Does diverse grazing behavior of suckler cows have an impact on predicted methane emissions?1

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ABSTRACT: A modeling study based on a dataset from a large-scale grazing study was used to identify the potential impact of grazing behavior and performance of diverse cow genotypes on predicted methane (CH₄) emissions. Lactating cows grazing extensive seminatural grassland and heath vegetation were monitored with Global Positioning System collars and activity sensors. The diet selected by cows of 3 different genotypes, Aberdeen Angus cross Limousin (AxL), Charolais (CHA), and Luing (LUI), was simulated by matching their locations during active periods with hill vegetation maps. Measured performance and activity were used to predict energy requirements, DMI, and CH₄ output. The cumulative effect of actual performance, diet selection, and actual physical activity on potential CH₄ output and yield was estimated. Sensitivity analyses were performed for the digestibility of intake, energy cost of activity, proportion of milk consumed by calves, and reproductive efficiency. Although with a better performance (P < 0.05), LUI required less total energy than the other genotypes (P < 0.001) as the other 2 spent more energy for maintenance (P < 0.001) and activity (P < 0.001). By selecting a better quality diet (P < 0.03), estimated CH₄ of CHA cow–calf pairs was lower than AxL (P = 0.001) and slightly lower than LUI (P = 0.08). Energy lost as CH₄ was 0.17 and 0.58% lower for LUI than AxL and CHA (P < 0.002). This study suggests for the first time that measured activity has a major impact on estimated CH₄ outputs. A 15% difference of the cow–calf pair CH₄ was estimated when using different coefficients to convert actual activity into energy. Predicted CH₄ was highly sensitive to small changes in diet quality, suggesting the relative importance of diet selection on heterogeneous rangelands. Extending these results to a farm systems scale, CH₄ outputs were also highly sensitive to reductions in weaning rates, illustrating the impact on CH₄ at the farm-system level of using poorly adapted genotypes on habitats where their performances may be compromised. This paper demonstrates that variations in grazing behavior and grazing choice have a potentially large impact on CH₄ emissions, illustrating the importance of including these factors in calculating realistic national and global estimates.

Key words: hill ground, lactating cows, seminatural vegetation

INTRODUCTION

Grasslands cover approximately 30 to 40% of the earth’s surface (White et al., 2000; Reid et al., 2004) and provide the opportunity to raise 30% of the total global livestock population, which contributes 25% of the total meat production from ruminant species (McLeod, 2011). There is considerable uncertainty in the prediction of CH₄ emissions from extensively managed ruminants on rangelands (Lassey, 2008). Therefore, understanding factors that can improve the accuracy of CH₄ predictions from these environments is critical for realistic inventories of emissions and for identifying routes for mitigation at farm, national, and global levels.

Various cattle breeds of diverse characteristics are used in cow–calf breeding systems (Roughsedge et al., 2001), which can differ in CH₄ emissions under controlled conditions (Estermann et al., 2002). Previous
studies have mentioned breed differences in the foraging behavior of cattle on rangelands (Funston et al., 1991; Hessle et al., 2008), which could lead to different use of the available energy. Diurnal grazing patterns affected CH₄ production (Lockyer and Champion, 2001; Dengel et al., 2011). However, the capacity of different breeds to select different diets of different digestibility or to modify their energy expenditure through different activity patterns and vegetation selection has not yet been considered in CH₄ evaluations. Studies involving grazing animals are usually performed using homogeneous pastures (McCaughey et al., 1999; Lockyer and Champion, 2001; Allard et al., 2007; Dengel et al., 2011), minimizing the foraging selection process. Due to the difficulty of measuring CH₄ in extensive hill environments, this study aims to assess in a modeling exercise the scale of potential differences in predicted CH₄ emissions as a result of the grazing activity of diverse genotypes by using actual data from a large scale study of grazing behavior of free-range beef cows—calves on seminatural hill vegetation.

MATERIALS AND METHODS

Database

A database from a large scale 4 yr study of grazing behavior (Umstätter et al., 2009) containing monthly BW and BW change (BWC) of lactating, pregnant spring calving cows and their calves was used in this study. This experiment was ethically reviewed and approved by the Scotland’s Rural College (SRUC) Animal Experiment Committee. This database contains information on horizontal and vertical movements measured on cows by Global Positioning System (GPS) collars (AgTrex BlueSky Telemetry, Aberfeldy, Scotland). Horizontal movements covered the x and y planes whereas vertical movements refer to the z plane. The GPS collars had integrated activity sensors, which measure minimum and maximum pitch and roll tilt. Information of activity and location is collected every minute. More details of the methodology can be found in Umstätter et al. (2008). The use of activity sensors enable the characterization of total hours of active and inactive time during the day (considering grazing, drinking, grooming, and walking as active time and lying, while sleeping, or ruminating and standing inactive as inactive time) based on the methodology developed for sheep by Umstätter et al. (2008). This information was collected from 3 genotypes representing 3 very divergent size and production characteristics: Aberdeen Angus cross Limousin (AxL; n = 15), known as a typical crossbred suckler cow type, Charolais (CHA; n = 15), a large sized cow viewed in the UK as suited to more intensive systems, and Luing (LUI; n = 15), a typical hardy hill cow believed to be well adapted to hill grasslands in Scotland. The methodology adopted to measure the behavior of the cows was considered the most appropriate given the characteristics of the extensively managed hill area where these experiments were performed.

Vegetation, Activity, and Diet Selection

Performance and activity data were collected from lactating cows of the 3 genotypes grazing extensive, seminatural hill grassland and heath during the summer (from July to September) over 4 consecutive years (2007 to 2010), with a mean stocking rate of 0.23 cow—calf/ha. The grazing study used 2 adjacent hills, Castlelaw Hill (Hill 1) and Turnhouse Hill (Hill 2), located in southeast Scotland at 55.87° N, 3.24° W and 55.85° N, 3.27° W, respectively. Hill 1 covers an area of 287 ha and has an altitudinal range from 245 to 488 m while Hill 2 covers an area of 187 ha and has an altitudinal range from 230 to 505 m. A detailed vegetation map of the study site was produced from aerial photography and field survey. An aerial photograph of the 2 hills was visually examined and the different vegetation patches present on the site were initially identified. The site was then visited to identify and classify the different vegetation types observed on the aerial photograph. The vegetation at over 240 ground control points was assessed and the GPS location, vegetation type, and structure were recorded. The vegetation data was then classified into 10 major plant community types. A vegetation map was then constructed from the field survey data using a supervised classification of the aerial photograph using ER Mapper image processing software (Version 6.4, Earth Resource Mapping, Perth, Australia). Validation of the map was then performed by field survey. Predominant indigenous species in the vegetation were dwarf shrubs Calluna vulgaris and Vaccinium myrtillus, grasses Nardus stricta, Agrostis capillaris, Festuca ovina, and Deschampsia cespitosa, the fern Pteridium aquilinum, and the rush Juncus effusus. Monthly values of dry matter digestibility (DMD) of these different plant species are described in Table 1.

The resulting activity and GPS data points were then linked to the vegetation maps using the Geographic Information System ArcGIS 9.2 (Environmental Systems Research Institute Inc., Redland, CA). In a review, Kilgour (2012) mentioned that for between 90 and 95% of the day animals are grazing, resting, or ruminating. With the information provided by the activity sensors, grazing activity (active time) can be differentiated from ruminating and resting (inactive time). As a result, combining information from activity sensors, GPS collars, and Geographic Information System (GIS), an estimation of the active time that cows spent on each vegetation type was obtained. De Vries and Daleboudt (1994) demonstrated that grazing time is the best predictor of patch selectivity.
Therefore, the actual measured active time was used in this study for simulating the diet selected by the cows. To simulate the diet selection, the time that cows spent active on each plant community was used as an equivalent surrogate measure of the proportion of species selected and present in the daily diet (Table 2). A predicted value of DMD of the selected diet was estimated for each month for each genotype for all years by multiplying the monthly digestibility value of each species with their proportion of time predicted previously. Cows spent some of their active time in habitats dominated by woodlands, scree, Ulex europaeus, and Luzula sylvatica. These areas were judged not to contribute with palatable forage for cattle feeding and their digestibility was assumed to be null when estimating their contribution to the total quality of the selected diet. It was assumed that cows consumed a diet that consisted of the dominant species within each plant community. There are many factors determining the quality of the selected forage while grazing communities of different plant species (Hodgson and Illius, 1996). However, measurements of, for example, the composition of the plant communities or the bulk density were not available. Given the extent of the area used for the experiments, the locations of the cows were unknown until data from the GPS collars were downloaded and analyzed. The 4-yr study was designed to characterize the natural behavior of cows grazing extensively managed rangelands without human intervention and the most appropriate remote sensing technology was adopted for those conditions.

To calculate distances walked, we summed up the mean activity time per day (hours) for the 3 different breeds and multiplied that with the mean speed of movement (km/h) during active times (speed × hours = distance). The activity per day was calculated from data collected with a 1-min resolution. However, mean speed was calculated from measures of location taken every 15 min.

This was done to reduce the GPS error whereby a stationary cow appears to move both horizontally and vertically. The 15-min interval was the best interval to calculate distances walked as the calculated average slope from the horizontal and vertical movement data matched the average slope calculated from the topographic map.

### Energy, Intake, and Methane Estimations

Metabolic energy requirements of lactating cows and calves at side (cow–calf) were estimated using prediction equations in Agricultural and Food Research Council (AFRC; 1993). These calculations were based on actual data on BW, BWC, pregnancy, and lactation stages, digestibility of the selected diet, and physical activity as horizontal and vertical meters walked per day.

The energy required for activity was initially predicted using the energy expenditure coefficient suggested by AFRC (1993; 2.6 and 28 J·kg BW\(^{-1}\)·m\(^{-1}\) horizontal and vertical, respectively). As different values for energy expenditure of grazing animals on the hill ground are available in the literature (Brosh et al., 2010; 0.62 and 5.17 J·kg BW\(^{-1}\)·m\(^{-1}\) horizontal and vertical, respectively), a sensitivity analysis was performed to study the impact on the results of using a more suitable coefficient of energy allowance.

The cow–calves on the experiment were towards the end of their lactation (wk 16 to 24) and at this stage it is generally known that calves are able to graze and ruminate. For instance, Le Du et al. (1976) reported values of grass intake between 0.7 to 3 kg OM calf\(^{-1}\)·d\(^{-1}\). However, little information is available in the literature regarding the milk:grass ratio of calves grazing extensive hill vegetation and in the present study this ratio was unknown. The ME for lactation was estimated to be proportional.
to the amount of milk the calves were estimated to consume. This was predicted from the total ME requirements of the calf depending on its actual BW and BWC, and it was assumed that the milk intake represented 50, 40, and 30% of the calves’ diet in July, August, and September, respectively. These proportions were selected as they were in agreement with the amount of milk production of beef cows of similar genotypes and stage of lactation (Funston et al., 1991; Wright et al., 1994; Sinclair et al., 1998a). Furthermore, a maximum milk production potential was determined by the equation milk yield (kg/d) = 8.0 × ln(0.121 × exp(−0.0048 × n)), in which n denotes week of lactation (AFRC, 1993) and lactation was limited by this amount. Under these assumptions, the estimated milk consumed by calves was always below the potential milk production of cows. Later, given the potential uncertainty of CH₄ outputs due to these assumptions, a sensitivity analysis of milk:grass ratio was also undertaken.

Based on the predicted energy content of the complete diet, weighted by differing amounts of hill grasses and differing DMD, DMI was then estimated as the amount of feed each cow and calf needed to cover their energy requirements (AFRC, 1993). As the predicted DMD adds potential error and uncertainty, a sensitivity analysis of this factor was performed.

The potential CH₄ emission was predicted by an equation for beef cattle based on this DMI value as CH₄ (g/d) = (35.1 × DMI (kg/d) + 14.7) × 1,000/1,400, modified from Yan et al. (2009). This equation was selected as it was developed from beef cows fed forage based diets and it is sensitive to changes of measured performance and diet quality. Methane outputs were expressed as absolute emission per animal (g·cow⁻¹·d⁻¹ and g·calf⁻¹·d⁻¹) and per cow–calf pair (g·cow–calf pair⁻¹·d⁻¹) and as energy loss as CH₄ per cow–calf pair per unit of GE intake (GEI; CH₄ yield = [pairCH₄ (MJ/d) x 100 (MJ)]/GEI (MJ/d)).

Means and deviations of observed individual performance were used to study the potential effect of measured activity on CH₄ emissions at the herd level. Methane emissions per kilogram of production (CH₄, kg/kg production) during July, August, and September (92 d) were estimated from a simple simulated breeding herd of 100 cows and 80 sellable calves, and divided per kilogram of calf BW produced in that period (calf BW minus calf birth BW). The CH₄ of the system was then estimated as: [cow–calf pair CH₄ × 100 × 92]/[(calf BW – calf birth BW) × 80]. Due to the uncertainty of the impact of reproductive efficiency on the final herd results, another sensitivity analysis was performed on this factor.

The cumulative effect of actual performance, diet selection, and physical activity on potential CH₄ output and yield was estimated in 5 incremental calculation tiers (Table 3), considering

<table>
<thead>
<tr>
<th>Tier</th>
<th>Performance</th>
<th>Activity</th>
<th>Diet</th>
<th>Actual values used</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Maintenance</td>
<td>Standard</td>
<td>Standard</td>
<td>BW</td>
</tr>
<tr>
<td>2</td>
<td>Actual</td>
<td>Standard</td>
<td>Standard</td>
<td>BW + performance</td>
</tr>
<tr>
<td>3</td>
<td>Actual</td>
<td>Actual</td>
<td>Standard</td>
<td>BW + performance + activity</td>
</tr>
<tr>
<td>4</td>
<td>Actual</td>
<td>Standard</td>
<td>Actual</td>
<td>BW + performance + diet</td>
</tr>
<tr>
<td>5</td>
<td>Actual</td>
<td>Actual</td>
<td>Actual</td>
<td>BW + performance + activity + diet</td>
</tr>
</tbody>
</table>

(1) actual variable BW but with identical performances (maintenance level only), an average DMD of the grazed vegetation (0.567 kg/kg DM), and a standard activity as recommended by AFRC (1993) for beef cows (0.0071 MJ kg⁻¹ d⁻¹),

(2) as (1) but with actual individual performance data, considering cows’ and calves’ BWC, lactation, and pregnancy (Table 4; Fig. 1),

(3) as (2) but using actual activity patterns (horizontal and vertical distances walked per day; Table 4) and again with average diet DMD,

(4) as (2) but with different diet DMD predicted by actual data on activity of cattle on different habitats and, as in (1) and (2), with standard activity, and

(5) all the actual effects from preceding tiers combined.

**Experimental Design and Statistical Analysis**

Two fenced grazing areas (Hill 1 and 2) with different proportions of the main vegetation types were used during the grazing study. In yr 1 (2007), 15 cows and calves of each genotype grazed together on Hill 1 for 4 wk (from July 3 to August 8) and then on Hill 2 for another 4 wk (from August 21 to September 20). In the subsequent 3 yr of the study (2008 to 2010), 2 genotypes were used each year for 8 wk, alternating genotype combinations subsequently (CHA and LUI from July 7 to September 10, 2008, AxL and LUI from July 2 to September 10, 2009, and AxL and CHA from July 5 to September 10, 2010). As a result, 3 repetitions from each genotype were obtained over the 4 yr of the study. Some animals were replaced during the experiment. Thus, a total of 44, 45, and 42 observations of performance were obtained for AxL, CHA, and LUI, respectively, with cows and calves independently weighed before and after each experimental period. No collars were lost during the experiment.

Average values per month for each year were available for the activity (h/d) and distances walked (km/d) for each genotype and the same for DMD of the selected diet. The DMD of selected diets (n = 27) was compared among genotypes using year, month, and grazing area (Hill 1 or 2) as covariates.
Table 4. Means ± SE of actual distances walked, BW, BW change (BWC), predicted DM digestibility (DMD) of the diet, intake, and methane outputs from Aberdeen Angus cross Limousin (AxL; n = 44), Charolais (CHA; n = 45), and Luing (LUI; n = 42) pregnant lactating cows with calves at side grazing seminatural hill grasslands

<table>
<thead>
<tr>
<th>Activity, m/d</th>
<th>AxL</th>
<th>CHA</th>
<th>LUI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horizontal</td>
<td>4,528.9 ± 331.00</td>
<td>4,718.0 ± 290.44</td>
<td>3,881.4 ± 309.27</td>
</tr>
<tr>
<td>Vertical</td>
<td>619.9 ± 20.20</td>
<td>636.1 ± 31.91</td>
<td>566.1 ± 34.14</td>
</tr>
<tr>
<td>BW, kg</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cows</td>
<td>711.9 ± 4.90b</td>
<td>785.1 ± 5.46a</td>
<td>622.3 ± 5.14a</td>
</tr>
<tr>
<td>Calves</td>
<td>183.3 ± 3.44a</td>
<td>181.2 ± 3.60a</td>
<td>168.0 ± 3.84a</td>
</tr>
<tr>
<td>BW change, g/d</td>
<td>-166.8 ± 29.40b</td>
<td>-143.9 ± 50.54b</td>
<td>63.7 ± 22.49a</td>
</tr>
<tr>
<td>Cow BWC</td>
<td>976.6 ± 19.09b</td>
<td>1,000.0 ± 13.03b</td>
<td>1,042.7 ± 14.97b</td>
</tr>
<tr>
<td>Calf BWC</td>
<td>520 ± 24.0a</td>
<td>502 ± 23.4a</td>
<td>495 ± 20.1b</td>
</tr>
<tr>
<td>Digestibility</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DMD, g/kg DM</td>
<td>486 ± 21.7b</td>
<td>520 ± 24.0a</td>
<td>495 ± 20.1b</td>
</tr>
<tr>
<td>Intake</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cow DMI, kg·d⁻¹</td>
<td>20.5 ± 0.37a</td>
<td>19.1 ± 0.28b</td>
<td>18.8 ± 0.33b</td>
</tr>
<tr>
<td>Cow GEI, MJ·d⁻¹</td>
<td>372.3 ± 6.50a</td>
<td>334.0 ± 5.46a</td>
<td>349.5 ± 5.42a</td>
</tr>
<tr>
<td>Methane¹</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CH₄, g·cow⁻¹·d⁻¹</td>
<td>524.3 ± 9.17a</td>
<td>489.7 ± 7.06b</td>
<td>481.8 ± 8.15b</td>
</tr>
<tr>
<td>CH₄, g·calf⁻¹·d⁻¹</td>
<td>150.3 ± 5.37a</td>
<td>125.2 ± 4.05a</td>
<td>161.1 ± 6.84a</td>
</tr>
<tr>
<td>CH₄, g·pair⁻¹·d⁻¹</td>
<td>674.5 ± 13.64a</td>
<td>614.9 ± 10.36a</td>
<td>642.9 ± 14.24a</td>
</tr>
<tr>
<td>CH₄, %GEI pair⁻¹·d⁻¹</td>
<td>7.89 ± 0.004b</td>
<td>8.30 ± 0.062a</td>
<td>7.72 ± 0.072a</td>
</tr>
<tr>
<td>CH₄, kg/kg production</td>
<td>0.56 ± 0.051a</td>
<td>0.53 ± 0.010a</td>
<td>0.57 ± 0.059a</td>
</tr>
</tbody>
</table>

¹Within a row, means without a common superscript differ (P < 0.05).
²GEI = GE intake.
³Predicted with the equation CH₄ (g/d) = [35.1 × DMI (kg/d) + 14.7] × 1,000/1,400; modified from Yan et al. (2009).
⁴Kilograms of CH₄ produced by the cow–calf pair during the 3 mo of experiment per kilogram of BW produced on farm assuming 20% of replacement rate, calculated as: [cow–calf pair CH₄ × 100 (herd) × 92 (d)]/[calf BW–calf birth BW) × 80 (sellable calves)].

Individual BW of cows and of calves was combined with average values of activity, distances walked, and DMD for modeling energy requirements, DMI, and CH₄. Within and between calculation tiers, genotypes were compared for their energy requirements, DMI, and predicted CH₄ emissions. The CH₄ output of the simulated herds were compared across genotypes using 3 repetitions (years) per genotype.

Results were analyzed in a completely randomized design with genotypes or calculation tiers as factors, using the GLM procedure of SAS (SAS Inst. Inc., Cary, NC). For comparisons among calculation tiers, the effect of tier and genotype interaction was analyzed. Preplanned contrasts were used to calculate differences among genotypes and calculation tiers. The MEANS procedure was used to calculate means and standard errors.

Sensitivity Analyses

Assumptions were made in this study to complete the dataset available from long-term experimental data. Assumptions affecting predicted energy requirements (such as energy cost of activity and milk consumed by calves), values of DMD of intake, and reproductive efficiency of cows are all likely to have a major and direct impact on the predicted values of CH₄ emissions and outputs from these type of systems (Reynolds et al., 2011; Ricci et al., 2013) but the relative importance of the variation of these factors on predicted CH₄ were not well understood. Therefore, sensitivity analyses were performed for each of these factors to understand the scale of the impact of using different assumptions and the likely error or uncertainty of using particular assumptions.

Calculations of the energy cost of activity were made using the coefficients for energy expenditure suggested by either AFRC (1993) or Brosh et al. (2010). They were applied to the actual observed data of horizontal and vertical distances walked to study the impact on the final results of the system by using more adequate coefficients than those used in current models.

The amount of milk consumed by calves represents an important part of both cow and calf energy requirements, having a direct effect on the final CH₄ results. Therefore, to illustrate the effect of a different milk:grass ratio of the calves’ diet on CH₄ estimation, 5 levels of milk consumption of 100, 75, 50, 25, and 0% for each of the 3 mo were used for simulation.

Values of DMD used in this study were obtained from the literature and were not measured on site as such in situ measurement of DMD intake of free ranging cattle grazing in complex habitats without potentially modifying behavior could not be undertaken. Therefore, a range of levels of DMD values (49, 50, 51, 52, 53, 54, 55, 60,
and 65%) for each of the 3 mo was used to simulate both the effect of cattle selecting different qualities of pasture intake and of using literature data for rangeland systems that have highly variable temporal and spatial distribution of vegetation quality.

To understand how scaling up from a relatively controlled and short time scale of measurement to the issues that affect farm systems, a fourth sensitivity analysis was performed. This assessed the potential effects of different reproductive efficiencies among genotypes on the overall CH₄ emissions at the cow–calf system level. A range from 60 to 100% of weaning rates were then applied to the herds to illustrate the impact of this efficiency factor that is likely to vary between farming systems and among breeds.

### RESULTS AND DISCUSSION

#### Activity

The total active time recorded on the database averaged 9.2 ± 0.27, 9.8 ± 0.48, and 10.2 ± 0.44 h·cow⁻¹·d⁻¹ for AxL, CHA, and LUI, respectively. On average, over the whole experiment CHA cows tended to walk more horizontal and vertical distances than AxL and LUI (Table 4). Results found in the literature are inconsistent regarding breed differences on activity patterns. With 6- to 9-yr-old lactating beef cows, Funston et al. (1991) observed that Simmental × Hereford cows tended to walk longer distances than pure Hereford and its crosses with Aberdeen Angus even though no differences in BW were reported. In a different trial of the same study, although prior differences in BW were observed, no differences in the distances walked were found among other breed types of younger cows (3 yr old). In contrast, Hessle et al. (2008) found that heifers of a traditional Swedish breed Vânæko (small frame) were more active than the larger CHA when grazing heterogeneous seminatural grasslands. In the present study, comparing data from 6- to 7-yr-old cows, CHA (heavier breed) tended to be more active than smaller frame genotypes (a traditional breed). These results differed from those reported by Hessle et al. (2008), probably due to the fact that they used a smaller grazing area (2.2 to 4.1 ha), younger cattle (8 mo old), and more homogeneous vegetation than those in the present study.

Minimum and maximum distances walked observed in the present study for all genotypes were 3.0 to 6.0 and 0.5 to 0.8 km·cow⁻¹·d⁻¹ in horizontal and vertical direction, respectively. These ranges are within values reviewed by Kilgour (2012) of daily distances walked from 1.7 to 12.6 km/d although ranges observed in the present study were greater than those reported previously from foothill grazing cows, which had a maximum of 3.6 and 0.12 km/d horizontally and vertically, respectively (Brosh et al., 2010). In the study by Brosh et al. (2010), cows were allocated to paddocks of 107 ha with an average stocking rate of 0.48 cows/ha. The paddocks used to collect the dataset of the present study were larger, with about half the stocking rate of Brosh et al. (2010), which could explain the greater distances observed.

#### Energy Requirements

As expected, energy required for maintenance ($P < 0.001$) and production ($P < 0.05$) differed among genotypes (Fig. 1), reflecting measured performance data. Physical activity contributed significantly to total ME required ($P < 0.001$). Combining the observed distances walked with the coefficients of energy allowance suggested by AFRC (1993), they represented 26, 29, and 23% of the total ME for AxL, CHA, and LUI, respectively ($P < 0.001$; Table 4).

#### Diet Selection and Intake

The estimated DMD of selected diets was significantly different for grazing area ($P < 0.001$), month ($P < 0.001$), and genotype ($P = 0.015$), without differences among years ($P = 0.90$). There was no effect of the interaction between genotype and month or grazing area ($P > 0.25$) on estimated DMD. The resulting DMD of the diet selected by CHA was significantly greater than AxL and LUI ($P = 0.006$ and 0.026, respectively), without differences between the last 2 ($P = 0.50$; Table 4). Estimated DMD of selected diets from cows of different genotypes grazing heterogeneous vegetation has not been reported previously. Estimated DMD values were lower and estimated DMI from back-calculations were higher than expected (Table 4). This suggests that actual values of DMD of the diet could have been higher as cows could have selected more than what was simulated. For simulation purposes, using the proportion of time spent on a particular plant community to estimate its importance on a daily basis was con-
Cattle grazing behavior and methane emissions considered the most appropriate approach to estimate monthly quality of the selected diet given the type of data available. This is in agreement with observed foraging selection in similar types of grassland, where the distribution of the grazing time was better explained by matching selectivity with digestibility of the selected patches (de Vries and Daleboudt, 1994). Therefore, the low values of DMD reflect the limited information available on quality of heterogeneous vegetation and the potential improvement of the quality of the diet due to selectivity. Although in vitro digestibility of the available grassland may be measured, this still does not reflect the fact that diverse cattle breeds may select a different diet quality, and therefore there is scope for considerable variation in true in vivo digestibility. As far as the authors are aware, this is the first attempt to combine GPS and activity sensor data with GIS maps for simulation purposes and further direct measurements are needed to validate the results obtained.

There was no difference on DMI between CHA and LUI ($P = 0.50$) whereas LUI tended to have greater GEI than CHA ($P = 0.06$; Table 4). The DMI of AxL cows was significantly higher than CHA ($P < 0.001$) and LUI ($P = 0.003$). Although the estimated DMD of the diet selected by AxL and LUI was similar, AxL cows required more energy than LUI, explaining the higher DMI of AxL cows. On the other hand, AxL and CHA required a similar amount of energy, but CHA selected a significantly higher quality diet and therefore AxL were required to eat significantly more than CHA cows. Little information is available regarding intakes of lactating beef cows on indigenous grasslands. Studying intake-related variables, Funston et al. (1991) observed that breeds of greater milk yield (Tarentaise x Simmental x Hereford) tended to have greater bite rate than pure Hereford, with no differences on grazing time and distances traveled on foothill grasslands. This supports the theory that breeds adapted to unfavorable conditions (i.e., Tarentaise vs. Hereford) have the ability to modify their grazing behavior to meet their requirements in these conditions.

**Methane Estimation**

Estimated CH$_4$ outputs from cow–calf pairs (CH$_4$pair; g·pair$^{-1}$·d$^{-1}$) differed among genotypes (Table 4). The CH$_4$pair from AxL was significantly greater than CHA ($P = 0.001$) and tended to be greater than LUI ($P = 0.08$), without differences between the last 2 ($P = 0.12$). The literature is not yet consistent on the effect of genotype on CH$_4$ emissions under highly controlled conditions such as respiration chamber based measurements. Previous studies did not find differences in CH$_4$ (L/d) outputs comparing Holstein vs. CHA × Simmental yearling heifers (Boadi and Wittenberg, 2002) while others comparing more divergent breeds did mention differences in CH$_4$ (g/d) emissions from Holstein vs. a Brazilian crossbred (Pedreira et al., 2009). Based on ratios of grass:milk consumption assumed for the main calculations, CH$_4$ emitted from calves contributes 22, 20, and 25% to the cow–calf pair emissions of AxL, CHA, and LUI, respectively (Table 4). Although differences were small, the energy lost as CH$_4$ from the cow–calf pair (% GEI·pair$^{-1}$·d$^{-1}$) was significantly lower for LUI ($P < 0.002$) and greater for CHA ($P < 0.001$; Table 4), indicating that LUI cow–calf pairs made a 0.17 and 0.58% more efficient use of the energy compared with the AxL and CHA, respectively. At 100% weaning rate, the CH$_4$ yield of the simulated system (CH$_4$pair kg/kg of calf BW produced) was not affected by genotype ($P = 0.85$; Table 4).

Nevertheless, there are typically differences in reproductive efficiency among genotypes and the impact of this factor was studied later in a sensitivity analysis. There is no information about CH$_4$ emissions from mature beef cows of different breeds grazing seminatural grassland, and therefore, conclusions about breeds from this modeling study must be drawn with caution. However, issues related to the grazing selectivity of different genotypes have not been considered before in CH$_4$ studies. Therefore, this modeling exercise illustrates that these factors have potential impact on CH$_4$ estimates and can contribute to reducing the uncertainty around CH$_4$ predictions from extensive livestock farming.

**Contribution of Actual Performance, Activity, and Diet Quality**

Calculation tiers were used to illustrate the cumulative effect and the relative importance of considering factors with potential impact on CH$_4$ prediction. The interaction between genotype and tier was significant ($P < 0.001$), indicating that the contribution of actual data on BW, performance, activity, and diet quality was different among genotypes (Table 3; Fig. 2). The estimated CH$_4$pair using standard values of diet quality and activity was significantly different among genotypes, reflecting their different BW (tier 1, $P = 0.013$) and performance (tier 2, $P = 0.031$). Including actual values of observed activity (tier 3), CH$_4$pair increased by 25, 29, and 19% for AxL, CHA, and LUI, respectively (Fig. 2), compared with the CH$_4$pair estimated using a standard value of activity recommended by AFRC (1993; tier 2). Therefore, the tendency observed on measured physical activity to differ among genotypes became significant in terms total CH$_4$ emissions of the system ($P = 0.004$). Considering the calculated diet quality selected by each genotype (tier 4), the CH$_4$pair increased by 29, 15, and 32% of the CH$_4$pair in tier 2 for AxL, CHA, and LUI, respectively, over those estimated with a similar diet for all of them (Fig. 2) and was significantly different among genotypes.
(P < 0.001). Smaller increments on CH₄ pair for CHA than the other genotypes between tiers 2 and 4 reflect that the estimated DMD for CHA was more similar to the assumed average DMD than the other breeds. Compared with previous calculation tiers, including actual activity and estimated quality of selected diet (tier 5), CH₄ pair was 23, 28, and 13% higher than tier 4 for AxL, CHA, and LUI, respectively, and was lowest for CHA (P = 0.004; Table 4). This modeling exercise illustrated that considering the physical activity and potential diet selection that these genotypes may have as a result of diverse measured activity patterns has a significant impact on the predicted CH₄ emissions. Lassey (2008) suggested that the uncertainty associated with “bottom-up” estimates of CH₄ production based on controlled experiments was ±21%. Although this author mentioned grazing selectivity as contributing uncertainty to CH₄ estimates, he did not mention grazing activity as another source of uncertainty for predicting CH₄ outputs from extensively managed livestock. Therefore, the present study provides clear evidence of the importance of differentiating the grazing behavior that the 3 genotypes are expressing, affecting not only the energy required for different physiological functions and performance but also their carbon budget through quality of the selected diet, their activity, and final amount of feed estimated to be consumed.

Methane emissions are only one part of the overall carbon budget and the environmental impact of cattle grazing systems. There are likely to be other impacts on fecal and urinary outputs of cattle and on resulting fluxes of the combination of these outputs and their location, together with grazing impacts, on a range of carbon fluxes of the rangeland vegetation and soils (Derner and Schuman, 2007). Moreover, distinctive selection “pressure” of cattle breeds could have a long-term impact on biodiversity associated with sensitive seminatural vegetation by varying their activity patterns on different vegetation species and disturbing the condition and balance of species of these types of habitats.

**Sensitivity Analyses**

**Energy Cost of Activity.** Using the conversion factors of activity into energy suggested by Brosh et al. (2010), CH₄ output was 92 g·cow⁻¹·d⁻¹ and 98 g·pair⁻¹·d⁻¹ (18 and 15%) lower than applying the AFRC (1993) suggested coefficients (P < 0.001). This variation in the results due to the use of diverse conversion factors can lead to strongly biased carbon budgets, raising the question of which of these coefficients is more suitable to use. There are enormous differences between the studies reported here. While AFRC (1993) assumed coefficients obtained by Ribeiro et al. (1977) with animals walking on treadmills with 0 and 6 degrees of gradient, Brosh et al. (2010) used an alternative method to predict energy expenditure *in situ* from animals grazing on the hill ground and expressing their natural behavior. Both studies provide estimates of the energy cost of activity; hence, it is a matter of deciding if observations from animals that are able to express their natural behavior are more reliable than those from unnatural but controlled conditions.

The Intergovernmental Panel on Climate Change (IPCC, 2006) Tier 2 methodology for predicting energy requirements of cattle considers the cost of activity as an increment of 17% on the energy requirements for maintenance of animals grazing in small areas with high grass availability and a 36% increment for those grazing open range areas where activity constitutes a significant cost. In the present study, based on AFRC (1993) coefficients, the energy cost of activity was 60, 64, and 54% of those for maintenance whereas based on the Brosh et al. (2010) coefficients they represented 20, 21, and 19% for AxL, CHA, and LUI, respectively. It is difficult to find a clear explanation in the literature of how the energy allowance for activity is estimated in other studies using simulation models and system analysis. Indeed, in many studies it is unclear whether it is accounted for or not. Again, this study illustrates the magnitude of bias that can be expected depending on the methodology used and assumptions made regarding this factor. More accurate and precise estimations of animals’ activity in free-range conditions are crucial to reduce the uncertainty on the estimations of environmental impact of these types of production systems.

**Diet Digestibility.** As described above, using estimated DMD based on measured different foraging patterns, CH₄ pair was greater for AxL followed by LUI and CHA (Table 4). Simulating equal DMD levels (assuming no diet selection took place), CH₄ pair from CHA would be similar to AxL (P > 0.50) and both greater than
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LUI ($P = 0.011$ and $P = 0.042$, respectively). The sensitivity analysis demonstrated that if the DMD of CHA intake is 20 g/kg DM greater than AxL (an increment of 4% of DMD, only 0.3 MJ of ME greater), CHA will produce less CH$_4$ pair emissions than the other 2 genotypes ($P < 0.004$). Further simulations demonstrated that CHA and AxL would have to increase their DMD by 20 and 30 g/kg DM (4 and 6% increment, 0.3 and 0.5 MJ more, respectively) to have lower CH$_4$ pair emissions than LUI ($P < 0.001$ and $P < 0.031$, respectively; Fig. 3). Given the large variation that can be expected on the quality of the vegetation over the year and between years, results from this modeling study suggest that the observed trends among genotypes of different foraging behavior and selectivity should be taken into account for upcoming CH$_4$ estimations of free-range cattle grazing in extensive conditions and identified in uncertainty analysis for producing farm, national, or global inventories of CH$_4$ emissions. These results also illustrate that independent of genotype, which in practice may have relatively little effect, underlying diet choice and overall diet digestibility is important in characterizing CH$_4$ outputs from cattle grazed on heterogeneous pastures.

Although this is a modeling study with associated uncertainty, both the sensitivity of DMD and the shift from tier 3 to tier 4 calculations (considering diet selection or not) reflects the importance of considering variable DMD on predicted CH$_4$ emissions due to diet choice, which is truly unknown in reality.

The results of diet choice and energy use, though, are in agreement with the theory that animals are able to change their behavior to optimize their foraging activity and intake (de Vries and Daleboudt, 1994). Some animals spend more energy on getting better food; others use less energy by accepting poorer food. It was further observed in the present study that this spontaneous behavior differed among genotypes and had a significant impact on predicted CH$_4$ emissions. Therefore, cows produce less CH$_4$ by eating better food but produce more CH$_4$ by needing more energy to walk further to find it.

**Milk Production.** After maintenance, milk production is the most important energy allowance for productive functions of the cow and changes in this flux will affect energy intake and losses. Compared with a calf whose diet consists of 100% milk, reducing it to 75, 50, 25, and 0% of the diet will reduce the cow’s CH$_4$ emissions on average for the 3 genotypes by 1, 15, 87, and 186 g/d, respectively (Fig. 4). However at the same time, replacing milk by grass in the calves’ diet will increase their CH$_4$ production. Increments of 1, 8, 48, and 102 g/d were estimated in calves’ CH$_4$ production by changing the milk proportion at the above mentioned levels (Fig. 4). As reducing the milk proportion of the calf’s diet has a major impact on the cow rather than the calf, the overall cow–calf pair CH$_4$ output was reduced by 0, 7, 40, and 84 g/d if the proportion of milk in the calf’s diet is 75, 50, 25, and 0% compared with 100% milk. The sensitivity analysis showed that changing the previous assumptions towards 100, 75, 50, or 25% will only affect cow–calf pair CH$_4$ emissions by ±3%. Although information regarding the proportion of milk in calves’ diets is scarce, this sensitivity analysis shows that the assumptions made for calculations, which were based on previous studies of milk production, provided solid information and little variation on the final results are likely to occur by any biased assumptions.

**Reproductive Efficiency.** Although there were no differences on predicted CH$_4$ outputs of the system (kg CH$_4$/kg production) among genotypes (Table 4), these results assumed 100% production efficiency as all cows in the experiment were rearing calves. This is certainly not the case in reality at the farm system level. Genotypes are often reported to differ in their
reproductive efficiency, with different responses under different types of production system. For instance, it has been reported that CHA cows under unfavorable conditions have poor reproductive rates (Sinclair et al., 1998b). This index is an example of a major measure of efficiency that should be considered when drawing conclusions about management options at the system level. With the same reproductive efficiency, CHA had slightly lower CH4 outputs per kilogram of production than AxL and LUI (Table 4). In this study, the sensitivity analysis demonstrated that a decrease of 5 and 7% in weaning rate of CHA can cancel out this difference between AxL and LUI, respectively (Fig. 5).

Historical data of conception rates collected in the last 4 yr (2009 to 2012) at the SRUC Beef Research Centre (Easter Howgate, Edinburgh, UK) showed the AxL cows as the most reproductively efficient genotype followed by LUI and CHA (80, 75, and 65% conception). With a 65% weaning rate, CHA herds will produce 94 g CH4/kg production (14%) more than that expected from AxL at 80% weaning rate and 51 g CH4/kg production (7%) more than LUI at 75% weaning rate. Weaning rates for CHA have been mentioned to be 60.9% (Lamb et al., 1992). Other authors have published conception rates below this value (Sinclair et al., 1998b; Muller et al., 2010; Pellegrini and Lopes, 2011; Vaz et al., 2012), meaning that weaning rates can be even lower than 60% for this genotype. For AxL weaning rates were described to be 80.6% (Lamb et al., 1992) and 96% for LUI cows (Scheider and Distl, 1994). Under similar conditions as evaluated in the present study where cows cannot reach their energy requirements and lose weight, reproductive performances may be compromised and differences among genotype performance could become even larger.

**Conclusion**

By introducing measured performance and activity data into a modeling study, this study has demonstrated for the first time that differences in energy requirements driven by diverse physical activity have a potential impact on predicted CH4 emissions of extensively managed cow–calf systems. Furthermore, the study shows how different genotypes may deal with these differences through altering their foraging behavior, diet selection, and activity patterns. Observed patterns of activity contributed significantly to determining the trend of the estimated CH4 emissions among genotypes. The use of coefficients to convert activity into energy more appropriate for the type of landscape and extensive management are crucial. A gap in the knowledge of the relationship between energy expenditure of animals grazing across a range of slopes was identified, which could help to explain large differences observed in the literature. Methane estimations were highly sensitive to changes in quality of the diet, highlighting the importance of considering animal selectivity on heterogeneous grasslands in future carbon budgeting. At the farm-system level, this study demonstrates that differences in CH4 outputs in response to diverse grazing behavior can be as important as varying reproductive efficiency. Information about CH4 emissions from beef cows grazing rangelands is scarce and extrapolations from housed or grazing studies under dissimilar conditions are at risk of underestimating the uncertainty of the predictions. This modeling exercise further helps to illustrate the need to assess grazing adaptability of some genotypes to more challenging environments to improve the efficiency of cattle breeding on heterogeneous grasslands, both in terms of environmental impact and food supply.

**LITERATURE CITED**


