entre eficiencia y reproducción será determinante para los sistemas criadores o donde la eficiencia productiva esté muy ligada al éxito reproductivo del rodeo.

1.3 HIPÓTESIS Y OBJETIVOS DEL TRABAJO

1.3.1 Hipótesis

Existe una asociación entre el RFI paterno y la RHP de vaquillonas evaluadas en sistemas pastoriles, especialmente durante la etapa de crecimiento, y, por lo tanto, el RHP puede ser utilizado para identificar animales eficientes en condiciones de pastoreo. A su vez, el RHP evaluado en vaquillonas de remplazo en sistemas pastoriles presentará una repetibilidad alta donde los animales más eficientes presentarán menores HP, sin diferencias en la respuesta productiva o reproductiva.

1.3.2. Objetivo general

Evaluar y cuantificar la eficiencia en el uso de la energía de vaquillonas Hereford en pastoreo mediante la cuantificación de la RHP y su relación con el RFI paterno.

1.3.3. Objetivos específicos

1. Cuantificar la relación entre la eficiencia paterna, medida a través del RFI, y la eficiencia individual, medida como RHP, de vaquillonas en pastoreo y la diferencia en la partición de la energía entre los grupos de alta y baja eficiencia, así como la performance reproductiva (experimento 1).
2. Determinar la repetibilidad de la RHP como medida de eficiencia de vaquillonas en pastoreo, evaluando las diferencias en consumo, HP y ER, las diferencias metabólicas (composición corporal y perfil metabólico-endócrino) y las diferencias en parámetros reproductivos entre los animales de alta y baja eficiencia (experimento 2).

1.4. ESTRUCTURA DE LA TESIS

La estructura central de la tesis consiste en dos artículos científicos. El primero titulado «Energy efficiency of grazing Hereford heifers classified by paternal residual feed intake» constituye el segundo capítulo de esta tesis y fue enviado a la revista *Journal of Animal Science* para su evaluación. Este tuvo como objetivo cuantificar la relación entre la eficiencia paterna, medida a través del RFI, y la eficiencia individual, medida como RHP, de vaquillonas en pastoreo y la diferencia en la partición de la energía entre los grupos de alta y baja eficiencia, así como la performance reproductiva (objetivo específico 1). Los resultados indicaron que las vaquillonas progenie (PHE**,** bajo RFI) fueron más eficientes (bajo RHP) en condiciones de pastoreo que las hijas de toros de baja eficiencia (PLE**,** alto RFI). A su vez, se observó una mayor ER sin diferencias en HP, EM o consumo de MS expresadas como unidades de $PV^{0,75}$, así como también una mayor eficiencia energética y alimentaria (mayor ER/EM y relación ganancia/consumo con una menor HP/GMD y RHP/GMD) en las hembras de PHE respecto a PLE, sugiriendo una reducción en los costos de energía de mantenimiento y/o un aumento en la eficiencia parcial de crecimiento. A su vez, las menores aunque significativas diferencias reproductivas detectadas en la primera estación reproductiva fueron a favor de PHE, aunque no se sostuvieron en el segundo parto.

El segundo artículo científico se titula «Energy efficiency and metabolic parameters of grazing Hereford heifers» y corresponde al tercer capítulo de la tesis. Se encuentra en proceso de revisión por parte de los coautores y será enviado a la revista *Journal of Animal Science.* El objetivo de este trabajo fue evaluar la repetibilidad de la RHP como medida de eficiencia de vaquillonas en pastoreo, las diferencias en el calor producido y la energía retenida entre los animales de alta y baja eficiencia y las diferencias metabólicas subyacentes a dichas diferencias, así como posibles diferencias en parámetros reproductivos (objetivo específico 2). Los resultados de este trabajo demostraron que la RHP presenta una alta repetibilidad en medidas consecutivas en pastoreo (74 % de las vaquillonas mantuvieron la categoría de eficiencia) aun bajo diferentes disponibilidades de alimento. Las vaquillonas eficientes mostraron menores HP, consumo de EM y MS, sin diferencias en ER, que sus pares ineficientes. Más aún, se estimaron menores requerimientos de ENM y EMM así como una mayor eficiencia parcial del uso de la EM consumida (*k*) para las vaquillonas más eficientes (bajo RHP; HH). Las hembras eficientes mostraron una actividad luteal más precoz, así como un menor intervalo servicio-concepción, a la vez que un parto más temprano en la estación que sus pares de baja eficiencia, probablemente asociado a un desarrollo más precoz del tejido adiposo.

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

2. ENERGY EFFICIENCY OF GRAZING HEREFORD HEIFERS CLASSIFIED BY PATERNAL RESIDUAL FEED INTAKE

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2.1. LAY SUMMARY

In recent years, residual feed intake (RFI) has become a widely used index to quantify feed efficiency. Nonetheless, although most of beef cattle systems in the world are pasture-based, RFI evaluation and research is usually performed in confinement conditions with little published information related to RFI for grazing beef cattle. In this context, residual heat production (RHP), estimated as the difference between actual heat production (HP) and the one expected based on maintenance and body weight (BW) gain requirements, appears as a way of identifying efficient animals without the need of measuring feed intake. In this study, we found that an association exists between paternal expected breeding value for RFI and RHP, increasing BW and gain, as well as retained body energy without affecting total heat production or metabolizable energy and dry matter intake, expressed as unit of metabolic body weight. We proved that the RFI measured in confinement could be useful to breeding efficient heifers in grazing conditions without permanent impacts in reproductive performance.

2.2. TEASER TEXT

Heifers´ energy efficiency on grazing conditions was positively correlated to paternal estimated breeding value for RFI with minor differences in reproductive performance, in favor of more efficient heifers, only during the first breeding and calving seasons. Thus, we demonstrated that RFI selection in confinement conditions is an effective tool in improving animal efficiency for growth in grazing conditions.

2.3. ABSTRACT

Residual feed intake (RFI) has become in a widely spread index of feed efficiency. Although most of beef cattle systems in the world are pasture-based, RFI evaluation and research is usually performed in confinement conditions. In this context, residual heat production (RHP) estimated as the difference between actual and expected heat production (HP), could allow to identify efficient animals. Thus, the aim of this work was to evaluate the relationship between paternal estimated breeding values (EBV) for RFI and beef heifer efficiency, measured as RHP, as well as its association with heifers' productive and reproductive performance on grazing conditions. Seventy-one 25 ± 0.8-month-old and seventy-four 24 ± 0.7-month-old Hereford heifers were managed as contemporary groups in spring 2019 and 2020, respectively. Heifers were sired by ten RFI evaluated bulls and classified into three groups according to the paternal EBV for RFI: five bulls of low RFI (high efficiency, pHE), two bulls of medium RFI (medium efficiency), and three bulls of high RFI (low efficiency, pLE). The experimental period lasted 70 days prior to their first insemination where HP was determined by the heart rate-O2 pulse technique. In addition, reproductive performances during the first and second breeding and calving seasons were recorded. Heifers' RHPs expressed as MJ/d and kJ/kg of $BW^{0.75}$ per d were positively correlated with paternal RFI EBVs ($P < 0.05$; $r > 0.60$). Moreover, BW and average daily gain (ADG) were greater ($P < 0.01$) for pHE than pLE heifers while, expressed as units of $BW^{0.75}$ per d, neither total HP nor metabolizable energy (ME) intake differed between groups, but pHE heifers had greater RE ($P < 0.01$) and lower RHP ($P < 0.05$) than pLE ones. Gross energy efficiency (RE/ME intake) was greater ($P < 0.001$) for pHE than pLE heifers while the HP/ADG and RHP/ADG were reduced ($P < 0.05$) and feed to gain ratio (ADG/DM intake) tended to be greater ($P = 0.07$) for pHE than pLE heifers. In addition, during the first breeding and calving seasons, small but significant ($P < 0.01$) differences in reproductive responses between groups suggested an earlier pregnancy in pHE heifers than the pLE group, differences that disappeared during the second breeding and calving seasons. Thus, heifers sired by high efficiency bulls measured as RFI were more efficient measured as RHP in grazing conditions, without significant differences in reproductive performance.

Keywords: beef cattle, rangelands, reproduction, residual heat production

2.4. LIST OF ABBREVIATIONS

ADF = Acid Detergent Fiber

ADG = Average Daily Gain

AI = Artificially Inseminated

BCS = Body Condition Score

BW = Body Weight

CL = Corpus Luteum

CP = Crude Protein

DM = Dry Matter

EBG = Empty Body Weight Gain

EBV = Estimated Breeding Value

EBW = Empty Body Weight

HP = Heat Production

HR = Heart Rate

ME= Metabolizable Energy

NDF = Neutral Detergent Fiber

OM = Organic matter

O2P = Oxygen Pulse

pHE = paternal High Efficiency group

pLE = paternal Low Efficiency group

RE = Retained Energy

RFI = Residual Feed Intake

RHP = Residual Heat Production

VO2 = Oxygen Consumption

2.5. INTRODUCTION

Feed and energy efficiency have been topics of extensive research in recent years as feed costs can account for up to 75% of total production cost in beef cattle systems (Nielsen et al., 2013). Moreover, most of feed consumed in cow-calf systems is associated to the supply of energy required for animal maintenance which represents 70 to 75% of the total annual energy requirements of the breeding cow (Ferrell and Jenkins, 1985). Over the last decade, residual feed intake (RFI), defined as the difference between actual feed intake and expected feed requirements for maintenance and body weight (BW) gain, has become in a widely spread index of feed efficiency (Berry, 2009; Moore et al., 2009). Genetic parameter estimates indicate that RFI is moderately heritable; a review by Berry and Crowley (2013) reported that RFI heritability varied between 0.07 and 0.62 with a mean of 0.33 ± 0.013, based on an extensive number of studies with growing animals. Moreover, a single generation of selection in favor of negative post-weaning RFI values improved efficiency of young bulls and heifers (Herd et al., 1997) and feedlot steers (Richardson et al., 1998).

Although most of beef cattle production is pasture-based, RFI is measured in confinement conditions with little published information related to RFI for grazing beef cattle, due to the difficulties of obtaining accurate individual records on feed intake. Wiley et al. (2016), working with bulls classified by RFI in confinement, reported that 47 ± 13% of animals maintained their ranking in grazing conditions and Trujillo et al. (2013) reported a moderate correlation (r = 0.50) between heifers' RFI measured consecutively in confinement and grazing conditions while Manafiazar et al. (2015) reported a lower correlation (r = 0.30) between RFI measured as growing heifers under dry-lot conditions and as pregnant cows in grazing conditions. In addition, although in confinement conditions RFI has been positively correlated with dry matter (DM) intake, with more efficient animals consuming less DM (Cantalapiedra-Hijar et al., 2018), herbage DM intake of previously ranked low or high RFI heifers or steers has not differed when evaluated under grazing conditions (Herd et al., 1998; Herd et al., 2002; Meyer et al., 2008; Lawrence et al., 2012; Oliveira et al., 2016). In contrast, other studies reported decreased herbage DM intake for low-ranked RFI heifers when evaluated consecutively (Trujillo et al., 2013) or as pregnant cows (Knight et al., 2015) at pasture. The scarce and contrasting results of RFI in grazing conditions are probably associated to the great difficulty of obtaining accurate measurements of DM intake in grazing animals (Lawrence et al., 2012)., as well as the characteristics of the grazing process (Lahart et al., 2020) which would also explain the variation detected between studies.

The heart rate-O2 pulse method (Brosh, 2007) could be of use to measure energy expenditure of free-range animals, thus, it could be used as an alternative to identify efficient animals in grazing conditions without the need to determine DM intake, as most of the metabolizable energy (ME) consumed is lost as heat. Thus, residual heat production (RHP) estimated as the difference between actual heat production (HP) and the one expected based on the animals' BW and level of production, could allow to identify efficient individuals: animals with lower RHP would be energetically more efficient since they would produce less heat than expected. Few studies have measured or estimated total HP in RFI-ranked animals and reported decreased HP, when expressed as a unit of $BW^{0.75}$, for low-RFI animals (Richardson et al., 2001; Basarab et al., 2003; Nkrumah et al., 2006; Chaves et al., 2015; Asher et al., 2018; Menezes et al., 2020). However, of the latter studies only two studies investigated RHP and its association with RFI (Richardson et al., 2001; Asher et al., 2018); Richardson et al. (2001) reported that the progeny of high RFI bulls had higher RHP per unit of gain in protein than the progeny of low RFI bulls, whereas Asher et al. (2018) found a positive association between individual RFI and RHP on young bulls fed a high-quality diet, although this relationship was not evident when animals were calves.

In this context, we hypothesized that there is an association between RFI and RHP, especially in the growing stages of the animals' development, and therefore RHP can be used to identify more efficient animals in grazing conditions. The objective of this work was to evaluate the relationship between paternal estimated breeding values (EBV) for RFI and beef heifer efficiency, measured as RHP, as well as the association with heifers' productive and reproductive performance on grazing conditions.

2.6. MATERIALS AND METHODS

The experiment was conducted during the springs of 2019 and 2020 at the Experimental Station of the Instituto Nacional de Investigación Agropecuaria, "Glencoe" (INIA; Paysandú, Uruguay; latitude: S 32º 00m 21s, longitude: W 57º 08m 01s). All experimental procedures were previously approved by INIA's Commission on Ethics in the Use of Experimental Animals (CNEA; 0009/11) and by the Animal Experimentation Committee of Universidad de la República (CHEA; 020300-001143-19). Temperature and relative humidity were recorded daily by a meteorological station located on the experimental site. During the first year of the measurement protocol (2019) the average daily temperature and relative humidity were 16.1°C and

77%, respectively. Whereas, in the second year (2020) the average daily temperature and relative humidity were 16.8°C and 71%, respectively.

2.6.1. Animals, experimental design, and measurement protocol

Seventy-one 25 ± 0.8-month-old and seventy-four 24 ± 0.7-month-old Hereford heifers were managed as contemporary groups in spring 2019 and 2020, respectively. At the beginning of the experimental periods, heifers weighted on average 262 ± 27 kg in 2019 and 272 ± 23 kg in 2020, with a mode of body condition score (BCS) of 4 in both years. Heifers were sired by ten RFI evaluated bulls and classified into three groups according to the paternal EBV for RFI (Ravagnolo et al., 2018; https://www.geneticabovina.com.uy): five bulls classified as low RFI (high efficiency, pHE; RFI EBV percentile ≤ 20; 62 heifers evaluated, n = 13 ± 5 per bull), two bulls classified as medium RFI (medium efficiency; 25 heifers evaluated, RFI EBV percentiles between 30 and 60; n= 13 ± 4 per bull), and three bulls classified as high RFI (low efficiency, pLE; RFI EBV percentiles □ 80; 58 heifers evaluated, n = 19 ± 7 per bull). Since they were born, heifers were managed as contemporary groups on grazing conditions (Campos grasslands; Allen et al., 2011) without supplementation and were weaned at 201 ± 33 days and 182 ± 40 kg without differences in BW corrected by age between groups.

Both years, the experimental period lasted 70 days prior to the first insemination when heifers grazed with an herbage mass of 2746 ± 1275 kg DM/ha; 10 ± 3 kg DM/kg BW of herbage allowance and 8 ± 3 cm of height, and a chemical composition of 86.5 ± 1.7% organic matter (OM), 7.73 ± 0.15% crude protein (CP), 70.72 ± 0.26% neutral detergent fiber (NDF), 43.79 ± 4.07% acid detergent fiber (ADF), and 7.93 ± 0.19 MJ/kg DM of ME. Herbage mass and height were recorded monthly by the comparative yield method (Haydock and Shaw, 1975) using ten reference quadrants (0.25 m2) corresponding to a 5-point calibration scale and 100 randomly selected quadrants for paddock sampling. Herbage samples of the 5-point scales were dried at 60 ºC and 1-mm ground to be composited according to the frequency of the scale point. Herbage pooled samples were analyzed for DM, CP, NDF and ADF and ash (AOAC, 2005; Van Soest et al., 1991).

During the experimental period, individual HP was assessed three times: at the first-third, during the mid-portion, and at the last-third of the experimental period, and the three measures were averaged for statistical analysis. Heifers were weighted (scale ID3000; True Test, Auckland, New Zealand) weekly after 12 h-fasting and BCS (scale 1 to 8; 1 = excessively thin and 8 = excessively fat; Vizcarra et al., 1986) was determined every 14-days by the same trained operator. At the end of the experimental period, heifers had their estrous cycles synchronized with two doses of 2 mL of prostaglandin (Glandinex, Laboratorio Universal Lab Ltda., Montevideo, Uruguay) ten days apart and were monitored for estrous by visual observation twice a day by two trained observers during 5 days after the last prostaglandin injection. All heifers showing estrus were artificially inseminated by two inseminators and thereafter, heifers were exposed to bulls 27 days after the first prostaglandin injection for a mating period that lasted 60 days. During the second mating period, primiparous cows were exposed to bulls at 73 ± 18 days of calving for 60 days.

2.6.2. Heat production measurements

Heat production was determined by HR-O2P technique (Brosh, 2007), as described by Talmón et al. (2020). This technique is based on the measurement of O2 consumption (VO2) as a mean to indirectly establish HP assuming 20.47 kJ/L O2 consumed (Nicol and Young, 1990). The VO2 of each animal is estimated through its HR and the O2 consumed per heartbeat (O2P) and it is calculated as VO2 = HR × O2P. The HR was recorded at 5 s intervals using Polar devices (Polar Electro Oy, Kempele, Finland), with a model H10 HR transmitter and a RCX3 data logger watch model for 4 to 5 continuous days. As O2P is the ratio between HR and O2, short-term (10 min) measures of both variables were conducted simultaneously. Oxygen consumption was measured using a face mask open-circuit respiratory system (Fedak et al., 1981), and a paramagnetic O2 analyzer model Servopro 1440 (Servomex, Crowborough, East Sussex, UK) to determine O2 concentration. To determine VO2 under standard conditions, relative humidity and temperature within the system were recorded by HygroClip S electronic sensor (Rotronic AG, Basserdorf, Switzerland), additionally, the air flux into the system was calculated by differential pressure measurement with a differential pressure transducer (Model 267; Setra; Boxborough; USA). The accuracy of the system was checked gravimetrically by N2 injection (N2 recovery) into the facemask (McLean and Tobin, 1990). The N2 recovery was 97 ± 3 and 99 ± 5 for 2019 and 2020, respectively. Heat production was calculated as specific HP (kJ/BW $^{0.75}$/d) = HR (beats/min) × O2P (mL O2/kg BW $^{0.75}$/beat) × 20.47 (kJ/mL O2) × 60 min/h × 24 h/d and daily HP (MJ/animal/d) = specific HP (kJ/BW $^{0.75}$/d) × BW $^{0.75}$ /1000.

2.6.3. Reproductive traits

Ovarian activity or pregnancy were determined by transrectal ultrasonographic examinations, using a real-time, Agroscan ALR 575 scanner with a 5/7.5 MHz - 60 mm transducer (ECM, Noveko International Inc., Quebec, Canada) before the AI synchronization protocol to record presence of corpus luteum (CL) and maximum follicle diameter, at day 30 after AI to record presence of CL or pregnancy (presence of an amniotic vesicle with an embryo with the heartbeat) and at 45 days after bull removal to determine total pregnancy and fetal age. Cows with follicles > 8 mm in without corpus luteum were considered in superficial anestrus and those with follicles ≤ 8 mm in diameter without corpus luteum were considered in deep anestrus anestrus according to Griffin and Ginther (1992) criteria (Clariget et al., 2016). The first service to conception interval was calculated as date of first conception minus date of service. Calving day was calculated using the date of calving of the first heifer of the season as reference (day 1). Calving to conception interval was determined using the fetal age determined by ultrasound at the end heifers' second breeding season minus date of first calving.

2.6.4. Calculations and statistical analysis

A linear regression of BW on day of study was fitted to each heifers' records to estimate changes in BW throughout the experimental period, this resulting in each cow having a model ($P < 0.05$, $r2 > 0.9$) that represented the BW evolution during the measurements. Average daily gain (ADG) was estimated as the slope of each regression. Predicted HP was calculated as the slope and intercept of a multiple linear regression of HP dependency on heifers' mid period $BW^{0.75}$ and ADG, using individual ADG as a proxy to individual retained energy (RE; Asher et al., 2018) and the RHP was calculated as the difference between measured and predicted HP. Retained energy was estimated using the empty body weight (EBW) and empty body weight gain (EBG) as: RE (MJ/d) = 0.266 × EBW $^{0.75}$ × EBG 1.097 according to NASEM (2016). Metabolizable energy intake was calculated as the sum of HP + RE and DM intake was estimated based on ME intake and herbage ME concentration (MJ/kgDM). Herbage ME concentration was estimated based on DM in vitro digestibility (DMIVD) of the forage as: DMIVD = 88.9 - (%FDA x 0.779) (NASEM, 2016).

Heart rate and O2P data were processed using R software to assess the quality of data (R Core Team, Viena, Austria) and later analyzed using SAS software (SAS University Edition, SAS Institute Inc., Cary, NC, USA). Pearson correlation and regression coefficients were estimated between heifers' RHP and paternal RFI EBV, as well as between paternal RFI EBV and productive and energy efficiency traits.

In addition, productive, reproductive and efficiency variables by paternal RFI EBV group (pHE *vs*. pLE groups) were estimated; heifers in the medium RFI EBV group were not considered in this analysis due to the smaller number of animals when compared with the other two groups. Productive and efficiency variables were analyzed with a mixed model using repeated measurements by the MIXED procedure where the model included paternal RFI EBV group and year as fixed effects and heifer within sire as random effect.

Reproductive traits were analyzed using the GLIMMIX procedure using binomial or Poisson distributions depending on the distribution of the variable. Cows that were not inseminated, were sold, died, or remained non-pregnant were censored on the respective dates during the analyses. Results are presented as least square means ± pooled standard errors and least square means were considered to differ when $P \leq 0.05$, and trends were identified when $0.05 < P < 0.10$.

2.7. RESULTS

2.7.1. Associations between paternal EBV for RFI and heifer RHP

Heifers' RHP, both expressed as MJ/d and kJ/kg of $BW^{0.75}$ per d, were positively correlated with paternal EBV for RFI ($P < 0.05$; $r > 0.60$; Figure 1A and 1B). Neither heifer total HP (MJ/d) or ADG (as g/d or g/kg$BW^{0.75}$ per d) nor estimated ME intake (as MJ/d or kJ/kg$BW^{0.75}$ per d) or DM intake (as kg/d or g/$BW^{0.75}$ per d) were correlated with paternal EBV for RFI ($P > 0.05$). However, when expressed as unit of kg$BW^{0.75}$, HP showed a positive correlation with paternal EBV for RFI ($r = 0.77$; $P < 0.05$; Figure 1C).

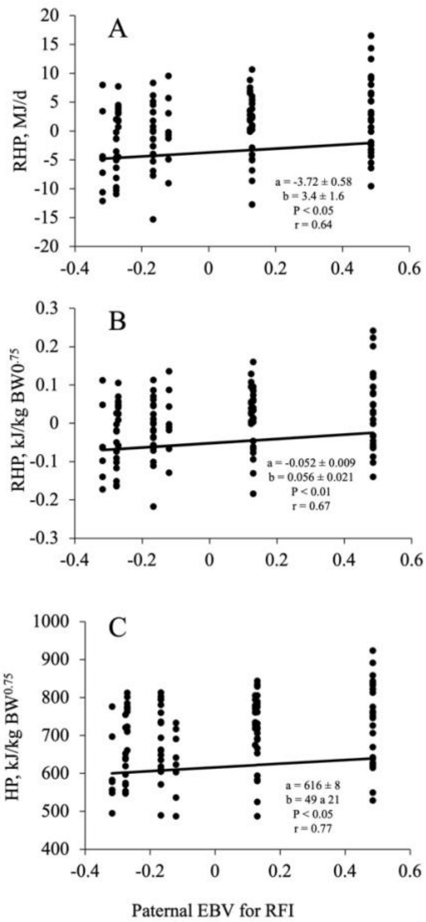

Figure 1. Relationship between heifers' residual heat production (RHP) expressed in MJ/animal/d (**A**) or kJ/$BW^{0.75}$ (**B**) and heat production in kJ/$BW^{0.75}$ (**C**) with paternal estimated breeding values (EBV) for residual feed intake (RFI).

2.7.2. Heifer body weight and gain, energy partitioning and efficiency for high and low paternal RFI groups

Body weight and ADG were greater ($P < 0.01$) for pHE than pLE heifers, while BCS mode was similar between groups (Table 1). Average HR was lower ($P=0.01$) while O2P tended to be greater ($P=0.06$) for pHE than pLE heifers (Table 1). Although HR varied along the day (data not shown), individual average HR did not vary across evaluated periods, with an average coefficient of variation (CV) of individual records of 2.6% in 2019 and 3.3% in 2020. Similarly, average CV of the difference between the two measures of individual O2P was 5.0% in 2019 and 5.2% in 2020, while Pearson correlation coefficients between the two individual O2P measures were 0.61 and 0.59 in 2019 and 2020, respectively.

Total HP, RE and ME intake (MJ/d) were greater ($P < 0.05$) in pHE than pLE heifers while RHP was lower ($P = 0.05$) in pHE than pLE group (Table 1). However, when expressed as units of $BW^{0.75}$ per d, total HP and ME intake did not differ ($P > 0.15$) between groups, but pHE heifers had higher RE ($P < 0.01$) and lower RHP ($P < 0.05$) than pLE ones. Estimated DM intake (kg/d) was greater ($P < 0.01$) for pHE than pLE heifers but no differences between groups were found on DM intake when expressed as percentage of $BW^{0.75}$ (Table 1).

Heifers in the pHE group had higher gross energy efficiency (RE/ME intake) than those in the pLE group ($P < 0.001$), while the ratios HP/ADG and RHP/ADG were lower ($P < 0.05$) and the gain to feed ratio (G:F; ADG/DM intake) tended to be greater ($P = 0.07$) in the pHE group than pLE heifers (Table 1).

Table 1. Body weight and average daily gain, and energy partitioning and efficiency of heifers sired by high and low RFI EBV bulls (pHE *vs*. pLE)

	Paternal RFI group			
	pHE	pLE	SEM	P-value
Initial body weight, kg	285	262	4	<0.001
Mid period body weight, kg	295	274	4	<0.001
Average daily gain (ADG), g/d	738	673	21	<0.01
Heart rate, beat/min	82	85	1	0.01
O_2 pulse, mL $O_2/BW^{0.75}$/beat	0.282	0.274	0.008	0.06
Energy partitioning, MJ/d				
Metabolizable energy intake (MEI)	61.6	58.3	1.0	<0.01
Retained energy (RE)	13.4	11.6	0.5	<0.001
Heat production (HP)	48.4	46.8	0.8	<0.05
Residual heat production (RHP)	-0.95	0.51	0.73	0.05
Energy partitioning, kJ/kg $BW^{0.75}$ per d				
Metabolizable energy intake (MEI)	868	862	13	0.67
Retained energy (RE)	191	172	6	<0.01
Heat production (HP)	678	693	10	0.15
Residual heat production (RHP)	-14	7	11	<0.05
DM intake (DMI), kg/d	7.16	6.78	0.12	<0.01
DM intake (DMI), g/$BW^{0.75}$ per d	109.3	108.6	1.6	0.67
Energy and feed efficiency				
RE/MEI	220	199	6	<0.001
Gain to feed ratio (ADG/DMI)	95	92	2	0.07
HP/ADG	65	70	2	<0.05
RHP/ADG	-26	8	15	<0.05

2.7.3. Heifer reproductive responses for high and low paternal RFI groups

There were more inseminated heifers from the pHE than pLE group ($P<0.01$). There were no differences between groups either in the percentage of cycling heifers before the first service (P = 0.16) or in the percentage of cow in superficial or deep anestrous (P = 0.72), but maximum follicle diameter was larger (P < 0.05) for pHE than pLE heifers (Table 2). Percentage of anestrous cows at day 30 of the first breeding season was lower (P < 0.05) for pHE than pLE heifers but not differences (P > 0.50) were detected between groups for total pregnancy percentage or service to conception interval. The pHE heifers calved earlier (P=0.05) in the season than pLE heifers (Table 2). No differences (P = 0.53) were observed on the percentage of cows leaving the breeding herd after the first season (5 *vs*. 10%, 3/62 *vs*. 6/58 for pHE *vs*. pLE, respectively). During the second breeding and calving seasons, neither pregnancy, cycling nor anestrous percentages at day 30 of breeding season nor total pregnancy percentage or first calving-conception interval differed (P > 0.36) between paternal RFI groups.

Table 2. Ovarian activity and reproductive performance in first and second breeding and calving seasons of heifers sired by high and low RFI EBV bull (pHE *vs*. pLE)

	Paternal RFI group		SEM	P-value
	pHE	pLE		
Ovarian activity previous AI				
Cycling, % (n/n)	34 (21/62)	22 (13/58)	-	0.16
Anestrous, % (n/n)	66 (41/62)	78 (45/58)	-	0.16
Superficial anestrus, % (n/n)	44 (27/62)	52 (30/58)	-	0.55
Maximum follicle diameter, mm	8.6	7.8	0.4	< 0.05
Maximum follicle diameter anestrous cows, mm	8.0	7.9	0.5	0.79
First breeding and calving seasons				
Inseminated heifers, % (n/n)	79 (49/62)	41 (24/58)	-	<0.01
Pregnant day 30, % (n/n)	42 (26/62)	38 (22/58)	-	0.81
Cycling day 30, % (n/n)	55 (34/62)	48 (28/58)	-	0.48
Anestrus day 30, % (n/n)	3 (2/62)	14 (8/58)	-	<0.05
Pregnancy, % (n/n)	97 (60/62)	95 (55/58)	-	0.67
Service to conception interval, d	16.7	16.9	2.1	0.51
Calving day, d	25	33	3	0.05
Second breeding and calving seasons				
Discarded after first breeding season, %	5 (3/62)	10 (6/58)	-	0.53
Pregnant day 30, % (n/n)	5 (3/59)	10 (5/52)	-	0.59
Cycling day 30, % (n/n)	44 (26/59)	48 (25/52)	-	0.36
Anestrus day 30, % (n/n)	51 (30/59)	42 (22/52)	-	0.57
Pregnancy, % (n/n)	88 (52/59)	83 (45/54)	-	0.58
Calving to conception interval, d	104.8	101.4	5.1	0.61

2.8. DISCUSSION

Our results demonstrated that heifers´ RHP measured in grazing conditions was positively correlated to paternal EBV for RFI, being feed and energy efficiency greater for pHE than pLE heifers as they had greater BW, ADG and RE without differences neither in total HP, nor in estimated DM or ME intake by unit of $BW^{0.75}$. In addition, we did not observe any major effect of paternal RFI EBV on reproductive performance during the two first breeding and calving seasons. Thus, selection by RFI measured in confinement conditions could be an effective selection criterion for improving animal efficiency in grazing conditions.

Indeed, it has been reported that feed efficiency measured as RFI is moderately heritable ($h^2 = 0.33 \pm 0.013$; Berry and Crowley 2013) and improved feed efficiency implies reductions of 3.8% to 5% of feedlot DM intake in the progeny of low *vs*. high RFI bulls (Herd et al., 1997, Richardson et al., 1998). Although genotype-by-environment interactions for RFI in growing beef cattle have been reported (Kenny et al., 2018), we showed that a single generation selection for RFI improve efficiency of grazing heifers, measured as RHP. Moreover, using the variance and covariance effects of the model estimated heritability of RHP was 0.33, in agreement with RFI heritability.

Although decreased DM intake has been associated with animals with lower RFI (high efficiency) in confined (Cantalapiedra-Hijar et al., 2018) and grazing (Trujillo et al., 2013) conditions, no correlation between paternal RFI EBV and estimated DM or ME intake was found in the present study. Moreover, when corrected by BW, neither DM nor ME intake per unit of $BW^{0.75}$ differed between pHE and pLE heifers. In agreement with our results, previous research indicated that in grazing conditions, a reduction of herbage DM intake in low-RFI ranked animals has not always been found (Meyer et al. 2008; Lawrence et al., 2012; Oliveira et al., 2016). Consistently, Bormann et al. (2010) reported no differences in DM intake of a high-roughage complete diet, offered ad-libitum for heifers sired by high and low RFI bulls. The difficulty of obtaining accurate individual measures of DM intake in grazing conditions has been noted as one of the main reasons of not finding differences in DM intake between RFI groups (Lawrence et al., 2012; Oliveira et al., 2016). In the present study, we avoided that difficulty as we determined animal efficiency based on HP and not on DM intake.

However, daily estimated DM and ME intakes (kg or MJ/d) were greater for pHE than pLE heifers as, pHE heifers had higher initial and final BW, ADG and more RE than pLE heifers, although they did not differ in weaning BW and were managed as a contemporary group not only during the experiments but also since birth. Feed intake is regulated by a combination of physical and metabolic mechanisms and is a function of meal size and frequency (Fitzsimons et al., 2017). Therefore, feeding behavior could contribute to explain the underlying variation in feed efficiency of beef cattle (Kelly et al., 2010; Fitzsimons et al., 2017, Cantalapiedra-Hijar et al., 2018). Kenny et al. (2018) conducted a meta-analysis of studies with growing beef cattle offered energy-dense high-concentrate diets and found that high-RFI cattle spent 0.12 more time eating than their low-RFI contemporaries with a 0.17 times higher DM intake which implied that efficient animals had a faster eating rate. Moreover, the space and time variation in nutrient supply that occurs under grazing conditions, make ingestive-digestive behaviors significant sources of inter-animal variation, indicating that the differential energy expenditures associated with the harvesting and defoliation processes must also be considered (Gregorini et al., 2008). It has been reported that efficient beef cows explore approximately 0.5 km/d further on rangelands than inefficient ones (Knight et al., 2015; Sprinkle et al., 2020). Knight et al. (2015) also found differences in the areas where high and low RFI cows grazed and hypothesized that efficient cattle could search out for higher quality forage to meet their nutritional needs, which may be located in different areas depending on the pasture. Thus, differences in the spatial exploration would be possibly an adaptation mechanism to grazing conditions, that in more restrictive nutritional situations as rangeland grazing, more efficient animals are able to make a better use of forage available and eventually, consume more forage or of better quality.

In agreement with our results, Herd et al. (1998) reported that low RFI grazing cows were 7% heavier that high RFI ones without differences in pasture DM intake. Also, Jones et al. (2011) found that low RFI cows were heavier while grazing both high- and low-quality pastures without differences in DM intake. Additionally, Sprinkle et al. (2020) working with high and low RFI cows grazing a low-quality forage reported that both groups had lower BCS, but the reductions in BCS and BW were greater and more variable for high than low RFI cows. This suggests that the greater reductions of BCS of inefficient cattle was due to greater maintenance requirements, and in combination with the lower losses in BW of more efficient cows could indicate an ability for adapting to poorer forage quality (Sprinkle et al., 2020). Therefore, the ability to adapt their ingestive-digestive behaviors and decreased maintenance energy requirements may explain differences in production responses, as well as in feed and energy efficiency between paternal RFI heifers' groups in rangelands when forage diminished in quantity and quality.

Our results showed a greater partitioning of consumed ME towards body reserves, indicated by RE, with a reduction in HP. Even though total HP (kJ/BW$^{0.75}$) did not differ between pHE and pLE heifers, paternal RFI EBV was positively correlated with HP expressed by unit BW$^{0.75}$. Few studies evaluated HP in high and low efficiency animals, and in agreement with our results, reported that HP (kJ/BW$^{0.75}$) showed a positive correlation with RFI (Basarab et al., 2003, Asher et al., 2018) or that it was increased between 8 and 21 % for high (low-efficient) than low-RFI animals (Nkurmah et al., 2006; Paddock, 2010; Menezes et al., 2020), suggesting decreased energy expenditure for maintenance in low than high RFI cattle. Total HP is the sum of HP for maintenance (HPm) and HP for production (HPp; Miron et al., 2008) and in the present study, total HP did not differ between paternal RFI groups but RE was 11% greater for pHE than pLE heifers, when corrected per unit of BW$^{0.75}$, indicating that greater HPp and lower HPm in efficient heifers could be expected. Nkrumah et al. (2006) and Chaves et al (20115) reported greater ME intake and RE with lower or similar HP while Menezes et al. (2020) and Asher et al (2018) found decreased ME intake and HP with similar or lower RE for high *vs*. low efficiency animals. Differences in techniques used to determine DM (ME) intake, RE, and total HP, as well as in diets, conditions, and type of animals among experiments could explain the discrepancies between studies. Nonetheless, relationships between ME intake, RE and total HP would indicate decreased HPm in more efficient animals in the previous studies. In agreement with these results, Menezes et al. (2020) reported reduced energy requirements for basal metabolism and ME for maintenance in high *vs*. low efficiency steers, without differences in the conversion efficiency of consumed ME (k).

The lower maintenance energy explains, at least partially, the increased efficiency observed. In the present study not only RE/ME intake but also G:F were, or tended to be, greater in pHE *vs*. pLE heifers. Other authors reported similar associations between RFI and RE/ME intake or G:F in steers or bulls in positive energy balance (Asher et al., 2018; Nkrumah et al., 2004). Moreover, our results show that HP/ADG and RHP/ADG were lower in pHE heifers compared to the pLE, suggesting that the partial efficiency for growth above maintenance could be also increased in pHE heifers (Cantalapiedra-Hijar et al., 2018). Asher et al. (2018) reported a negative correlation between HP/ME intake and RFI but similarly to our results, found that RHP was positively correlated ($r = 0.33$, $P = 10$) with RFI or was lower in efficient than in inefficient calves (~300 – 570 kg) in positive energy balance. In addition, Richardson et al. (2001) reported a positive correlation ($r = 0.46$, $P < 0.05$) between RHP/kg of protein gain and paternal RFI EBV and 35% less RHP/kg of protein gain in low than high RFI steers, while no differences in RHP per kg of fat gain between groups were observed. Similarly, in the present work, it could be expected that body gain tissue had a greater protein to fat ratio than later in life, given the age of heifers evaluated during the growth phase. Although not consistent, several studies have associated RFI with changes in body composition, with small but significant increases in carcass leanness and reductions in carcass fatness (Richardson et al., 2001; Basarab et al., 2011; Lancaster et al., 2009). Therefore, it could be suggested that low RFI animals were more efficient in depositing body protein and/or in maintaining it when deposited, probably associated to decreased protein turnover, which is an energetically expensive process (Cantalapiedra-Hijar et al., 2018).

There are relatively few studies that have examined the association between RFI and fertility or maternal productivity. Previous research indicated that pregnancy, calving or weaning rate were not associated with RFI, or decreased in low *vs*. high RFI beef cows (Kenny et al., 2018). Later calving dates were reported in heifers with low RFI (high efficiency), associated to a later puberty and lower levels of body fat (Arthur et al., 2005; Basarab et al., 2011; Shaffer et al., 2011). In agreement with these results, we did not find any major effect in the reproductive performance of pHE *vs*. pLE heifers. However, pHE (high efficiency) group had higher percentage of inseminated heifers and lower percentage of heifers in anestrus 30 d after the start of breeding season in the first breeding and calving season, in contrast with previous reports (Shaffer et al., 2011, Kenny et al., 2018). Efficient heifers (pHE) also had an earlier calving date, suggesting an earlier pregnancy during the first breeding season than pLE heifers. This agrees with Knight et al. (2015) who found that high efficiency cows got pregnant earlier and, consequently, bred 16 d earlier than low efficiency ones. The observed differences in the first breeding and calving seasons, in our study, could be attributed to BW differences between groups that could imply different development and a latter puberty in the pLE heifers. These differences between pHE and pLE heifers disappeared during the second breeding and calving seasons, which could indicate that as heifers finished their development, the impact in the reproductive performance was minimized.

2.9. CONCLUSIONS

Heifers sired by high efficiency bulls, measured as RFI, were more efficient in grazing conditions measured as RHP. Greater RE without differences in HP, ME or DM intake expressed as a unit of $BW^{0.75}$ as well as feed and energy efficiency (increased RE/ME and G:F and decreased HP/ADG and RHP/ADG) were observed for pHE than pLE heifers, suggesting a reduction in maintenance energy cost and/or an increase of the partial efficiency for growth. The slight differences observed in reproductive performance during the first breeding and calving seasons were in favor of pHE heifers but differences between paternal RFI groups were not maintained thereafter during the second breeding and calving seasons.

2.10. DISCLOSURE

The authors declare no conflicts of interest.

2.11. LITERATURE CITED

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3. ENERGY EFFICIENCY AND METABOLIC PARAMETERS OF GRAZING HEREFORD HEIFERS

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3.1. ABSTRACT

Over the years, feed and energy efficiency in cattle has gained international interest, especially since its improvement has a significant impact not only on the profits but also on the environmental footprint of beef production where residual feed intake (RFI) has become the preferred index to determine feed efficiency in beef cattle. Nevertheless, the biggest downside of RFI is that its measurement requires to accurately determine individual feed intake, which leads to the need to carry out RFI trials in confinement conditions. In this context, residual heat production (RHP), defined as the difference between observed and predicted heat production, presents as an alternative to determine efficiency in grazing conditions as it is independent from feed intake. The aim of this work was to evaluate the repeatability of RHP and study its relationship with metabolic and endocrine as well as reproductive variables. Seventy-four Hereford heifers were used and at the beginning of the experimental period; heifers were 18 ± 0.7-month-old and weighted on average 278 ± 26 kg. Heat production (HP) was determined at the beginning (March to May; fall) and at the end (September to November; spring) of the experiment using the heart rate (HR)-O2 pulse (O2P) technique (Brosh, 2007) to classify heifers according with the residual heat production (RHP). Efficient heifers showed lower HP ($P < 0.01$), ME ($P < 0.01$) and DM intake ($P < 0.01$) without differences in RE (only in spring). During fall, average daily gain (ADG) was not included in the estimated HP model; therefore, although as in RFI, RHP should be independent of BW and ADG, a trend for greater ADG and RE was found for efficient heifers when compared with inefficient ones. Decreased maintenance requirements (NEm, and MEm) as well as higher partial efficiency of use of consumed ME (k) were estimated for more efficient heifers (low RHP; HH) while efficient heifers showed an earlier luteal phase and a shorter service-conception interval and calved earlier in the season, probably associated to an earlier development of fat tissue. Excluding glucose, no mayor differences were found in the plasma metabolites between groups, although during fall, high efficiency animals showed positive correlations with cholesterol and negative ones with NEFA plasma concentrations.

3.2. LIST OF ABBREVIATIONS

ADF = acid detergent fiber

ADG = average daily gain

BW = body weight

CP = crude protein

DM = dry matter

EBG = empty body weight gain

EBW = empty body weight

EG = efficiency group

HE = high efficiency

HH = yearly high efficiency group

HP = heat production

HR = heart Rate

LE = low efficiency

LL= yearly low efficiency group

ME = metabolizable energy

NDF = neutral detergent fiber

OM = organic matter

O2P = oxygen pulse

RE = retained energy

RFI = residual feed Intake

RHP = residual heat production

VO2 = oxygen consumption

3.3 INTRODUCTION

Over the years, feed and energy efficiency in cattle has gained international interest, especially since its improvement has a significant impact not only on the profits but also on the environmental footprint of beef production. In this sense, residual feed intake (RFI) has become the preferred index to determine feed efficiency in beef cattle (Berry and Crowley, 2012). This index has been indicated as moderately heritable (h2 = 0.33 ± 0.013; Berry and Crowley, 2012) and repeatable for steer and heifers fed the same diet (r = 0.42-0.50; Durunna et al., 2011; Durunna et al., 2012) or different diets (r = 0.62; Kelly et al., 2010). In addition, RFI has been described as a complex multifaceted trait, under the control of many biological processes among which, feeding behavior, feed digestibility, tissue metabolism, and heat production (HP) have been reported as the main ones (Kenny et al., 2018; Cantalapiedra-Hijar et al., 2018). Indeed, decreased total HP associated with reduced energy expenditure for maintenance has been related with low-RFI (more efficient) bulls (Menezes et al., 2020) and decreased protein turnover, an energetically expensive process, has been suggested to explain not only the reduction in the maintenance cost but also a greater partial efficiency for growth above maintenance (Cantalapiedra-Hijar et al., 2018). Indeed, although not always consistent, plasma urea has been reported to be reduced for low-RFI animals, suggesting decreased protein degradation (Richardson et al., 2004; Kelly et al., 2010; Jorge-Smeding et al., 2021) maybe stimulated by an increased insulin sensitivity associated to leanness of more efficient animals (Richardson et al., 2004). Moreover, low RFI values have been associated with leaner animals (Richardson et al., 2001), especially when fat was not considered as a covariable in the determination of the index (Basarab et al., 2011).

Nevertheless, the biggest downside of RFI is that its measurement requires to accurately determine individual feed intake which leads to the need to carry out RFI trials in confinement conditions although most of the worldwide beef production is conducted on grazing systems. In this context, residual heat production (RHP) defined as the difference between observed and predicted heat production, presents as an alternative to determine efficiency in grazing conditions as it is independent from feed intake. Previously, we have demonstrated a positive association between paternal RFI and individual RHP on beef replacement heifers on grazing conditions (Marín et al., 2022), which would indicate RHP as a useful index to determine energy efficiency in grazing animals. Nonetheless, the repeatability of RHP as well as its relationships with body composition and metabolic parameters have not been studied. We hypothesized that RHP will have a moderate to high repeatability and that efficient heifers will produce less heat without differences in productive or reproductive responses. Thus, the objective of this work was to evaluate the repeatability of RHP for replacement heifers in grazing conditions and to identify productive, metabolic, and reproductive differences between heifers differing in RHP.

3.4 MATERIALS AND METHODS

The experiment was carried out during the year 2020 at the Experimental Station of the Instituto Nacional de Investigación Agropecuaria, "Glencoe" (INIA; Paysandú, Uruguay; latitude: S 32º 00 m 21 s, longitude: W 57º 08 m 01 s). All experimental procedures were previously approved by INIA's Commission on Ethics in the Use of Experimental Animals (CNEA; 0009/11) and by the Animal Experimentation Committee of Universidad de la República (CHEA; 020300-001143-19).

The experiment was carried out on grazing conditions (Campos grasslands; Allen et al., 2011) without supplementation and all animals grazed the same native pasture that averaged 3246 ± 385 kg DM/ha of herbage mass and 10 ± 4 kg DM/kg BW of herbage allowance with 9 ± 4 cm of height and a chemical composition of 86.3 ±1.4 % organic matter (OM), 6.3 ±1.9 % crude protein (CP), 71.4 ±1.3 % neutral detergent fiber (NDF), 47.1 ±0.6 % acid detergent fiber (ADF), and 7.7 ±0.1 MJ/kg DM of metabolizable energy (ME). Temperature and relative humidity were recorded daily by a meteorological station located on the experimental site. During fall, the average daily temperature and relative humidity were 16.3 °C and 74 %, respectively. Whereas, in spring, the average daily temperature and relative humidity were 16.8 °C and 71 %, respectively.

3.4.1 Animals and experimental design

Seventy-four Hereford heifers born during the year 2018 managed as a contemporary group since birth were used. Heifers were weaned at 227 ± 22 days and 213 ± 30 kg in March 2020. At the beginning of the experimental period, heifers were

18 ± 0.7-month-old and weighted, on average, 278 ± 26 kg with a mode of body condition score (BCS) of 4.

Heat production (HP) was determined at the beginning (March to May; fall) and at the end (September to November; spring) of the experiment using the heart rate (HR)-O2 pulse (O2P) technique (Brosh, 2007) to classify heifers according with the residual heat production (RHP). Predicted HP was calculated as the slope and intercept of a multiple linear regression of HP dependency on heifers' mid period $BW^{0.75}$, average daily gain (ADG) and rump fat thickness (in spring) or only in mid period $BW^{0.75}$ (in fall), using individual ADG, estimated as the slope of the linear regression of individual BW and day of study, as a proxy to individual retained energy (RE; Asher et al., 2018) and the RHP was calculated as the difference between measured and predicted HP. Thus, each season, two RHP groups were formed: the high efficiency (HE) one with negative RHP and the low efficiency (LE) with positive RHP. Thus, heifers were classified in four groups (efficiency groups; EG): heifers that had negative RHP both seasons (HH), heifers that had positive RHP both seasons (LL), heifers that had negative RHP in fall but had a positive one in spring (HL) and heifers that had positive RHP in fall, but it became negative in spring (LH).

3.4.2 Heat production measurements

The HR-O2P technique is based on the measurement of O2 consumption (VO2) as a mean to indirectly establish HP assuming 20.47 kJ/L O2 consumed (Nicol and Young, 1990) where the VO2 of each animal is estimated through its HR and the O2 consumed per heartbeat (O2P). At each season (fall and spring), the HP measurement period lasted 70 days during which individual HR was recorded at 5 s intervals for 4 to 5 continuous days using Polar devices (Polar Electro Oy, Kempele, Finland) three times: at the first-third, during the mid-portion and at the last-third of the measurement period and averaged for statistical analysis. Additionally, as O2P is the ratio between HR and O2, short-term (10 min) measures of both variables were conducted simultaneously twice per season. Oxygen consumption was measured using a face mask open-circuit respiratory system (Fedak et al., 1981) and a paramagnetic O2 analyzer model Servopro 1440 (Servomex, Crowborough, East Sussex, UK) to determine O2 concentration. To determine VO2 under standard conditions, relative humidity and temperature within the system were recorded by HygroClip S electronic sensor (Rotronic AG, Basserdorf, Switzerland); additionally, the air flux into the system was calculated by differential pressure measurement with a differential pressure transducer (Model 267; Setra; Boxborough; USA). The accuracy of the system was checked gravimetrically by N2 injection (N2 recovery) into the facemask (McLean and Tobin, 1990). The N2 recovery was 98 ± 2 and 99 ± 5 for autumn and spring, respectively. Heat production was calculated using the following equations (Eq. 1; Eq. 2):

$$\text{Specific HP (kJ/BW}^{0.75}\text{/d)} = \text{HR (beats/min)} \times \text{O2P (mL O2/kg BW}^{0.75}\text{/beat)} \times 20.47 \text{ (kJ/mL O2)} \times 60 \text{ min/h} \times 24 \text{ h/d} \quad (1)$$

$$\text{Daily HP (MJ/animal/d)} = \text{specific HP (kJ/BW}^{0.75}\text{/d)} \times \text{BW}^{0.75} /1000 \quad (2)$$

3.4.3 Data and sampling collection

Heifers were weighted (scale ID3000; True Test, Auckland, New Zealand) from 18 to 26 month of age (March to November); weekly during the experimental periods of fall and spring, and monthly during winter (June to August). Additionally, at 20, 23, and 26 months of age (fall, winter and spring, respectively), rib eye area (area of the longissimus dorsi muscle measured in cm2), rump fat thickness a (subcutaneous rump fat depth over the gluteus muscle on the rump, measured in mm) and back fat thickness (subcutaneous fat over the longissimus dorsi muscle between the 12th and 13th rib, measured in mm) were determined by ultrasonography by the same operator using a real-time, B mode scanner with a linear array transducer of 3.5 MHz (Aloka SSD 500 Echo camera, Over-seas Monitor Corp. Ltd., Richmond, BC) and images were analyzed using the software Biosofts (Bio-tronics Inc., Ames, Iowa, USA).

Two blood samples were collected monthly, 11 ± 2 days apart, by coccygeal venipuncture into tubes with lithium heparin (BD Vacutainer tubes; Becton Dickinson, Franklin Lakes, NJ, USA), refrigerated, centrifugated (2000 g, 15 min) within 3 h after collection and plasma stored at -20 ºC until analyses were performed.

3.4.4 Metabolite and hormone analyses

Plasma glucose, non-esterified fatty acids (NEFA), β-hydroxybutyrate (BHB), cholesterol and urea concentrations were determined monthly by spectrophotometry using a 96-well microplate reader (Multiskan FC, Thermo Fisher Scientific Inc., MA, USA) and commercial kits: glucose, cholesterol and urea concentrations were determined with kits from Biosystems S.A. (Costa Brava, Barcelona, Spain), while NEFA and BHB concentrations were determined with kits by Randox Laboratories Ltd. (Ardmore, UK). All samples were determined in the same assay for each metabolite and for all determinations the intra and inter-assay coefficient of variation (CV) were less than 10 %. Insulin concentrations were determined in three plasma samples (at 20, 23, and 26 months of age; fall, winter, and spring, respectively) using immunoradiometric assays (IRMA) with a commercial kit (INS-IRMA; DIA Source Immune Assays S.A., Belgium). All samples were analyzed in a single assay where the limit of detection was 0.9 µIU/mL and intra-assay CV for control low (20.93 µIU/mL) and high (79.77 µIU/mL) were 5.4 % and 3.2 %, respectively. Progesterone concentrations were determined in all samples by a direct solid-phase radioimmunoassay (RIA) busing a commercial kit (MP biomedicals, LLC, Ohio, USA). All samples were analyzed in a single assay, the limit of detection was 0.021 ng/mL and intra-assay CV for control low (1.01 ng/mL) and high (5.44 ng/mL) were 8.5 % and 7.7 %, respectively. Days to first luteal phase was defined as the day when plasma P4 increased above the threshold value of 1 ng/mL.

3.4.5 Reproductive response

At the end of the experimental period, heifers had their estrous cycles synchronized with two doses of 2 mL of prostaglandin (Glandinex, Laboratorio Universal Lab Ltda., Montevideo, Uruguay) ten days apart and were monitored for estrous by visual observation twice a day by two trained observers during 5 days after the last prostaglandin injection. All heifers showing estrus were artificially inseminated by two inseminators and, thereafter, heifers were exposed to bulls 27 days after the first prostaglandin injection for a mating period that lasted 60 days. Service to conception interval was estimated as conception date minus date of first service with the conception date was calculated as calving date minus 283. Calving day was calculated using the date of calving of the first heifer of the season as reference (day 1) and calf weight at birth and weaning were registered.

3.4.6 Calculations and statistical analyses

Retained energy was estimated using the empty body weight (EBW) and empty body weight gain (EBG) as: RE (MJ/d) = 0.266 × $EBW^{0.75}$ × EBG 1.097 according to NASEM (2016). Metabolizable energy intake was calculated as the sum of HP + RE and DM intake was estimated based on ME intake and herbage ME concentration (MJ/kgDM). Herbage ME concentration was estimated based on DM in vitro digestibility (DMIVD) of the forage as: DMIVD = 88.9 - (%FDA x 0.779) (NASEM, 2016) and dry matter intake (DMI) was estimated as ME intake divided by ME pasture concentration. The revised quantitative insulin sensitivity check index (RQUICKI) was estimated according to Perseghin et al. (2001) i.e. RQUICKI = 1/ [log(Glucose, mg/dl) + log(Insulin, μU/ml) + log(NEFA, mmol/l)].

Heart rate and O2P data were processed using R software to assess the quality of data (R Core Team, Vienna, Austria) and later analyzed using SAS software (SAS University Edition, SAS Institute Inc., Cary, NC, USA). Productive and efficiency variables during fall and spring measurements were analyzed separately with a model that included RHP groups (HE *vs*. LE) as a fixed effect using the MIXED procedure with the compound symmetry (CS) as the covariance structure, and the Kenward-Roger procedure was used to adjust the denominator degrees of freedom.

Overall results of productive, efficiency and metabolic parameters variables were analyzed with a mixed model using repeated measurements with the MIXED procedure. The model included EG (HH *vs*. LL), heifers' age or date of sampling and their interaction as fixed effects and heifer as a random effect. The first-order autoregressive (for evenly spaced data; AR(1)) or spatial power law (for unevenly spaced data; SP(POW)) were used as the covariance structures and the Kenward-Rogers procedure was used to adjust the denominator degrees of freedom. Days to first luteal phase, service to conception interval and calving day were analyzed using the GLIMMIX procedure with Poisson distribution and log transformation specified whereas calf birth and weaning weight and cow BW at calving were analyzed using the MIXED procedure. The model included only EG as fixed effect.

Pearson correlations between fall and spring RHP as well as between productive, energy efficiency and metabolic variables were estimated with the CORR procedures using all heifers evaluated (n = 74). Net energy requirements for maintenance (NEm) and the partial efficiency of use of ME (k) were obtained using a linear model between HP and ME intake for HH and LL heifers where the intercept of the model represents the NEm (kJ/EBW$^{0.75}$/d) and 1-slope represents k. Metabolizable energy intake for maintenance (MEm) was estimated as NEm/k. Results are presented as least square means ± pooled standard errors and least square means were considered to differ when $P \leq 0.05$, and trends were identified when $0.05 < P < 0.10$.

3.5 RESULTS

3.5.1 Heifers' energy efficiency

During fall, there were no differences in BW between RHP groups, but HE heifers tended to have greater ($P = 0.08$) ADG but reduced ($P < 0.01$) HR and O2P than LE ones (Table 1). High efficiency heifers had decreased ($P < 0.01$) ME intake and total HP and tended to have greater ($P = 0.09$) RE than LE ones, both, when expressed as MJ/d (data not shown) and kJ/kg BW$^{0.75}$ per d (Table 1). Consistent with fall results, during spring there were no differences between RHP groups in BW and ADG, while both HR and O2P were reduced ($P < 0.01$) for HE than LE heifers (Table 1). Similarly, ME intake and total HP, expressed as MJ/d (data not shown) and kJ/kg BW$^{0.75}$ per d, were reduced ($P < 0.01$) for HE than LE heifers but there were no differences in RE between RHP groups. Gross energy efficiency (RE/ME intake) was greater ($P < 0.05$) for HE than LE heifers during both, fall and spring (Table 1). Pearson correlation between fall and spring RHP was 0.53 with 55 of 74 (74 %) heifers maintaining their efficiency group between seasons (n = 31 and n = 24 for HH and LL, respectively) while 19 heifers changed their efficiency status (n = 11 and n = 8 for HL and LH, respectively; Figure 1).

Table 1. Heifer body weight and gain, and energy partitioning and efficiency for high and low efficiency heifers in fall and spring.

	Efficiency group			
	High	Low	SEM	P-value
Fall				
Number	42	32	-	-
Initial body weight, kg	267	271	6	0.53
Final body weight, kg	269	273	6	0.52
Average daily gain (ADG), g/d	136	72	37	0.08
Heart rate, beat/min	68	72	1	<0.01
O_2 pulse, mL $O_2/BW^{0.75}$/beat	0.243	0.274	0.005	<0.01
Energy partitioning, kJ/kg $BW^{0.75}$ per d				
Metabolizable energy intake (MEI)	521	595	12	<0.01
Retained energy (RE)	33	17	9	0.08
Heat production (HP)	489	578	9	<0.01
Residual heat production (RHP)	-43	56	9	<0.01
Gross energy efficiency (RE/ME intake)	0.053	0.024	0.014	0.04
Spring				
Number	39	35	-	-
Initial body weight, kg	270	274	5	0.48
Final body weight, kg	300	304	6	0.48
Average daily gain (ADG), g/d	624	625	31	0.98
Heart rate, beat/min	71	77	1	<0.01
O_2 pulse , mL $O_2/BW^{0.75}$/beat	0.267	0.295	0.005	<0.01
Energy partitioning, kJ/kg $BW^{0.75}$ per d				
Metabolizable energy intake (MEI)	773	888	19	<0.01
Retained energy (RE)	159	159	9	0.98
Heat production (HP)	563	668	13	<0.01
Residual heat production (RHP)	-57	64	11	<0.01
Gross energy efficiency (RE/ME intake)	0.204	0.178	0.008	<0.01

Additionally, average CV between the two measures of individual O2P was 5.3 % in fall and 5.2 % in spring, while Pearson correlation coefficients between the two individual O2P measures were 0.67 and 0.59 for fall and spring, respectively. When comparing the individual average O2P of each season, the average CV between the fall and spring measures was 7.3 %, while the Pearson correlation between coefficients was 0.61. Moreover, when comparing the individual average HR of each season, the average CV between the fall and spring measures was 6.0 %. Residual heat production was positively correlated with HP ($P < 0.01$, $r > 0.86$), and MEI ($P < 0.01$, $r > 0.70$) but tended to be ($P = 0.08$, $r = -0.21$) or was ($P < 0.01$, $r = -0.47$) negatively correlated with RE/MEI for fall and spring, respectively.

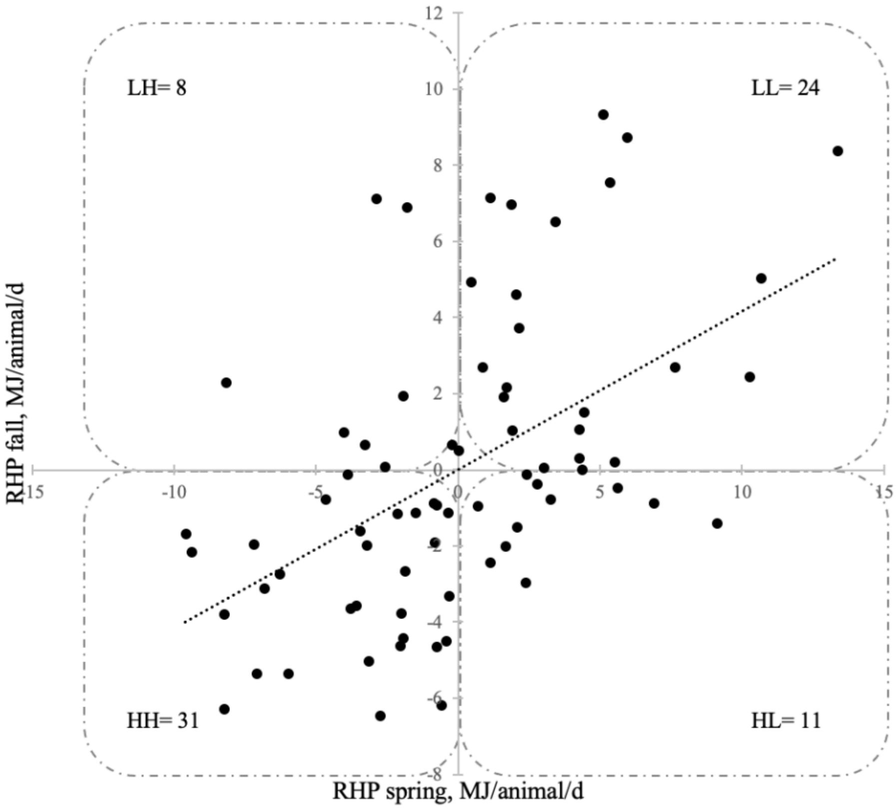

Figure 1. Relationship between spring and fall residual heat production (RHP). Each quadrant corresponds to an efficiency group where the first letter indicates fall and the second one spring efficiency.

The average ME intake and HP for HH and LL heifers were 615 *vs*. 717 ± 13 kJ/BW$^{0.75}$ per d and 521 *vs*. 631 ± 11 kJ/BW$^{0.75}$ per d, respectively. Regressions of HP on ME intake (kJ/BW$^{0.75}$) were found to be high and significant ($r > 0.86$; $P < 0.01$; Figure 2) for both, HH and LL heifers and both, regression intercept and slope were greater for LL than HH heifers indicating that HH heifers had a reduced fasting heat production and increased partial efficiency of use of ME (k; 1 – slope) than LL heifers (259 *vs*. 290 and 0.58 *vs* 0.52, for NEm and k, respectively).

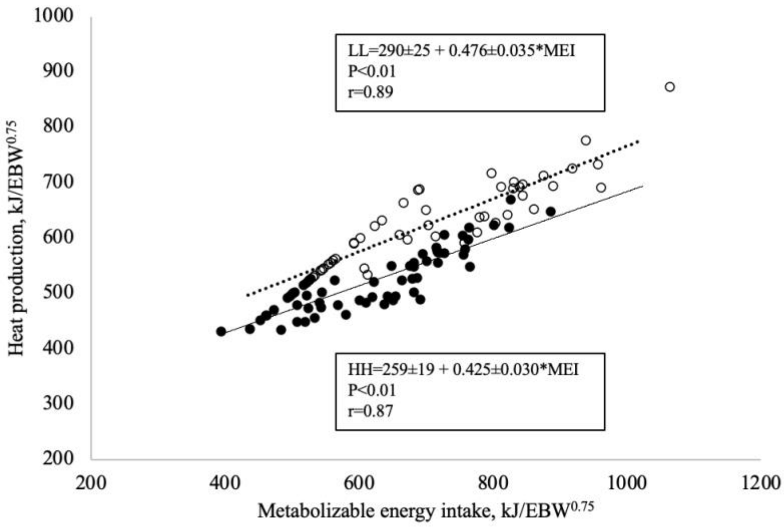

Figure 2. Relationship between heat production (kJ/EBW$^{0.75}$) and metabolizable energy intake (kJ/EBW$^{0.75}$) for high efficiency (HH) and low efficiency (LL) heifers. The solid line represents the linear regression of HP in ME intake for HH and the dotted line in LL.

3.5.2 Productive and reproductive performance of high *vs*. low efficiency heifers

When comparing the HH and LL groups, the difference between average RHP between them was 7.38 MJ/d and 119 kJ/BW$^{0.75}$/d (Table 2). Neither heifers BW nor ADG differed between EG, and although BW showed small changes during fall and winter and increased in spring, it was not affected by the EG by heifers age interaction (Table 2; Figure 3A) nor was ADG. Rib eye area and back fat depth increased ($P < 0.01$) as heifers got older (20 to 26 months of age; from fall to spring) but were not affected by EG or by the interaction of EG by heifers age (Table 2). Rump fat depth was not affected by any of the effects tested.

Estimated DM intake both, expressed as kg/d or as g/BW$^{0.75}$ per d were less ($P < 0.01$) for HH than LE heifers and was greater ($P < 0.01$) during spring than fall (26 *vs*. 20 months of age). In addition, there was a trend for the interaction between EG and heifers age ($P \leq 0.09$) as differences between EG in DM intake were accentuated in spring (Table 2; Figure 3B). Thus, gain to feed ratio was greater ($P < 0.01$) for HH than LL heifers (Table 2) and for spring than fall (100 *vs*. 21 g/kg DM, respectively). Dry matter intake was positive correlated ($P < 0.01$, $r > 0.70$) with RHP while gain to feed ratio was negatively correlated ($P \leq 0.05$, $r = -0.22$ and $r = -0.51$ for fall and spring, respectively).

Table 2. Body weight, body weight gain, body composition, dry matter intake and energy and feed efficiency of heifers classified by overall efficiency group.

	Eficiency group			P-value		
	HH	LL	SEM	EG	Age	EG x Age
Number	31	24	-	-	-	-
Residual heat production (MJ/d)						
Mean	-3.40	3.98	0.58	<0.01	0.93	0.30
Median	-3.14	3.20	-	-	-	-
Residual heat production (kJ/kg $BW^{0.75}$ per d)						
Mean	-55	64	10	<0.01	0.90	0.35
Median	-48	49	-	-	-	-
Body weight (kg)	276	280	6	0.48	<0.01	0.98
Average daily gain (ADG, g/d)	135	134	16	0.96	-	-
Body composition						
Rib eye area, cm^3	29	29	1	0.66	<0.01	0.97
Back fat depth, mm	1.7	1.7	0.1	0.93	0.03	0.25
Rump fat depth, mm	1.7	1.7	0.1	0.70	0.23	0.57
DM intake (DMI), kg/d	4.9	5.8	0.1	<0.01	<0.01	0.07
DM intake (DMI), g/$BW^{0.75}$ per d	79	92	2	<0.01	<0.01	0.09
Energy and feed efficiency						
RE/ME intake	0.14	0.10	0.01	<0.01	<0.01	0.57
Gain to feed ratio (ADG/DMI), g/kg	70	51	4	<0.01	<0.01	0.59

At the beginning of the experiment there were no differences between efficiency groups in heifers showing luteal activity (4/31 and 1/24 for HH and LL, respectively), but days to first luteal activity, service to conception interval and calving day were reduced (P < 0.01) for HH than LL heifers (Table 3). Nonetheless, there were no differences in birth or weaning weight of first calf nor in cow's BW or body condition score at calving.

Table 3. Reproductive performance of heifers that maintained the fall assigned efficiency group.

	Efficiency group			
	HH	LL	SEM	P-value
Number	31	24	-	-
First luteal activity, d	225	256	17	<0.01
Service to conception interval, d	12	16	1	<0.01
Calving day	21	25	1	<0.01
Calf birth weight	35	35	2	0.63
Calf weaning weight	176	173	6	0.48

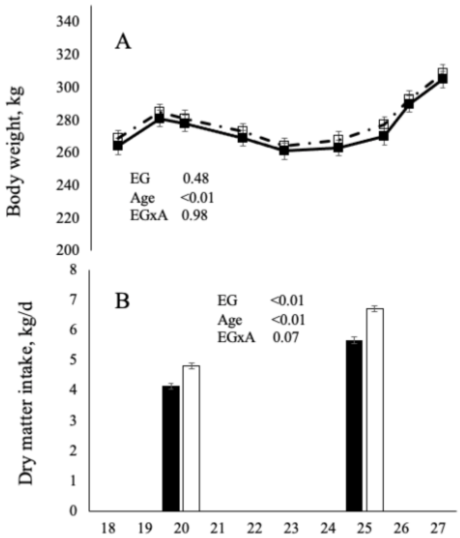

Figure 3. Body weight (**A**) and dry matter intake (**B**) of high efficiency group heifers (bold line or solid bar) and low efficiency group heifers (dashed line or empty bar).

3.5.3 <u>Metabolic and endocrine profile of high *vs*. low efficiency heifers</u>

Glucose concentrations were greater (P < 0.01) for HH than LL heifers throughout the year (Figure 4A). However, neither NEFA, BHB, cholesterol, urea, insulin nor urea concentrations differed between EG (Figures 4B to 4G). All metabolite concentrations were affected by date of sampling (P < 0.01) as glucose and urea concentrations increased from fall to spring while serum NEFA and BHB peaked at the end of winter and cholesterol concentrations decreased from fall to winter to increase again during spring. Serum insulin concentrations were not affected by EG, date of sampling or its interaction (Figure 4F). Neither glucose to insulin ratio nor RQUICKI were affected by EG or its interaction with date of sample; nonetheless, they were affected by date as increased in spring (P < 0.01; data not shown). Average serum P4 concentrations were low during fall and winter and increased during spring (P < 0.01) but were not affected neither by EG nor by its interaction with date of sampling (Figure 4G). During fall, using all animals, significant correlations between RHP and NEFA (P < 0.05; r = 0.21) and RHP and cholesterol (P < 0.01; r = -0.23) were detected.

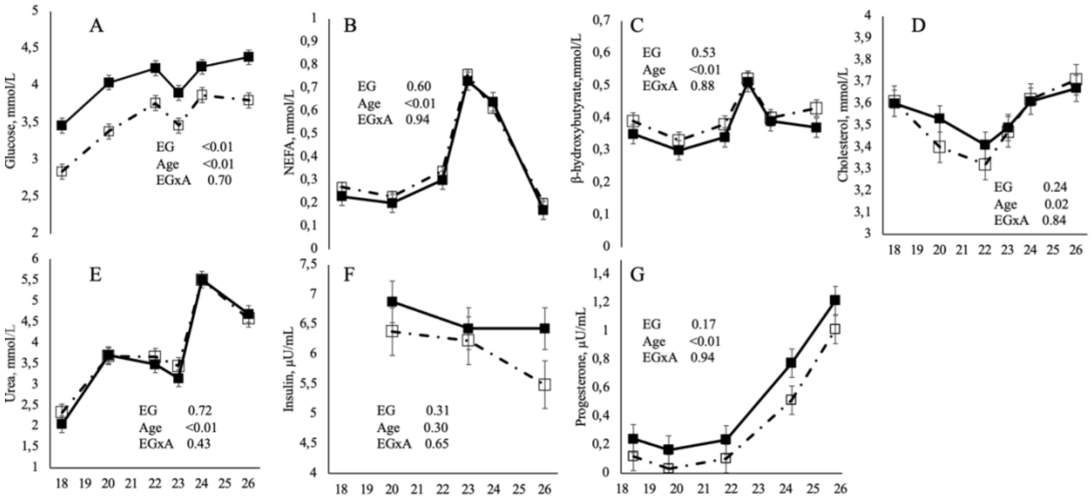

Figure 4. Blood serum glucose (**A**), non-esterified fatty acids (**B**), β-hydroxybutyrate (**C**), cholesterol (**D**), urea (**E**), insulin (**F**) and progesterone (**G**) concentrations of high efficiency group heifers (bold line) and low efficiency group heifers (dashed line). EG = efficiency group, EGxA = interaction between efficiency group and age

3.6 DISCUSSION

The RHP proved to be a repeatable trait, at least when animals are young, given that 74 % of evaluated heifers maintained the fall assigned efficiency group on spring. Also, the energy partitioning of efficient *vs*. inefficient animals was the same in both seasons: efficient heifers produced less heat without differences in RE or BW while having a lower ME intake. There was no apparent major effect of the studied metabolites on efficiency nor there was a significant effect of efficiency on body composition.

In our experiment, RHP showed a moderate to high repeatability where 74 % of heifers maintained the fall assigned EG in spring. These finding indicated that RHP could be a robust efficiency index. Similarly, it has been proven than RFI is a repeatable trait in beef cattle; moderate correlations (r = 0.40 to 0.62) have been reported between two consecutive measure periods of RFI for steers and replacement heifers fed the same (Kelly et al., 2010; Durunna et al., 2011; Durunna et al., 2012) and between RFI measured as postweaning heifers and as mature cows offered pelleted diets or diets with different forage proportion (Archer et al., 2002; Hafla et al., 2013). However, Durunna et al. (2011) reported a lower correlation (r = 0.33) between RFI measurements in steers fed different diets (growing *vs*. finishing) and Lahart et al. (2020) determined that the correlation of RFI for steers and heifers across three different diets (grass plus silage, grazed grass, and high concentrate) was only 0.25.

During spring, we observed that variation in HP was explained by $BW^{0.75}$ (0.48; $P < 0.01$), ADG (8.66; $P < 0.05$) and rump fat thickness (-3.45; $P < 0.01$), while in fall, probably due to seasonal variation in herbage quantity and/or quality on Campos rangelands (Berretta et al., 2000), heifers' DM intake, thus ADG, were limited. The low ADG and RE during this period (< 150 g/d and 35 kJ/$BW^{0.75}$ per d) as well as the fact that almost half of the heifers evaluated were not gaining BW, would indicate that heifers' energy intake was near maintenance. Indeed, ADG was not included in the model to predict HP as its estimate was not significant and only $BW^{0.75}$ (0.47; $P < 0.01$) was. Therefore, although as in RFI, RHP should be independent of BW and ADG, a trend for greater ADG and RE was found for HE when compared with LE heifers during fall. Indeed, during fall, 55 % (17/31) of the heifers classified as HH, but only

21 % (5/24) of those classified as LL had ADG greater than 0. In agreement with our result, Adreini et al. (2020) comparing low *vs*. high RFI steers in ad libitum and restricted (75% ad libitum intake) feeding periods, reported decreased RE during feed restriction only for high-RFI steers, which was associated with a greater decrease in NEm in low than high-RFI animals during restriction.

In the present work, during fall and spring, both, HR and O2P were lower for HE then LE heifers, which is consistent with previous research using RFI as the efficiency index that reported decreased HR (Hafla et al., 2013) and O2P (Paddock, 2010; Chaves et al., 2015) for efficient than inefficient animals. This decrease in HR and O2P would suggest that feed efficiency could be associated to reduced metabolic rates, resulting for lower maintenance energy expenditure or a greater partial efficiency of use of consumed ME (Cantalapiedra-Hijar et al., 2018). Moreover, HH heifers consumed 15 % less of ME and produced 20 % less HP than LL heifers without differences in RE, indicating a greater partitioning of consumed ME towards RE than HP. Total HP is the sum of heat production for maintenance (HPm) and production (HPp; Miron et al., 2008), so it could be expected that HPp would be similar between EG as they did not differ in RE; thus, a reduced HP for HH heifers would be due to reduced HPm. Furthermore, the intercept of the regressions of HP on ME intake (kJ/BW$^{0.75}$ per d) for HH *vs*. LL heifers indicated that the net energy requirements for maintenance (NEm; or the HP when ME intake is equal to zero) were 11 % higher for LL than HH heifers. Estimates of NEm were in the range of the reported by Menezes et al. (2020) for low and high-RFI Nellore bulls but lower than the estimated for Andreini et al. (2020) for Angus-cross steers. Nevertheless, these authors observed a greater difference between RFI groups (18 to 20 % increase in NEm for high *vs*. low RFI animals). Moreover, the MEm, identified as the value where ME intake is equal to HP (or the NEm divided by the k), was 447 *vs*. 558 kJ/BW$^{0.75}$ for HH and LL, respectively, representing a 25 % increase for MEm for LL than HH heifers, in contrast to Menezes et al. (2020) who did not find differences in k between high and low-RFI Nellore bulls (k = 0.64), we estimate that k was 10 % greater for HH than LL heifers (0.58 *vs*. 0.52, respectively). Differences between our and these studies (low NEm and k) could be probably due to type of diet (pasture grazing *vs*. total mixed ration offered in confinement) and level of intake. Richardson and Herd (2004), analyzing a series of experiments in cattle divergently selected for RFI, and Cantalpiedra-Hijar et al. (2018), reviewing the biological determinants of variation of feed efficiency, indicated that reduced maintenance energy expenditure would be in the basis of feed efficiency evaluated as RFI.

Not only ME intake but also estimated DM intake was different between HH and LL and, considering all heifers used in the study, both ME intake and DM intake showed a positive high ($P < 0.01$; $r = 0.70$) phenotypic correlation with RHP. Despite BW and ADG no differing between groups, LL heifers had greater DM intake than HH ones. Difference in DM intake between HH and LL was about 1 kg DM/d, value similar to the one reported by Andreini et al. (2020) for high and low RFI steers in confinement conditions both with restricted and ad libitum diets. Greater differences were reported by Asher et al. (2018) who found that average DM intake ranged between 35 to 48 % between the most and least efficient animals measured as RFI. By definition (Koch et al., 1963), animals with lower RFI are considered more efficient because they eat less than expected and several authors have confirmed that for total mixed diets under confinement (Nkrumah et al., 2006; Chaves et al., 2015; Menezes et al., 2020) or in grazing conditions (Trujillo et al., 2013) the least efficient group consumes significatively more DM than the efficient group, expressed both as kg/d or %$BW^{0.75}$. However, several authors have not been able to find differences in forage DM intake in animals of different efficiency (low *vs*. high RFI) under grazing conditions (Meyer et al. 2008; Lawrence et al., 2012; Oliveira et al., 2016). The different methods to determine DM intake, whether is measured directly or estimated as in this work, as well as the difficulty to obtain accurate measure of intake in grazing conditions, could explain the differences between studies.

The greater DM intake by inefficient animals could explain, at least partly, the differences in maintenance energy expenditure as higher DM intake of high *vs*. low RFI animals has been associated to lower HP and decreased mass of gastrointestinal tract viscera (Renand and Krauss, 2002; Basarab et al., 2003), being the high metabolic costs of these organs a high proportion of NEm (Ferrell and Jenkins, 1985; Fitzsimons et al., 2017). In addition, greater DM intake could also imply greater energy expenditures associated with the digestion process and decreased efficiency with which dietary energy will be captured by the gastrointestinal tract as passage rate would increase. Previous works observed a negative association between digestibility and RFI in animals in confinement where the most efficient animals were associated with greater digestibility (Richardson and Herd, 2004; Bonilha et al., 2017; Kenny et al., 2018; Cantalapiedra et al., 2018). Furthermore, Richardson and Herd (2004), using a variety of beef cattle breeds, concluded that the differences between animals in their digestive ability explained 10 % of the variation in RFI. However, it is not clear if the greater digestibility is associated with characteristics inherent to more efficient animals or is only a consequence of a lower passage rate due to a lower DM intake (Cantalapiedra et al., 2018; Kenny et al., 2018). In addition, decreased DM intake of more efficient animals, especially in grazing conditions, could also imply lower energy expenditure for activity (Fitzsimons et al., 2014). In this sense, Kenny et al. (2018) found that high RFI cattle spent 12 % more time eating than low RFI animals, and that the latter ones had a 17 % higher DM intake, indicating they also had a higher intake rate than low RFI animals. Similar data have been reported for pregnant cows of several beef breeds on diets with a high proportion of forage (Basarab et al., 2007; Hafla et al., 2013; Fitzsimons et al., 2014). Greater eating times and intake rates have been associated with increased MEm in grazing animals (Di Marco and Aello, 2001).

Although HH consumed less DM intake than LL heifers, they had greater plasma glucose concentrations, which would indicate that this animals consumed a diet of higher quality due to the selection process (i.e, less fiber; Hardison et al., 1954) or had more efficient rumen degradation or digestion process (i.e. increased propionic; Richardson and Herd, 2004; Bonilha et al., 2017) or had an increased hepatic gluconeogenesis (Casal et al., 2018) as suggested for more efficient animals (low-RFI). However, this higher glucose concentration in the more efficient heifers was not accompanied by higher plasma insulin concentrations or by a differential sensitivity of peripheral tissues (estimated through the RQUICKI) to this hormone. The results in the literature regarding glucose and insulin concentrations in animals of different efficiency are not consistent since greater (Nascimento et al., 2015; Foroutan et al., 2020), similar (Kolath et al., 2006, Xi et al., 2016) or lower (Richardson et al., 2004, Zhang et al., 2022) concentrations associated with high-efficiency animals (low RFI) have been reported. Discrepancies between studies regarding differential blood concentrations of key metabolites and hormones, associated with feed intake, growth, body composition, and nutrient partitioning and utilization, between low- and high-efficiency animals are probably because, among other factors, of the intake level, type of diet and prandial activity on these variables.

Alternatively, it has been suggested that the decrease in protein turnover, an energetically expensive process, would explain not only the reduction in maintenance cost but also a greater partial efficiency for growth above maintenance (Cantalapiedra-Hijar et al., 2018) and lower plasma urea concentrations have been reported in more efficient (low RFI) animals, suggesting decreased protein degradation (Richardson et al. 2004; Kelly et al., 2010; Jorge-Smeding et al., 2021) stimulated by greater insulin sensitivity associated with higher body protein content (Richardson et al., 2004). However, in our work, and in agreement with other research (Lawrence et al., 2011; Broleze et al., 2020; Guarnido-Lopez et al., 2022), neither plasma concentrations of urea or insulin nor insulin sensitivity (RQUICKI) or rib eye area differed between HH and LL heifers. Guarnido-Lopez et al. (2022) observed a positive association between protein turnover and RFI in finishing steers fed a diet based on corn silage but not when the diet was less dense (based on pasture silage), and, in agreement with other authors (Lahart et al., 2020; Jorge-Smeding et al., 2021), indicated differences between diets affect the biological mechanisms that explain feed efficiency.

Several authors had associated feed efficiency (as RFI) with leaner animals (Arthur et al., 2001; Basarab et al., 2007; Berry and Crowley, 2013) and differences in rate of protein and fat deposition would also affect ADG as energy density is greater for fat than protein. Nonetheless, we did not detect differences in back fat thickness between EG, and although rump fat thickness was a significant factor in the model used to estimate HP, it showed a negative correlation with it. In the present study, the lack of differences in back fat thickness between EG could be the result of heifers' age and development in limiting nutritional conditions. In spring, when herbage growth increased, and more herbage was available, contrary to previous work (Arthur et al., 2001; Basarab et al., 2007; Berry and Crowley, 2013), a small difference was detected in favor of HH heifers in rump fat thickness, an early developing fat tissue, deposited at a younger age than backfat tissue. A meta-analysis of studies conducted with beef cattle fed energy-dense diets concluded that RFI was neither associated with final or carcass muscle area nor with back fat depth during the growing phase (Kenny et al., 2018). Similarly, Asher et al. (2018) did not find any association between several postmortem carcass traits studied and RFI or RHP for Holstein steers.

Previous research (Roberts et al., 2007; Lines et al., 2014; Herd et al., 2011) did not detect differences between low and high RFI heifers or cows when fed at maintenance level or in restricted feeding, which was associated with a low RFI variation. Thus, these latter authors suggested that variation in appetite would contribute more to variation in RFI as higher feed intake would determine higher fat deposition without differences in energy efficiency. However, in this work, although variation in RHP was less in fall than spring, we were able to detect differences in fall when heifers were grazing in more restrictive conditions. Furthermore, although plasma NEFA and BHB did not differ between RHP heifers, in agreement with previous reports for RFI (Richardson et al. 2004, Lawrence et al. 2011), during fall, in agreement with the trend for greater ADG, plasma NEFA concentrations were positively correlated while cholesterol concentrations were negatively correlated with RHP, indicating more negative energy balances (Astessiano et al., 2014) when feeding was restricted, in the less efficient heifers despite they consumed more. Therefore, in this work, although the variance for RHP was lower in fall than spring, differences between HH and LL heifers would be the result of differential energy utilization efficiency.

There are few and equivocal reports linking feed efficiency with reproductive traits, being gain in efficiency usually reported in detriment of reproductive traits (Kenny et al., 2018). Indeed, later calving dates were reported in heifers with low RFI (high efficiency), associated to a later puberty and lower levels of body fat (Arthur et al., 2005; Basarab et al., 2011; Shaffer et al., 2011). In contrast, we found that more efficient heifers (low RHP; HH), despite not showing differences in P4 concentrations with LL ones, had earlier luteal activity, beginning one month before than in inefficient heifers without differences in age but associated with greater rump fat thickness.

Consistently, low RHP heifers had a shorter service to conception interval and calved earlier in the season without differences in the calf weight than high RHP heifers as it has been reported that an earlier ovarian cyclicity would improve conception rates (Butler et al., 2001). However, in agreement with previous research in RFI (Arthur et al., 2005; Basarab et al., 2007; Broleze et al., 2020), maternal productivity at the first calving did not differ between groups since the calf weight at birth and weaning weight showed no difference between HH ad LL heifers.

3.7 CONCLUSIONS

The RHP proved to be a repeatable trait even though grazing conditions, thus, nutrition, were more restrictive in fall than spring. More efficient heifers showed lower HP, ME intake and DM intake without differences in RE than inefficient ones. Decreased maintenance requirements (NEm, and MEm) as well as higher partial efficiency of use of consumed ME (k) were estimated for more efficient heifers (low RHP; HH). More efficient heifers showed an earlier luteal phase and a shorter service-conception interval and calved earlier in the season, probably associated to an earlier development of fat tissue.

3.8 DISCLOSURE

The authors declare no conflicts of interest.

3.9 LITERATURE CITED

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4. DISCUSIÓN GENERAL Y CONCLUSIONES

4.1 DISCUSIÓN

Los sistemas productivos de base pastoril son complejos y no suelen ser entendidos o manejados fácilmente (Turner et al., 2013), en especial por su dependencia en la producción de forraje que presenta cambios inter- e intraanuales (Soca et al., 2007). En Uruguay, los sistemas ganaderos constituyen una actividad de gran importancia socioeconómica debido a la relevancia del rubro en lo que respecta a exportaciones (DIEA, 2022). A pesar de esto, la competencia que ha enfrentado el rubro por el uso de la tierra, así como el aumento de los costos productivos en general, ha llevado a que se apunte a una mejoría de la eficiencia de los sistemas (producir más y mejor con menos recursos) sin que esto resulte en un detrimento medioambiental. A su vez, en el ámbito global, existe una demanda creciente de alimentos que hace necesario un aumento de la producción agrícola, y de carne en particular, y se ha demostrado que el aumento de la productividad por unidad de área y, por lo tanto, un incremento de la eficiencia de producción, es más ventajoso, en términos ambientales, que el aumento del área destinada a producción (Tilman et al., 2011). En sí, el aumento de la eficiencia de los sistemas criadores dependerá, entonces, de los resultados productivos y/o reproductivos de estos, donde la eficiencia individual será determinante de la eficiencia global del sistema; animales más eficientes serían, por consiguiente, aquellos que puedan mantener su nivel productivo con un menor requerimiento de alimento sin comprometer su performance reproductiva.

Es así que este trabajo buscó evaluar una metodología -la RHP- para la identificación de animales eficientes en condiciones en pastoreo. El RFI es el parámetro de eficiencia más ampliamente difundido, pero presenta la limitante de que su determinación se realiza en un entorno productivo muy diferente al de los sistemas criadores basados en pasturas nativas o naturales. Aunque la evaluación de RFI requiere alimentación *ad libitum* en confinamiento, esta situación difiere mucho de la mayoría de los sistemas criadores donde las hembras son manejadas en pastoreo y están sujetas a las variaciones en la disponibilidad y calidad del alimento.

En este trabajo, demostramos que a pesar de las diferencias en el tipo (ración mezclada vs. forraje) y suministro (confinamientos vs. pastoreo), la selección genética de toros por RFI se tradujo en vaquillonas más eficientes (menor RHP), existiendo una relación positiva entre las variables RHP de la vaquillona de remplazo y el EBV paterno para RFI (exp. 1), estimando que la RHP parecería ser moderadamente heredable (exp. 1). Por otra parte, al categorizar las vaquillonas por su eficiencia individual de acuerdo con la RHP medida en dos momentos de la recría (otoño y primavera), se observó que esta variable era repetible por lo menos durante la etapa de crecimiento y desarrollo a pesar de que las condiciones de alimentación difirieron entre ambos momentos de medición (mantenimiento vs. ganancia de PV; exp. 2). Futuros trabajos deberán explorar la relación entre el EBV paterno para RFI y la eficiencia individual medida como RHP, así como la repetibilidad de la RHP para otros estados fisiológicos de la vaca de cría (gestación y lactación). Cabe destacar que 52 % (16/31) y 29 % (9/31) de las vaquillonas del grupo HH pertenecían a padres con un percentil de EBV para RFI ≤ 20 y ≥ 80, respectivamente, mientras que 42 % (10/24) y 25 % (6/24) de las vaquillonas del grupo LL pertenecían a padres con un percentil de EBV para RFI ≤ 20 y ≥ 80, respectivamente. A su vez, de las vaquillonas con padres con percentil de EBV para RFI ≤ 20, el 42 % (16/38) pertenecieron al grupo HH y el 25 % (10/38) al grupo LL.

Estudios previos han señalado que menores costos de energía para mantenimiento estarían explicando una porción importante la variación individual en RFI (Herd et al., 2004, Cantalapiedra-Hijar et al., 2018). De hecho, algunos estudios han evaluado la HP en animales de alta y baja eficiencia (bajo y alto RFI) y mostraron que la HP disminuye en animales más eficientes, lo que sugiere una disminución del gasto energético de mantenimiento (Basarab et al., 2003, Nkurmah et al., 2006, Paddock, 2010, Asher et al., 2018, Menezes et al., 2020). En nuestro tabajo, la HP (kJ/$PV^{0,75}$ por d) si bien no difirió entre vaquillonas PHE y PLE, se correlacionó positivamente con el EBV paterno para RFI (exp. 1) y fue menor en las vaquillonas de HH que de LL (exp. 2). En acuerdo con Hafla et al. (2013), en ambos trabajos, los grupos de alta eficiencia (PHE y HH; exp 1 y 2, respectivamente) presentaron menores HR. Sin embargo, el O_2P no difirió cuando las vaquillonas fueron clasificadas de acuerdo con la eficiencia paterna (exp.1), pero fue menor cuando fueron clasificadas de acuerdo con su eficiencia individual (exp. 2). Resultados similares fueron reportados por Chaves et al. (2015), lo que indica una menor actividad metabólica (Brosh, 2007) en los animales más eficientes (menor RHP).

Cuando los resultados de consumo y partición de la energía fueron expresados en relación con el $PV^{0,75}$ (kJ/$PV^{0,75}$ por d), las vaquillonas de PHE presentaron una mayor ER sin diferencias en la HP total o en el consumo de EM que las del grupo PLE (exp. 1), mientras que las vaquillonas HH presentaron igual ER y menor HP total y consumo de EM que las LL tanto en otoño como en primavera (exp. 2). La HP total de calor es la suma de la HPm y la HPp (Miron et al., 2008). Por lo tanto, la mayor o similar ER indicaría que la HPp sería mayor o igual, mientras que la HPm sería menor (ya que la HP total sería igual o menor) para las vaquillonas más eficientes (PHE y HH, respectivamente). Resultados comparables fueron reportados previamente (Nkurmah et al., 2006, Chaves et al., 2015, Asher et al., 2018, Menezes et al., 2020) para novillos y vaquillonas en crecimiento. Mas aún, en acuerdo con Menezes et al. (2020), la regresión de HP en el consumo de EM (exp. 2) mostró que el requerimiento de ENM (cuando consumo EM es igual a cero) fue 11 % menor para las vaquillonas HH que LL. Asimismo, la eficiencia de utlización de la EM (k; 1 – pendiente de la regresión) fue mayor para las vaquillonas más eficientes (HH), lo que indica diferencias en el metabolismo de los nutrientes entre grupos de animales. En acuerdo con la información previa (Nkrumah et al., 2006, Asher et al., 2014, Asher et al., 2018), y consistente con los menores requerimientos de ENM y/o mayores eficiencia de utilización de la EM (k), en ambos experimentos, las vaquillonas más eficientes (PHE y HH) presentaron mayores relaciones ER/consumo EM y GMD/consumo MS que las vaquillonas menos eficientes (PLE y LL).

El menor requerimiento de ENM en las vaquillonas más eficientes (PHE y HH) se reflejó en consumos de MS y EM en relación con el $PV^{0,75}$ que no difirieron, pero en GMD y ER mayores (exp. 1) o en menores consumos de MS y EM sin diferencias en GMD y ER (exp. 2). En general, de manera similar a lo observado en el exp. 2 cuando las vaquillonas fueron clasificadas de acuerdo con su RHP individual, menores consumo de MS se han asociado con animales de bajo-RFI (alta eficiencia) tanto en confinamiento (Cantalapiedra-Hijar et al., 2018) como en pastoreo (Trujillo et al., 2013). Sin embargo, varios autores han sido incapaces de encontrar diferencias en el consumo de MS forraje en animales de diferente eficiencia (bajo vs. alto RFI) en condiciones de pastoreo (Meyer et al. 2008, Lawrence et al., 2012, Oliveira et al., 2016) pero sí se ha reportado que animales de bajo RFI o alta eficiencia presentaban PV mayores o menores pérdidas de PV o BCS cuando estaban en condiciones extensivas de producción (Herd et al., 1998, Jones et al., 2011, Sprinkle et al., 2020). En acuerdo con estos resultados en el exp. 1, cuando las vaquillonas fueron clasificadas de acuerdo con el RFI paterno, a pesar de que fueron manejadas como un grupo contemporáneo desde el nacimiento, el PV inicial y final, así como el GMD, fueron mayores para las vaquillonas PHE que PLE. El comportamiento ingestivo-digestivo de animales en pastoreo se ha sugerido como un mecanismo de adaptación a estas condiciones (Gregorini et al., 2008), donde diferencias en el exploración espacial podrían determinar que, en condiciones restrictivas, animales más eficientes pudieran hacer un mejor uso del forraje disponible y, eventualmente, consumir forraje de mejor calidad y/o tener menor gasto energético por actividad (Richardson y Herd, 2004, Knight et al., 2015, Sprinkle et al., 2020, Lahart et al., 2020).

Por otra parte, el mayor consumo de MS de los animales ineficientes podría también explicar los mayores requerimientos de ENM, ya que mayores consumos de MS en animales menos eficientes se asociaron a mayores pesos de las vísceras del tracto gastrointestinal (Renand y Krauss, 2002, Basarab et al., 2003) e investigaciones previas han establecido que los altos costos metabólicos de estos órganos constituyen una alta proporción de la ENM (Ferrell y Jenkins, 1985, Fitzsimons et al., 2017). A su vez, un mayor consumo de MS implicará gastos mayores asociados a este proceso y este, una menor eficiencia con la que se capturará la energía consumida por mayores tasas de pasaje. Trabajos anteriores observaron una asociación negativa entre digestibilidad y RFI en animales en confinamiento, es decir que los animales más eficientes tuvieron asociadas mayores digestibilidades (Richardson y Herd, 2004, Bonilha et al., 2017, Kenny et al., 2018, Cantalapiedra-Hijar et al., 2018). Más aún, Richardson y Herd (2004) concluyeron que las diferencias entre animales en su habilidad digestiva explicaban un 10 % de la variación del RFI. Sin embargo, no es claro si esta mayor digestibilidad está asociada a características inherentes a los animales más eficientes o es solamente una consecuencia de una menor tasa de pasaje por un menor consumo de MS (Cantalapiedra-Hijar et al., 2018, Kenny et al., 2018). Claramente, el consumo y digestibilidad de la MS, así como el comportamiento en pastoreo, son áreas que deberán ser exploradas en futuros estudios sobre eficiencia en animales en pastoreo.

Menores consumos de MS en las vaquillonas HH se asociaron con mayores concentraciones de glucosa en plasma (exp. 2), lo que indicaría una mayor calidad de la dieta consumida (selección), o un proceso de degradación ruminal o digestión más eficiente (*i.e.*: propiónico; Richardson y Herd, 2004, Bonilha et al., 2017) o un incremento de la gluconeogénesis hepática (Casal et al., 2018) como fue sugerido para animales más eficientes (menor RFI). Sin embargo, esta mayor concentración de glucosa en las vaquillonas más eficientes no se acompañó de mayores concentraciones de insulina en plasma ni de una sensibilidad diferencial de los tejidos periféricos (estimada a través del RQUICKI) de esta hormona. Los resultados en la literatura con respecto a las concentraciones de glucosa e insulina en animales de diferente eficiencia no son consistentes, ya que se ha reportado mayores (Nascimento et al., 2015, Foroutan et al., 2020), similares (Kolath et al., 2006, Xi et al., 2016) o menores (Richardson et al., 2004, Zhang et al., 2022) concentraciones asociadas a animales de alta eficiencia (bajo RFI). Probablemente, las discrepancias entre estudios en relación con las concentraciones en sangre diferenciales de metabolitos y hormonas clave, asociados con el consumo de alimento, el crecimiento, la composición corporal y la partición y utilización de los nutrientes, entre animales de baja y alta eficiencia, se deba a que estas variables están influenciadas, entre otros factores, por el nivel de consumo, el tipo dieta y la actividad prandial.

Alternativamente, se ha sugerido que la disminución del *turnover* proteico, un proceso energéticamente costoso, explicaría no solo la reducción en el costo de mantenimiento, sino también una mayor eficiencia parcial para el crecimiento por encima del mantenimiento (Cantalapiedra-Hijar et al., 2018). De hecho, aunque no siempre consistente, se han reportado menores concentraciones de urea en plasma en animales más eficientes (bajo RFI), lo que sugiere una disminución de la degradación de proteínas (Richardson et al., 2004, Kelly et al., 2010, Jorge-Smeding et al., 2021) estimulada por una mayor sensibilidad a la insulina asociada al mayor contenido proteico corporal (Richardson et al., 2004). Sin embargo, en nuestro trabajo (exp. 2), y de acuerdo con otros reportes (Lawrence et al., 2011, Broleze et al., 2020, Guarnido-Lopez et al., 2022), ni las concentraciones circulantes de urea o insulina, ni el RQUICKI, ni la deposición de proteína en la carcasa medida por ultrasonido (área de ojo de bife) difirieron entre vaquillonas HH y LL. Guarnido-Lopez et al. (2022) observaron en novillos en engorde una asociación positiva entre el *turnover* proteico y el RFI en animales alimentados con una dieta basada en ensilaje de maíz, pero no cuando la dieta era menos densa, basada en ensilaje de pastura, lo que indica diferencias entre dietas en los mecanismos biológicos que explican la eficiencia alimenticia (o RFI), lo que sería clave a la hora de considerar la eficiencia en animales en pastoreo (Lahart et al., 2020).

La información de eficiencia alimenticia evaluada como RFI en situaciones de restricción alimenticia es limitada (Andreini et al, 2020). En el exp. 2, durante el otoño, probablemente debido a la variación estacional en la cantidad y/o calidad del forraje en los pastizales de Campos (Berretta et al., 2000), se registraron bajas GMD y ER (< 150 g/d y 35 kJ/PV^{0,75} por d), lo que indicaría que el consumo de energía de las vaquillonas estaba cerca de mantenimiento. Más aún, el consumo de MS representó el 1,8 % del PV (vs. 2,5 % de PV en primavera) y las menores HR y O_2P registradas en otoño que en primavera confirmarían la limitación del consumo de MS. De hecho, el efecto GMD no fue significativo en el modelo para predecir HP, y se perdió la independencia entre RHP y GMD, observándose una tendencia a mayores GMD en HE que LE. Adreini et al. (2020), al comparar novillos con bajo vs. alto RFI evaluados con alimentación *ad libitum* y restringidos (75 % de ingesta *ad libitum),* encontraron una disminución de ER durante la restricción de alimentación solo para novillos con alto RFI, y esto se asoció a una menor disminución de los requerimientos de ENM durante la restricción en estos animales. En nuestro trabajo, durante el otoño, el 55 % (17/31) de las vaquillonas clasificadas como HH, pero solo el 21% (5/24) de las clasificadas como LL tenían GMD > 0. Más aún, durante este período de medición, las concentraciones en plasma de NEFA se correlacionaron positivamente, mientras que las concentraciones de colesterol se correlacionaron negativamente con el RHP, lo que indica balances energéticos más negativos (Astessiano et al., 2014) cuando la alimentación fue restringida en las vaquillonas menos eficientes a pesar de que estas consumían más. Probablemente, estos resultados se expliquen por una adaptación diferencial en los costos de mantenimiento en situaciones restrictivas de alimentación entre animales de alta y baja eficiencia (Andreini et al., 2020). Sin embargo, Lines et al. (2014) no detectaron diferencias entre vaquillonas de bajo y alto RFI cuando eran alimentadas a nivel de mantenimiento y Herd et al. (2011) si bien encontró que EBV para RFI-posdestete y RFI-feedlot se asoció con una mejora en la eficiencia de las vacas alimentándose con pasturas de calidad media o alimentadas en corral sin restricción, no mejoró la eficiencia en alimentación cuando las vacas estaban en una situación de alimentación restringida, asociándolo a una menor variación en esta característica en condiciones de mantenimiento. De hecho, Roberts et al. (2007) reportaron varianzas para RFI menores para vaquillonas en alimentación restringida (80 % *ad libitum*) que en *ad libitum;* resultados similares encontramos en este trabajo cuando comparamos la variación de RHP en otoño vs. Primavera, donde, además, las hembras del grupo de alta eficiencia presentaron varianzas menores que el grupo de baja eficiencia. La menor variación en RFI reportada cuando los animales se encontraban en alimentación restringida sugirió que la variación en el apetito contribuiría mucho más a la variación en RFI de las vaquillonas con un mayor consumo de alimento, lo que determinaría una mayor deposición de grasa sin diferencias en eficiencia energética (Roberts et al., 2007, Lines et al., 2014). Sin embargo, como mencionamos anteriormente, no detectamos diferencias en composición corporal por ultrasonido en otoño entre vaquillonas HH y LL y en primavera, si bien el espesor de grasa en P8 fue significativo en el modelo de RHP, correlacionó negativamente con esta variable y tampoco difirió el espesor de grasa subcutánea entre los dos grupos. Por lo tanto, en este trabajo, si bien la varianza para RHP fue menor en otoño que primavera, las diferencias entre vaquillonas HH y LL sería resultado de una eficiencia de utilización de la energía diferencial. Es claro que se requiere más investigación sobre la medición de la eficiencia en animales con nutrición restringida, situación típica para las vacas de carne durante gran parte del año en sistemas de producción basados pasturas nativas o naturales.

Los trabajos que han estudiado la asociación entre RFI y la fertilidad o la productividad materna son escasos. Investigaciones previas indicaron que la tasa de preñez, parto o destete no se asoció con RFI, o disminuyó en vacas de carne de bajo vs. alto RFI (Kenny et al., 2018). Contrario a lo reportado en la bibliografía, en ambos experimentos, las vaquillonas más eficientes (PHE y HH) presentaron una respuesta reproductiva más temprana (evidenciada por menos días a fase luteal o menores intervalos servicio-concepción, y/o días de parto y mayor porcentaje de vaquillonas inseminadas). Varios autores han asociado fechas de parto más tardías en vaquillonas de bajo RFI (alta eficiencia) a pubertades más tardías y menores niveles de grasa corporal (Arthur et al., 2005, Basarab et al., 2011, Shaffer et al., 2011). Sin embargo, las vaquillonas más eficientes (PHE y HH) presentaron mayores PV (y, por lo tanto, posiblemente mayores niveles de grasa; exp 1) o mayor porcentaje de engrasamiento medido por ultrasonido a nivel del P8 (exp. 2), lo que podría explicar nuestros resultados, ya que la pobre respuesta reproductiva ha sido asociada a animales más magros más que a la eficiencia en sí (Kenny et al., 2018). Esta respuesta reproductiva temprana favorable a las vaquillonas de alta eficiencia se perdió en el segundo entore (exp. 1) y no reflejaron en una productividad materna diferente al primer parto (exp. 2), ya que el peso de los terneros al nacer y destete no se diferenciaron entre grupos de eficiencia.

4.2 CONCLUSIONES

La variable RHP mostró estar correlacionada con el EBV paterno para RFI, siendo una medida repetible y heredable, lo que permitiría su uso en un programa de selección a la vez que aparentaría ser una medida de eficiencia robusta, ya que se asoció a la eficiencia energética y alimenticia. Los resultados de ambos experimentos indicaron una menor actividad metabólica y un menor requerimiento de energía de mantenimiento por parte de las vaquillonas de alta eficiencia (clasificadas de acuerdo al RFI paterno o RHP individual) sin perjuicio de la performance reproductiva. Futuros trabajos deberán continuar explorando la RHP como medida de eficiencia para animales en pastoreo, validarla con medidas conjuntas de RFI y RHP e incluir otros estados fisiológicos o funciones productivas (gestación-lactación) y niveles de alimentación (mantenimiento vs. ganancia) representativas del sistema criador de base pastoril, así como las bases biológicas que explican esta característica.

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