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1 **Temperament and dominance relate to feeding behaviour and activity in beef**

2 **cattle: implications for performance and methane emissions**

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16 Short title: Behaviour alter performance and methane in cattle

17

18 **Abstract**

19 In beef cattle, feeding behaviour and activity are associated with feed efficiency and

20 methane (**CH_4**) emissions. This study aimed to understand the underlying traits

21 responsible for the contribution of cattle behaviour to individual differences in feed

22 efficiency, performance and CH_4 emissions. Eighty-four steers (530±114 kg body

23 weight) of two different breeds (crossbreed Charolais and Luing) were used. The

24 experiment was a 2×2×3 factorial design with breed, basal diets (concentrate vs.

25 mixed) and dietary treatments (no additive, calcium nitrate, or rapeseed cake) as the

main factors. The individual dry matter intake (**DMI**; kg) was recorded daily and the body weight was measured weekly over a 56-day period. Ultrasound fat depth was measured on day 56. Based on the previous data, the indexes average daily gain, food conversion and residual feed intake (**RFI**) were calculated. The frequency of meals, the duration per visit and the time spent feeding per day were taken as feeding behaviour measures. Daily activity was measured using the number of steps, the number of standing bouts and the time standing per day. Agonistic interactions (including the number of contacts, aggressive interactions, and displacements per day) between steers at the feeders were assessed as indicators of dominance. Temperament was assessed using the crush score test (which measures restlessness when restrained) and the flight speed on release from restraint. Statistical analysis was performed using multivariate regression models. Steers that spent more time eating showed better feed efficiency ($P=0.039$), which can be due to greater secretion of saliva. Feeding time was longer with the mixed diet ($P<0.001$), Luings ($P=0.009$) and dominant steers ($P=0.032$). Higher activity (more steps) in the pen was associated with poorer RFI, possibly because of higher energy expenditure for muscle activity. Frequent meals contributed to a reduction in CH_4 emissions per kg DMI. The meal frequency was higher with a mixed diet ($P<0.001$) and increased in more temperamental ($P=0.003$) and dominant ($P=0.017$) steers. In addition, feed intake was lower ($P=0.032$) in more temperamental steers. This study reveals that efficiency increases with a longer feeding time and CH_4 emissions decrease with more frequent meals. As dominant steers eat more frequently and for longer, a reduction in competition at the feeder would improve both feed efficiency and CH_4 emissions. Feed efficiency can also be improved through a reduction in activity.

Selection for calmer cattle would reduce activity and increase feed intake, which may improve feed efficiency and promote growth, respectively.

Keywords

Livestock, Greenhouse gas emissions, Growth, Mitigation, Social behaviour

Implications

Reducing methane emissions and increasing the production efficiency are key goals to make livestock production sustainable. At an animal level, these can be accomplished through changes in feeding behaviour and activity of cattle. We found that a reduction of cattle dominance and temperament can work as strategies to manipulate feeding behaviour and activity towards more sustainable livestock. Herd management for reducing feeding competence will promote longer and more frequent meals benefiting feed efficiency and methane emissions. In turn, breeding for calmer cattle can have two effects, reducing activity which benefits efficiency and increase feed intake promoting growth.

Introduction

Livestock are an important contributor to anthropogenic greenhouse gas (**GHG**) emissions. Enteric fermentation from non-dairy cattle accounted for 21% of the total emissions from agriculture in the period between 2002 and 2012 (FAOSTAT, 2014). The main GHG emitted by cattle is methane (**CH_4**) which has a warming potential 25 times higher than carbon dioxide.

Feed efficiency and growth performance have repeatedly been found to be associated with feeding behaviour in beef cattle (Nkrumah *et al*., 2007; Kelly *et al*.,

75 2010). For example, a longer feeding time (Schwartzkopf-Genswein *et al*., 2002) and

76 more frequent feeding bouts (Schwartzkopf-Genswein *et al*., 2011) are associated

77 with higher productivity (average daily gain) in feedlot cattle, and a better feed

78 efficiency (**FCR**). However, it is less clear how feeding behaviour affects efficiency

79 for different breeds and diets.

80 Physical activity can influence total energy expenditure and feed efficiency

81 (Susenbeth *et al*., 1998; Herd *et al*., 2004). According to different studies reviewed

82 by Herd *et al*. (2008), beef cattle that are more efficient may engage in less daily

83 activity which may have evolved as a mechanism to minimise energy expenditure.

84 However, there are no studies on how differences in feeding behaviour and activity

85 in the pen affects CH_4 emissions in beef cattle.

86 Feeding behaviour and activity are determined by dominance and temperament. For

87 instance, a dominant animal would be able to access resources as it wished,

88 whereas a subordinate might have to adapt to dominant group member preferences.

89 Temperament reflects repeatable between-individual differences in behavioural

90 responses to a challenging situation. Excitable temperaments measured during

91 routine handling have been associated with higher activity in undisturbed group pens

92 of beef cattle (MacKay *et al*., 2013). Cafe *et al*. (2011) found that excitable steers

93 (castrated males) showed shorter feeding bouts and lower feed intake when kept in

94 groups. These behavioural differences could contribute to the improved growth and

95 feed efficiency in calmer beef cattle found previously (Voisinet *et al*., 1997; Turner *et*

96 *al*., 2011). This study aimed at understanding the contribution of cattle behaviour to

97 individual differences in feed efficiency, performance and CH_4 emissions. Therefore,

98 we investigated the association between feeding behaviour and activity with feed

4

99 efficiency and CH_4 emissions and whether this can be predicted by temperament

100 and dominance in beef cattle.

101

102 **Materials and methods**

103 *Animals and experimental design*

104 This experiment was part of a larger project to investigate the effect of cattle breed

105 types, concentrate/fibre ratio and dietary CH_4 mitigation strategies on performance,

106 efficiency and CH_4 (Duthie *et al.* 2015; Troy *et al.* 2015).

107 The experiment followed a 2 x 2 x 3 factorial design, with two breeds of cattle, two

108 basal diets and three dietary additive treatments. Eighty-four castrated male beef

109 cattle (steers) (Charolais-sired (**CHx**) n=42; Luing n=42) of 530±114 kg body weight

110 were housed at the SRUC Beef Research Centre. Steers were allocated to one of 6

111 pens of 72 m^2 each, with 14 steers per pen balanced for breed (an equal number of

112 CHx and Luing), sire and live weight (**BW**). Pens were provided with saw dust

113 bedding, *ad libitum* access to a water trough and were equipped with automated

114 feeding stations (HOKO feeders, INSENTEC B.V., Markenesse, The Netherlands;

115 Supplementary Figure S1) providing *ad libitum* access to feed. The number of HOKO

116 feeders within each pen was either five feeders (four of the pens) or six feeders (two

117 of the pens). Feeders were filled once a day using a forage wagon with a diet that

118 consisted of either 52:48 (Mixed) or 8:92 (Concentrate) forage:concentrate ratio (%,

119 dry matter basis) with no additive (Control), calcium nitrate or rapeseed cake as

120 dietary treatments. The composition of the diets and the distribution of diets and

121 additives according to pen can be found in Duthie *et al.* (2015).

122 Steers were either born and raised at SRUC Beef Research Centre or purchased

123 from Scottish farms during the summer of 2013 and were given eight weeks to adapt

5

124 to the facilities and feeding system before the beginning of the experiment. The last

125 four weeks of that period doses of additives were gradually increased to allow steers

126 adapt to dietary treatments. On arrival the steers were fed a standard finishing diet

127 for eight weeks before the experiment started. Subsequently, recordings of feed

128 intake, BW and fat depth were taken over 56 days (referred ahead as 56-day test) to

129 assess the residual feed intake (**RFI**). RFI is a feed efficiency measure calculated as

130 the difference between the actual and predicted feed intake required for the level of

131 production achieved (Basarab *et al*., 2003). Methane emitted by the steers at the

132 feeders was assessed on a daily basis. Steers were recorded during 56-day test

133 using two cameras per pen. The cameras covered the complete space available to

134 the steers.

135 The temperament of the steers was recorded three times throughout the 56-day test

136 by observation of their behavioural response to handling associated with routine

137 weighing.

138 All variables assessed are represented in Figure 1 according to the day of

139 measurement along the 56-day period.

140

141 *Residual feed intake estimation*

142 The automatic feeders recorded the weight of feed consumed during each feeding

143 event 24 h a day for each steer from which the dry matter intake **(DMI)** was

144 calculated. Steers were weighed weekly from the beginning until the end of the RFI

145 assessment period. Fat depth at the 12th -13th rib intercostal space was measured

146 ultrasonically (Aloka 500 machine, BCF technology Ltd, Scotland, UK) at the end

147 (between d 57 and 58) of the RFI assessment period. Growth was modelled by linear

148 regression of BW against test date to describe ADG, and metabolic live weight at

149 mid test **(MLW)** was calculated as BW*0.75. Feed conversion ratio (FCR)

150 corresponds to the average DMI (kg/ day) /average daily gain **(ADG)**. Following

151 Duthie *et al.* (2015), RFI was calculated as the deviation in actual DMI (kg/day) from

152 predicted DMI based on linear regression of actual DMI on ADG, MBW and FD.

153

154 *Measurement of methane emissions*

155 During the 56-day RFI measurement period, individual enteric CH_4 emissions were

156 measured using gas sampling hoods located over the HOKO feeders. As described

157 in Troy et al., 2016, the system consists of two head hoods with two large vacuum

158 pumps used to evacuate air from the hoods that pumped the sampled air into an

159 instrumentation cabinet that housed the gas analyser.

160 The respiration gas was sampled each day of the whole experiment when the steers

161 were feeding and visits shorter than one min were not taken into account for CH_4

162 sampling as there was insufficient time to allow the gas analyser to equilibrate.

163

164 *Behavioural assessments*

165 *Feeding behaviour.* Feeding behaviour was monitored automatically during the RFI

166 period using the HOKO feeders which recorded every time each steer entered the

167 feeder providing the number and the duration of feeding events per steer per day.

168 The feeders measured the weight of feed consumed during each visit. Feeding

169 events were then refined by eliminating visits in which no feed was consumed and

170 those shorter than 1 min in duration. The daily feed intake was divided by the

171 percentage of DM of the diet to calculate the DMI. The average number of feeding

172 events per day (***nFeed_bout***), the duration per visit (***bout_length***) and the total time

173 spent feeding per day (***dFeed_time***) were calculated. Data from days on which the

7

174   steers were weighed were excluded due to the risk that weighing could disrupt

175   feeding patterns. Due to the risk that weighing could disrupt feed intake patterns,

176   data from days on which the steers were weighed were excluded from the data

177   analysis.

178

179   *Activity.* Activity was assessed by fitting every steer with an IceTag® sensor

180   (IceRobotics Ltd, Edinburgh, UK; Supplementary Figure S2) which remotely and

181   continuously measured activity. As described by MacKay *et al.* (2013), IceTags are

182   triaxial accelerometers that function predominantly as pedometers when attached to

183   the leg of a steer, providing the orientation of the device 16 times per second. This

184   data was used to calculate the percentage of time that the steer was standing

185   (**Standing**), a count of the number of standing bouts (**nStdBout**) and the number of

186   steps (**nSteps**) per day using criteria presented in Tolkamp *et al.* (2011). The Motion

187   Index, as an indicator of the overall activity of the steer, was calculated using the

188   average magnitude of acceleration on each of the 3 axes (Kokin *et al.*, 2014). The

189   IceTags were attached on a hind leg, between the hock and fetlock joints for two

190   periods of 28 consecutive days. Two periods were required to allow data to be

191   downloaded and Icetags to be reformatted for further use. The first period occurred

192   from week 1 until week 5 of the RFI period and the second period started on week 6

193   and finished one week after the end of the RFI period. Data from the day on which

194   the IceTags were fitted and removed were discarded since they did not represent the

195   data for a full day and included locomotion during handling.

196

197   *Dominance.* Dominance was assessed *a posteriori* from the recorded images using

198   Observer XT 11.5 software (Noldus, Wageningen, The Netherlands). The analysis

199 was based upon an adapted ethogram from MacKay *et al.* (2013) assessing

200 agonistic interactions between steers at the HOKO bin feeders in the home pen. As

201 the number of feeders was lower than the number of steers, they often engaged in

202 agonistic interactions to displace others in order to access the feed. Fresh feed was

203 added every morning (approximately at 8:00 h AM) and observations were made

204 thereafter. During pilot observations in the current study little interaction was

205 observed after 1.5 hours following food provision, so samples of 90 minutes were

206 used. Behaviour was recorded on two consecutive days a week (Tuesday and

207 Wednesday) on weeks 1, 3, 5 and 7 of the 8-week RFI trial. These days were

208 selected as they involved the least disturbance of the steers for routine procedures.

209 All observations were performed by a single observer.

210 For each observation, the date of the observation, time of the interaction, behaviour

211 of the aggressor, and identity of the aggressor and recipient were recorded. The

212 variables measured were the number of events involving physical contact

213 (***Cont_Total***), number of aggressive interactions (***Aggr_Total***) and number of

214 displacements (***Displ_Total***) as defined by MacKay *et al.* (2013). The aggression

215 index (***Aggr_Ind***) provided information on the proportion of interactions in which the

216 steer acted as an aggressor (index values close to 1 indicated that the steer was

217 more often the aggressor than recipient). The displacement index (***Displ_Ind***)

218 summarised the proportion of displacements that the steer initiated relative to all

219 displacements it was involved in, giving a general impression of social status

220 (Galindo and Broom, 2002).

221

222 *Temperament assessment.* Temperament was assessed by performing a crush

223 score (**CS**) and a flight speed (**FS**) test, as described by Turner *et al.* (2011), both

224 undertaken during routine weighing in a chute (i.e. crush) on three occasions (day 8,

225 22 and 43 of the RFI assessment period). Steers were moved in groups from their

226 home pen to a holding pen that led to a semi-circular single-file race and then the

227 crush. Each steer was confined in the crush with its head secured in the bail. CS of

228 the steer was monitored based on signs of restlessness on a six point scale for 10 s

229 providing a categorical behavioural score based upon the reaction to being

230 restrained (Turner *et al*., 2011). Steers that struggled the most violently received a

231 high score. The weight was recorded and the steer was released directly into a

232 straight race. In the race, a digital flight speed meter consisting of two motion

233 sensors (located 1m and 5m from the crush exit) recorded the time taken to travel

234 the intervening 4m as a measure of the FS (m/s). CS and FS were recorded on each

235 of the 3 test days.

236

237 *Statistical analysis*

238 Analyses were carried out with the Statistical Analysis System version 9.4 (SAS

239 Software; SAS Institute Inc, Cary, NC, USA; 2002–2008). Variables were checked

240 for normality using Kruskal-Wallis tests.

241 Initially, a Pearson's correlation (Proc Corr) matrix was created between explicative

242 variables of the same behaviour group, for example temperament and dominance

243 variables that explain feeding behaviour and activity models and at the same time

244 activity and feeding behaviour variables that explain the performance and CH_4

245 models. This sought to identify measures that provided similar information and those

246 that required separate inclusion in multivariate models. Subsequently, the effect of

247 temperament and dominance (both the raw and index traits) on feeding behaviour

248 and activity was calculated by analysis of variance using linear mixed models (Proc

249   Mixed) firstly by univariate models and thereafter by multivariate models. Similarly,

250   the impact of feeding behaviour and activity on CH_4 and performance was assessed

251   using Proc Mixed. For every outcome variable (performance, CH_4, feeding behaviour

252   and activity) 'diet' and 'breed' were used as explanatory variables and 'pen' as a

253   random effect. Dietary treatment (Control, Nitrate, Rapeseed cake) had no effect on

254   feeding behaviour, temperament, activity and dominance, therefore it was not

255   included in the model. In the univariate models, the association of feeding behaviour

256   and activity with performance and CH_4 emissions was assessed using each of the

257   variables. The same procedure was undertaken to assess the association of

258   temperament and dominance with feeding behaviour and activity. Each individual

259   variable that showed a P-value lower than 0.25 became a candidate for the

260   multivariate model. The candidate variables were then added into the multivariate

261   model in a stepwise fashion. If two of the selected traits were highly correlated (r

262   >0.9) a selection was made to remove one from the analyses. The retained trait was

263   that which showed the least correlation with other traits, therefore maximising

264   independence relative to other traits. Candidate variables were kept in the model

265   with significance of P<0.05. When candidate variables showed significant effects the

266   rate of each component of variation was calculated using REML (restricted maximum

267   likelihood). Statistical significance was assumed at P ≤ 0.05 and tendencies at P ≤

268   0.1 for all analyses.

269

270   **Results**

271   *Association of feeding behaviour and activity with performance and methane*

272   *emissions*

11

273   The effects of basal diet, breed and additives on performance and CH_4 emissions

274   were reported in Duthie *et al.* (2015) and Troy *et al.* (2015), respectively. The main

275   results found were that steers fed with a concentrate diet ate less (DMI) ($P < 0.001$),

276   were more efficient (lower RFI) ($P < 0.01$) and produced less CH_4 (g/kg DMI) than

277   those fed with a mixed diet ($P < 0.001$). Also, steers fed the mixed diet produced

278   17% less CH_4 (g/kg DMI) when nitrate was added ($P < 0.01$). CHx steers had lower

279   DMI (kg BW; $P < 0.01$), greater ADG ($P < 0.01$) and were more efficient (lower RFI;

280   $P < 0.01$) than Luing steers. No effect of dietary additives was found in any of the

281   performance traits.

282   Table 1 provides mean values for feeding behaviour and activity for the two breeds

283   and diets. The models that best explained the influence of feeding behaviour and

284   activity on performance and CH_4 emissions are shown in Table 2. FCR showed a

285   non-parametric distribution and was transformed using logarithm base 10. Neither

286   feeding behaviour nor activity had a significant impact on DMI, ADG or FCR.

287   Feeding behaviour determined RFI by the interaction between diet*dFeed_time

288   suggesting that steers fed a mixed diet were more efficient (decreased RFI) when

289   the time spent feeding was higher ($P = 0.039$) but no effect was detected in

290   concentrate-fed steers. There was also a tendency for lower RFI in steers that were

291   less active, as shown by taking fewer *nSteps* ($P = 0.071$). Methane emissions (g /kg

292   DMI) were lower in steers that ate more frequently (*nFeed_bouts*) ($P = 0.041$) and

293   spent a shorter time standing ($P = 0.037$).

294

295   *Association between temperament and dominance with feeding behaviour*

296   Table 1 provides mean values for feeding behaviour, dominance and temperament

297   for each breed. The number of feeders in each pen did not affect feeding or social

298 behaviour. In addition, there was no difference between breeds in their temperament

299 and temperament was not affected by diet. Table 3 shows the models that describe

300 the effect of diet, breed, temperament and dominance on feeding behaviour. Mixed

301 fed and calmer steers ingested more DMI as indicated by the negative association

302 between DMI and diet (P = 0.001) and AvgeFS (P = 0.0319). The frequency of feed

303 bunk visits (*nFeed_bouts*) was influenced by diet, temperament and dominance.

304 Steers fed a forage diet ($P<0.0001$) and those that were temperamental (*AvgeFS*; P

305 = 0.0026) and dominant (*Displ_Tot*; P = 0.0207) visited the feeder more often.

306 Feeding bout length (*bout_length*) was influenced by breed, temperament (*AvgeFS*)

307 and dominance (*Displ_Tot*). CHx steers (P = 0.0497), those with poorer

308 temperament (*AvgeFS*; P = 0.0397) and greater dominance (*Displ_Tot*; P = 0.0002)

309 had shorter feeding bouts. Total feeding time (*dFeed_time*) was determined by diet

310 (P = 0.0001), breed (P = 0.0067) and dominance (*Displ_Index*; P = 0.0299) and was

311 lower in CHx steers those fed with a concentrate diet and in subordinate steers.

312

313 *Association of temperament and dominance with activity*

314 The models that explain the effect of diet, breed, temperament and dominance on

315 activity are shown in Table 4. Breed affected *Standing* ($P < 0.001$) and *nSteps* (P =

316 0.0110), indicating that CHx steers stood for a shorter period but had a higher

317 number of steps. The number of standing bouts (*nStdBout*) was affected by *AvgeCS*

318 (P = 0.0005) meaning that more temperamental steers had more frequent standing

319 bouts. No other associations between temperament, dominance and activity were

320 found.

321

322 **Discussion**

323 The main aim of the study was to assess the effects of feeding behaviour and activity

324 on performance, feed efficiency and CH_4 emissions. Research on beef cattle have

325 indicated the capacity of temperament (Nkrumah *et al.*, 2007) and dominance

326 (Gonzalez *et al.*, 2008) to affect feeding behaviour and activity patterns, this

327 association was also assessed to understand the underlying traits that drive

328 variations in productivity and CH_4. Understanding the associations between these

329 traits might constitute the basis for designing breeding, handling and management

330 strategies to improve efficiency and mitigate GHG emissions in beef cattle. The

331 results show that feed efficiency (RFI) was not influenced by feeding behaviour and

332 activity (except in interaction with diet type) but that CH_4 emissions (g /kg DMI) were

333 lower when steers ate more frequently and spent less time standing. Feeding

334 behaviour itself was influenced by temperament and dominance whereby

335 temperamental and dominant steers ate more frequently but in shorter bouts. For

336 temperamental steers, this reduced their daily DMI whilst for dominant steers it

337 increased their total daily feeding time. Activity was unaffected by dominance but

338 temperamental steers had more frequent standing bouts. The analysis accounted

339 also for the breed, diet and use of dietary additives which offers the possibility to

340 understand the effect of feeding behaviour and activity on performance and CH_4

341 emissions in a selected range of diets and breeds that are commercially relevant.

342

343 *Effect of feeding behaviour and activity on growth performance and methane*

344 *emissions*

345 In the current study, feeding behaviour largely had no effect on DMI or ADG,

346 contrasting with several studies reporting a significant association. Assessing DMI,

347 Nkrumah *et al.* (2007) have reported that a high feeding duration is correlated with

348 high feed intake for time spent at the feeder and time consuming feed, (r=0.27 and

349 0.33, respectively). Regarding growth, Schwartzkopf-Genswein *et al.*, (2002)

350 reported a positive correlation (r=0.38) between bunk attendance duration and ADG,

351 which were similar to what Hicks *et al.* already stated in 1989. Nkrumah *et al.* (2007)

352 found that the number of visits to the feeder and feeding bout duration correlated

353 with ADG (r=0.25 and 0.18 respectively). These associations could not be confirmed

354 in this study suggesting that individual attributes of feeding behaviour were poor

355 predictors of DMI and ADG in this population. The reason for the discrepancy with

356 the mentioned studies is unclear. However, we hypothesise that the way data was

357 analysed might have had an effect. For instance, both Schwartzkopf-Genswein *et al.*,

358 (2002) and Nkrumah *et al.* (2007) used Pearson correlations to assess associations

359 whereas in our study multivariate ANOVA models were used accounting for several

360 factors such as breed, diet, weight or pen, which might have restricted the

361 association likelihood estimation between explained and explanatory variables.

362 Feed efficiency was assessed in this study using two different measures: FCR and

363 RFI. Traditionally, feed efficiency has been expressed as the ratio of feed intake to

364 BW gain (FCR). We did not find any effect of activity and feeding behaviour on FCR

365 but only a breed and MLW effect. RFI has been suggested to be a better estimate of

366 feed efficiency as it is independent of growth and body size (Crews, 2005). The

367 association between RFI and feeding time in the mixed diet fed steers shows that

368 steers that spent a longer time eating the less nutrient-dense diet made more

369 efficient use of the feed. An increased daily time spent eating may increase total

370 salivary secretion (Beauchemin *et al.*, 2008). Saliva modulates rumen pH, which

371 usually is beneficial for rumen fermentation (Owens *et al.*, 1998) and likely improving

372 digestion of the nutrients. In addition, an increase in the time spent eating can be a

consequence of a reduction in intake rate (g/min). It is likely that the accessibility of fibrolytic microbiota to feed will increase if the intake rate is low and meals are frequent rather than if feeding occurs rapidly in large bouts. Increased saliva production can be a consequence of higher ruminating times (González et al., 2012). Forage-based diets stimulate a greater time spent ruminating per day and per unit of intake compared to diets with higher concentrate proportion (Faleiro et al., 2011). This may be the reason why the effect of feeding time on feed efficiency is more evident with fibrous compared to concentrate-based diets.

There was a tendency ($P = 0.071$) for greater activity (more frequent steps) to be associated with poorer feed efficiency (RFI). This finding agrees with other studies. Herd *et al.* (2004) attributed a 5% contribution of activity to the total variation in RFI found between cattle lines divergently selected for high and low RFI. Richardson *et al.* (1999) reported that the variation in RFI explained by daily pedometer count could reach up to 10%. Breeding or managing steers in such a way that they show diminished activity and energy depletion may be effective in improving feed efficiency.

This experiment also investigated the possible effect of feeding behaviour and activity on enteric CH_4 emissions. Respiration chambers, the gold-standard approach for CH_4 assessment, require the isolation of a steer, which affects feed intake (Llonch *et al.*, 2016b) and possibly feeding behaviour and activity. The hoods fitted above the feeders in the home pen, which have been shown to robustly measure CH_4 emissions in group-housed steers (Troy *et al.*, 2016), were regarded as the preferable method to study the association of CH_4 emissions with feeding behaviour and activity.

397 The results of the current study show that steers with frequent feeding bouts

398 (*nFeed_bouts*) emitted less CH_4. One could hypothesise that this association is due

399 to changes in rumen retention time and digestibility. The association between DMI,

400 retention time and feed digestibility has been confirmed by several studies (Colucci

401 *et al.*, 1982; Shaver *et al.*, 1986; DeVries and von Keyserlingk, 2009). In 1988,

402 Ørskov *et al.*, reported that variation in ruminal retention time among cattle might be

403 explained by differences in DMI but also by differences in feeding behaviour. In this

404 sense, it could be argued that a steer showing highly distributed feeding patterns will

405 improve the digestion of feed and increase the production of CH_4, however the

406 results of this study show the opposite.

407 An explanation for the apparently beneficial effect of frequent feeding visits on CH_4

408 emissions could result from the way that CH_4 was sampled in this study. Enteric CH_4

409 is mostly exhaled during respiration; therefore, less frequent but longer feeding bouts

410 would allow a greater level of CH_4 to accumulate. On the contrary, steers that visited

411 the feeder more frequently but for shorter visits may have performed much of their

412 chewing and rumination out of the feeder. However, as our analysis found no

413 relationship between *bout_length* and CH_4 emissions, the impact of this artefact may

414 not have been great. Alternatively, increased activity around the pen could also

415 facilitate gas distribution within the rumen, easing rumen gas exhalation in more

416 active steers.

417

418 The results also revealed that steers that spent the longest time standing emitted

419 more CH_4. In turn to the association between activity and feed efficiency we

420 hypothesise that activity might influence, or be influenced by, feeding behaviour. For

421 instance, the association between higher CH_4 emissions and a greater standing time

422   could potentially result from more time spent at the feeder, which is actually where

423   the CH_4 was monitored in this experiment. In a study conducted with respiration

424   chambers, Nkrumah *et al.* (2006) found a positive relationship between feeding time

425   and CH_4 emissions. Using a laser detector, Chagunda *et al.* (2013) found that during

426   feeding, cows produced a 34% more, measured in ppm, CH_4 than when idle. In our

427   study we found an association between feeding visits and CH_4 emissions. Thus it is

428   possible that steers showing more activity in the pen also show more feeding activity,

429   which ultimately affects CH_4 emissions. Although it is not possible to establish which

430   is the cause and the consequence in such relationship, activity in the pen could still

431   partially explain variations in CH_4 emissions and be used to monitor them in beef

432   cattle production.

433

434   *Association between temperament and dominance with feeding behaviour and*

435   *activity*

436   According to our results, feeding behaviour is partially explained both by

437   temperament and dominance traits. Although no change in total feeding duration

438   was shown, more temperamental steers visited the feeder more frequently, had

439   shorter meals and a decreased feed intake. MacKay *et al.* (2013) also found that

440   temperamental steers eat less feed per day. Van Reenen *et al.* (2005) suggested

441   that in response to any challenging stimuli, temperamental steers will exhibit an

442   active coping response manifest as a greater behavioural reaction relative to the

443   level of internal stress they are experiencing compared to less temperamental

444   steers. This may suggest that temperamental steers are more reactive to external

445   stimuli (i.e. social interactions) increasing the likelihood of disruption of feeding

446   events leading to a large number of shorter feeding bouts with a reduction in total

447 feed intake. As discussed in the previous section, more frequent feeding bouts leads

448 to a decrease in CH_4 emissions. Additionally, the reduction in feed intake by

449 temperamental steers may have implications for both feed efficiency and CH_4

450 emissions. Using the same population of steers, Llonch *et al.* (2016 a,b)

451 demonstrated that a decrease in feed intake results in an increase in feed efficiency

452 but also in CH_4 emissions per kg of DMI, possibly due to a reduction in passage rate.

453 At the same time, Llonch *et al.* (2016a) demonstrated that the population group of

454 steers considered more temperamental also showed a lower ADG (kg/day)

455 compared to calm steers, possibly due to increased energy expenditure. Thus,

456 breeding for less temperamental steers would have multiple and contrasting effects

457 on efficiency and CH_4 emissions. Calmer steers will show poorer feed efficiency but

458 increased growth and will have a controversial effect on CH_4 emissions, due to

459 effects on eating frequency and DMI. The goal is to complement this breeding

460 strategy with appropriate feeding management to counteract the decrease in feed

461 efficiency (when increasing intake) which could be achieved by promoting longer

462 times spent eating, therefore improving digestion of feed.

463 A similar association between feeding behaviour and dominance was seen as

464 between feeding behaviour and temperament. The relationship between feeder

465 access and dominance behaviour has been extensively described in cattle (Harb *et*

466 *al.*, 1985; DeVries and von Keyserlingk, 2009; Gonzalez *et al.* 2008, 2012) where it

467 is generally accepted that dominant steers limit access of subordinates to feed. In

468 this study, a strong association was found between feeding behaviour and total

469 displacements or displacement index, whereby dominant steers showed more

470 frequent but shorter feeding bouts. This result suggest that if subordinate steers can

471 be fed at their wish they will probably show a similar pattern than dominant steers,

472 with frequent and short feeding bouts, and as discussed earlier, potentially reduce

473 CH_4.

474 The results also show that dominant steers spent a greater time feeding compared to

475 subordinates which they could achieve since they were not displaced so frequently.

476 The same association was found by De Vries *et al.* (2004) who showed that

477 subordinate cows have to adapt to the feeding patterns of dominant animals and

478 access feed when it is available which results in less frequent but longer feeding

479 bouts and less time spent eating than dominants. In our experiment, the increased

480 daily feeding time did not affect DMI which suggests that dominant steers must have

481 slowed their ingestion rate. The impact of greater feeding time, potentially due to

482 higher dominance rank, on RFI have been discussed in the previous section

483 whereby a longer time feeding, in fibrous fed steers, is associated with greater feed

484 efficiency. Strategies to reduce dominance behaviour (e.g. by increasing the feeding

485 space or reducing the stocking rate) will increase both the frequency and the

486 average time spent eating by the herd which in this study simultaneously improved

487 efficiency and reduced CH_4 emissions and at the same time reduces agonistic

488 behaviour thereby benefiting animal welfare.

489 Evidence was found indicating that decreased activity, in the form of fewer steps, is

490 associated with greater feed efficiency. On the other hand our results show that

491 temperamental steers were more active (more frequent standing bouts) which

492 confirms the results of MacKay *et al.* (2013) who found that steers with high flight

493 speed were most active in the home pen. In this regard, the effect of activity on feed

494 efficiency could be partially mediated by temperament. More temperamental steers

495 are more reactive to potentially threatening external stimuli. As a result, the energy

496 expenditure dedicated to body movement is likely to be higher which may decrease

497   the quantity of resources that can be dedicated to growth and compromise efficiency.

498   An association between temperament and feed efficiency has been reported by

499   Voisinet *et al.* (1997) and Nkrumah *et al.* (2007). In contrast, Llonch *et al.* (2016a)

500   could not find such a relationship but temperamental steers grew more slowly.

501   Presumably in the latter study, the DMI was also reduced to some extent in more

502   temperamental steers which reduced the impact on feed efficiency. Minimising the

503   effects of activity on RFI offers a strategy to improve efficiency. Improving

504   temperament may be a potential way to reduce activity with down-stream benefits for

505   growth rate and efficiency.

506

507   **Conclusions**

508   More time spent feeding on fibrous diets is associated with greater feed efficiency

509   possibly due to greater secretion of saliva and increased access of microbiota to

510   fibre. Dominant steers were able to eat for a longer period each day which suggests

511   that management aimed towards reducing competition for feed could help to

512   increase the average herd feeding time and improve feed efficiency. More frequent

513   feeding bouts contributed to a reduction in CH_4 per feed intake. Dominant steers

514   accessed the feeders more frequently suggesting that if access to feed is not

515   restricted steers show a pattern of frequent but short feeding bouts. Temperamental

516   steers reduced feed intake which previous studies have found to increase feed

517   efficiency but to reduce growth rate and increase CH_4 emissions per feed intake.

518   Steers that were more active in the pen had a poorer RFI, presumably because of

519   the energetic demands of body movement. Considering that activity is partly

520   explained by temperament, management or breeding strategies that improve

21

521 temperament will reduce activity and ought to benefit feed efficiency if the opposing

522 effects on increased feed intake are controlled.

523

524 **Acknowledgements**

533

534 **Conflict of interest**

535 Authors declare that we do not have any conflict of interest

536

537 **Ethics**

538 This experiment was approved by the Animal Experiment Committee of SRUC in

539 accordance with the requirements of the UK Animals (Scientific Procedures) Act

540 1986.

541

542 **Software and data repository resources**

543 Data has not been deposited in an official repository.

544

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658   **Figure 1** *List of performance and behaviour variables assessed each day during an eight-week assessment period in beef cattle*

659
660   *Agg_Total: number of aggressive interactions; Displ_total: number of displacements; Displ_Index: the aggression index is the proportion of interactions in
661   which the steer acted as a displacer; nFeed_bout: average number of feeding events per day; dFeed_time: the total time spent feeding per day; bout_length:
662   duration per visit; Standing: percentage of time that the steer was standing; nStdBout: a count of the number of standing bouts; Standing: percentage of time
663   that the steer was standing; nSteps: number of steps per day; AvgeFS: average of the flight speed test; AvgeCS: average of the Crush Score.

Table 1 *Mean (± SEM) of each dominance, feeding behaviour, activity and temperament trait according to breed and diet in beef*

cattle

	Charolais-sired Diet			Luing Diet					
	Concentrate	Mixed		Concentrate	Mixed		P-value diet (Charolais)	P-value diet (Luing)	P-value breed
	Mean	Mean	SEM	Mean	Mean	SEM			
Dominance									
Agg_total	0.22	0.19	0.017	0.27	0.23	0.018	0.49	0.21	0.07
Displ_total	0.59	0.56	0.019	0.56	0.54	0.018	0.69	0.72	0.21
Displ_Index	-2.03	-2.01	0.020	-1.99	-1.98	0.030	0.66	0.95	0.28
Feeding behaviour									
nFeed_bout	28.8[b]	45.4[a]	2.258	27.9[b]	41.8[a]	2.073	<0.001	<0.001	0.21
dFeed_time (s)	5784.6[b]	8755.5[a]	278.589	6795.5[b]	9366.5[a]	308.313	<0.001	<0.001	0.005
Bout_length (s)	237.0[b]	216.4[b]	10.054	271.1[a]	261.6[a]	12.616	0.51	0.70	0.008
Activity									
nStdBout	65.3	66.1	6.359	67.2	66.2	7.755	0.95	0.98	0.94
Standing (min)	916.8[b]	941.9[b]	12.236	1016.0[a]	1003.7[a]	10.99	0.31	0.61	0.001
nSteps	1221.7[a]	1316.1[a]	31.166	1140.4[b]	1134.2[b]	45.816	0.13	0.75	0.029
Motion Index	4383.7[a]	4438.0[a]	146.970	3880.7[b]	3504.3[b]	735.931	0.87	0.29	0.97
Temperament									
AvgeFS (m/s)	1.80	1.59	0.074	1.50	1.56	0.074	0.19	0.71	0.14
AvgeCS	1.75	1.85	0.129	1.51	1.68	0.136	0.58	0.55	0.34

[a,b,c] Values within a row with different superscripts differ significantly at *P*<0.05.

Agg_Total: number of aggressive interactions; Displ_total: number of displacements; Displ_Index: the aggression index is the proportion of interactions in which the steer acted as a displacer; nFeed_bout: average number of feeding events per day; dFeed_time: the total time spent feeding per day; bout_length: duration per visit; nStdBout: a count of the number of standing bouts; Standing: percentage of time that the steer was standing; nSteps: number of steps per day; Motion Index: indicator of the overall activity of the steer, was calculated using the average magnitude of acceleration on each of the 3 axes; AvgeFS: average of the flight speed test; AvgeCS: average of the Crush Score.

673 **Table 2** *Mean (±SEM) weight of each diet, breed, feeding behaviour and activity trait with a significant effect on multivariate models*

674 *of performance and CH$_4$ emissions in beef cattle*

Outcome variable	Intercept	Fixed effects	Feeding behaviour	Activity
DMI (kg)	11.99±0.1934	diet (CONC; *b*= -1.0691±0.2826)***		
ADG (kg/d)	0.78±0.2993	diet (CONC; *b*= -0.11±0.050)* breed (CHx; *b*=0.14±0.049)** MTLW (*b*= 0.0015±0.000)**		
FCR (kg/kg)	1.807±0.1576	breed (CHx; *b*=-0.15±0.028)*** MLW (*b*=0.0006±0.000)*		
RFI	1.687±0.6406	diet (CONC; *b*=-2.44±0.786)** breed (CHx; *b*=-0.37±0.139)**	Diet*dFeed_time (b=-0.00014±0.000)*	Steps (*b*= 0.0006±0.000)†
CH$_4$ (g/kgDMI)	7.244±1.4449	diet (CONC; b=-3.499±0.8067)***	nFeed_bouts (*b*=-0.0146±0.0081)*	Standing (*b*=0.0038±0.0018)*

675 †, *, ** or *** symbols refer to a tendency, $P < 0.05$, $P < 0.01$ and $P < 0.001$.
676 DMI: Dry Matter Intake; ADG: Average Daily Gain; FCR: Feed Conversion Ratio; RFI: Residual feed Intake; CH$_4$: methane; CONC: concentrate; CHx:
677 Charolais sired; nFeed_bout: average number of feeding events per day; dFeed_time: the total time spent feeding per day; Standing: percentage of time that
678 the steer was standing; nSteps: number of steps per day.

Table 3 *Mean (±SEM) weight of each diet, breed, temperament and dominance trait with a significant effect on multivariate models*

of feeding behaviour in beef cattle

Outcome variable	Intercept	Fixed effects	Temperament variables	Dominance variables
DMI (kg)	13.028±0.5008	Diet (CONC; b=-0.9454 0.2763)***	AvgeFS (b=-0.5920±0.2946)*	
nFeed_bouts	21.459±5.764	Diet (CONC; b=-15.5341±3.1593)***	AvgeFS (b=6.493±2.092)**	Displ_Tot (b=20.235±8.555)*
bout_length (min)	466.23±43.518	Breed (CHx; b=-30.615±15.383)*	AvgeFS (b=-34.498±16.468)*	Displ_Tot (b=-257.3±66.109)***
dFeed_time (min)	1321±1719.94	Diet (CONC; b=-2614.48±282.73)*** Breed (CHx; b=-794.51±284.60)**		Disp_Index (b=1905.22±860.46)*

681   †, *, ** or *** symbols refer to a tendency, P< 0.05, P < 0.01 and P < 0.001.
682   DMI: Dry Matter Intake; nFeed_bout: average number of feeding events per day; bout_length: duration per visit; dFeed_time: the total time spent feeding per
683   day; CONC: concentrate; CHx: Charolais sired; Displ_total: number of displacements; Displ_Index: the aggression index is the proportion of interactions in
684   which the steer acted as a displacer; AvgeFS: average of the flight speed test; AvgeCS: average of the Crush Score.

685 **Table 4** *Mean (±SEM) weight of each diet, breed, temperament and dominance trait with a significant effect on multivariate models*

686 *of activity in beef cattle*

Outcome variable	Intercept	Fixed effects	Temperament variables	Dominance variables
nStdBout	32.076±10.909		(AvgeCS; 19.84±5.466)***	b=
Standing (min)	612.59±7.035	Breed (CHx; *b*=-48.073±9.826)***		
Steps	1180.31±100.92	Breed (CHx; *b*=120.01±54.004)*		

687 †, *, ** or *** symbols refer to a tendency, P< 0.05, P < 0.01 and P < 0.001.
688 Standing: percentage of time that the steer was standing; nStdBout: a count of the number of standing bouts; nSteps: number of steps per day; CHx:
689 Charolais sired; AvgeCS: average of the Crush Score

Temperament and dominance relate to feeding behaviour and activity in beef cattle: implications for performance and methane emissions

Llonch P, Somarriba M, Duthie CA, Troy S, Roehe R, Rooke J, Haskell MJ and Turner SP

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Supplementary material

Figure S1. Detail of the Hoko feeders used in the study to assess feeding behaviour and methane emissions. The blue part contains the feed and records each time a steer accesses the feeder. On top of it, the transparent cover contains the gas exhaled, which was vacuumed towards a gas chromatograph.

Figure S2. Pictures of the IceTag® sensor (IceRobotics Ltd, Edinburgh, UK) put on the steers to monitor activity. The first picture represents the sensor, the second is the cover to protect the sensor and the third picture shows the exact location on the steers' legs. Copyright: IceRobotics Ltd.