

Scotland's Rural College

## Relationships between feeding behaviour, activity, dominance and feed efficiency in finishing beef steers

Haskell, MJ; Rooke, JA; Roehe, R; Turner, SP; Hyslop, JJ; Waterhouse, A; Duthie, C-A

*Published in:*  
Applied Animal Behaviour Science

*DOI:*  
[10.1016/j.applanim.2018.10.012](https://doi.org/10.1016/j.applanim.2018.10.012)

Print publication: 01/01/2019

*Document Version*  
Peer reviewed version

[Link to publication](#)

### *Citation for published version (APA):*

Haskell, MJ., Rooke, JA., Roehe, R., Turner, SP., Hyslop, JJ., Waterhouse, A., & Duthie, C-A. (2019). Relationships between feeding behaviour, activity, dominance and feed efficiency in finishing beef steers. *Applied Animal Behaviour Science*, 210, 9-15. <https://doi.org/10.1016/j.applanim.2018.10.012>

### **General rights**

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

### **Take down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25

Relationships between feeding behaviour, activity, dominance and feed efficiency in finishing beef steers

Marie J. Haskell\*, John A. Rooke, Rainer Roehe, Simon P. Turner, James J. Hyslop, Anthony Waterhouse and Carol-Anne Duthie

\*SRUC, West Mains Road, Edinburgh EH9 3JG, United Kingdom

Corresponding author: Marie Haskell; Phone: +44 (0)1316519366; Fax: +44 (0)131 535 3121; E-mail: marie.haskell@sruc.ac.uk

26

27 Abstract

28 To increase the profitability and sustainability of beef production systems, the  
29 use of animals with high feed efficiency is preferred. Efficient animals eat less than  
30 their peers for the same or better growth. This efficiency can be measured using feed  
31 conversion ratios (FCR) and residual feed intake (RFI) parameters. However, the  
32 biological mechanisms, particularly those related to the animal's behaviour and  
33 personality, are poorly understood. An individual animal's behaviour, such as its  
34 activity levels, may contribute to efficiency. Feed intake is also a factor in efficiency,  
35 and therefore, social dominance rank may also indirectly affect efficiency through its  
36 influence on feeding behaviour. This experiment investigated the effects of dominance  
37 on feeding behaviour, as well as of dominance and activity on average daily gain  
38 (ADG), FCR and RFI in two breeds of beef cattle. The study used a 2 x 2 design with  
39 80 cattle of two breed-types (Charolais-cross (CHx) (n=41) and Luig (n=39)) and two  
40 diets (a concentrate-based diet (CONC) and a mixed forage and concentrate diet  
41 (MIXED)). For each individual steer, FCR and RFI were measured over a 56-day  
42 performance test. Feed intake, patterns of feeding behaviour, activity and dominance  
43 were also measured. Feed intake was affected by dominance, with more dominant  
44 steers having significantly higher dry matter intakes ( $P=0.001$ ) and feeding rates  
45 ( $P=0.006$ ) suggesting that dominant animals had priority of access to the feeders.  
46 Steers with higher ADG had higher intakes and performed more standing bouts. Steers  
47 with better FCR values performed more standing bouts and younger animals had better  
48 FCR. For RFI there was also an interaction between breed and variation in length of  
49 the feeding events, showing that Luig steers with more consistent feed bout lengths  
50 had better RFI, with no association shown for CHx steers. There was no direct effect of

51 dominance on ADG, FCR or RFI. However, the effect of dominance on feed intake  
52 suggests that measures of performance in any study may be affected by feeder-space  
53 allocation. The associations between standing bouts and feeding bouts with efficiency  
54 measures also suggest that individual animal behavioural characteristics influence  
55 efficiency and that overall efficiency of all animals may be improved by allowing  
56 animals to express individual patterns of behaviour.

57

58 Key words: activity, dominance, efficiency, beef cattle, feeding behaviour

59

60

61

## 62 **1. Introduction**

63       Increasing the production outputs or growth of animals for a fixed amount of feed  
64 is seen as a means of reducing costs and improving profitability in beef production  
65 systems (Archer et al., 1999; Arthur et al., 2004). The term ‘feed efficiency’ is used to  
66 describe the relationship between feed inputs and growth outputs, with efficient  
67 animals being those that grow well but consume less feed compared to others in their  
68 cohort. As well as improving farm profitability, increasing feed efficiency is an  
69 important means of reducing the environmental impact associated with beef  
70 production. Ruminants are responsible for an important proportion (between 6-8-%) of  
71 the global anthropogenic methane emissions (Gerber et al., 2013).

72       A great deal of research has focussed on achieving improvements in feed efficiency  
73 in beef production systems worldwide (e.g. Archer et al., 1999; Arthur et al., 2004;  
74 Basarab et al., 2003). A number of measures have been developed to quantify feed  
75 efficiency. Feed conversion ratio (FCR) measures the amount of feed required per unit  
76 of growth (e.g. Archer et al., 1999; Robinson and Oddy, 2004), while residual feed  
77 intake (RFI) is the difference between an animal’s actual feed intake and its expected  
78 intake requirements for growth and maintenance estimated using others in its cohort in  
79 a given production system (Archer et al., 1999; Koch et al., 1963). Thus an animal that  
80 eats less than expected over the test period will be more efficient and have a negative  
81 RFI value (Richardson et al., 2002).

82       Given the link to productivity, it is not surprising that research into feed efficiency  
83 has most entirely focussed on animal-level factors affecting productivity, such as breed  
84 and diet (e.g. Basarab et al., 2003; Golden et al., 2008), but little is known about the  
85 underlying biological causal factors, such as behaviour or physiology. In a review of  
86 the subject, Herd et al. (2004) suggested that there were a number of factors that may

87 contribute to individual differences in efficiency including activity, feed intake and  
88 digestion, metabolism and thermoregulation. Studies have investigated the relationship  
89 between overall activity and RFI. A study by Richardson et al. (2000) has shown that  
90 inefficient animals with high RFI scores took a greater number of steps per day than  
91 animals with better efficiency. A higher step-count in steers with poor RFI scores has  
92 also recently been confirmed by Llonch et al., (in press), but has not been shown in a  
93 number of other studies with beef cattle (e.g. Hafla et al., 2013; Lawrence et al., 2011).  
94 Higher activity has also been associated with poor efficiency in other species (Luiting  
95 et al., 1994).

96 The direct relationship between feeding behaviour and efficiency has already been  
97 investigated in a number of studies. The results suggest that efficient animals (those  
98 with low RFI scores) have a shorter duration of feeding each day (Basarag et al., 2007;  
99 Durunna et al., 2011; Lancaster et al 2009; Nkrumah et al., 2007) and fewer feeding  
100 events per day (Durunna et al., 2011; Golden et al, 2008; Kelly et al., 2010; Lancaster  
101 et al 2009; Nkrumah et al., 2007). Steers with a higher frequency of feeding events had  
102 lower (more favourable) FCR values (Nkrumah et al., 2007).

103 However, other behavioural traits may also be important, particularly those that can  
104 affect feed intake and feeding behaviour. The social dominance rank of the animal is  
105 known to affect feeding behaviour. High social dominance rank generally infers  
106 priority of access to resources (Syme, 1974) which includes access to food (e.g.  
107 McPhee et al., 1964). In dairy cattle, it has been shown that in situations where there is  
108 limited access to feed, animals of low dominance rank or younger animals can be  
109 displaced from the feeder by higher-ranking animals (Gibbons et al., 2009; Huzzey et  
110 al., 2006). Low-ranking animals may also avoid approaching feeders when dominant  
111 animals are present. Both of these factors will affect feeding frequency and duration.

112 Fewer studies have been carried out in beef cattle, but they also suggest that dominance  
113 affects access to feed (Stricklin and Gonyou, 1981; Llonch et al., in press).

114 The hypothesis that dominance may affect feeding behaviour in beef cattle has  
115 relevance for the assessment of feed efficiency. Typically, feed efficiency trials are  
116 carried out using automatic feed bins that record the amount of feed consumed by each  
117 animal. However, the number of bins provided is normally lower than the number of  
118 animals, which may create a situation of competition. For instance, Golden et al (2008)  
119 had 1 bin to every 3 animals, while Fitzsimmons et al., (2014) had 1 bin per eight to  
120 nine animals. Thus, in these situations, dominance rank may influence feed intake and  
121 patterns of feeding behaviour, which may have an indirect affect on the individual  
122 animal's ability to express its full potential for efficiency.

123 The first hypothesis of this study is that dominance will affect feed intake in a  
124 typical feed efficiency trial in which there are fewer automatic feeders than there are  
125 animals. Secondly, we hypothesis that dominance, activity and feeding behaviour  
126 affect efficiency.

127

## 128 **2. Materials and Methods**

129 The behavioural data were taken as part of an overall trial that investigated the  
130 growth, efficiency and methane emissions of two breed types of beef cattle on two  
131 types of diet. The experiment was of a 2 x 2 factorial design, with 2 breeds of steers  
132 and two diets. Two commercially relevant beef breeds were used: Charolais-crossbreds  
133 (CHx; n=41) and purebred Luing steers (n=39). This design contrasted the fast-  
134 growing Charolais with the hardier Scottish Luing breed (a Beef Shorthorn x Highland  
135 Cattle composite). Two diets (as total mixed rations) were generated using a diet  
136 mixing wagon and consisted of forage to concentrate ratios (g/kg DM) of either

137 500:500 (Mixed: 12.0 MJ/kg DM; 500g/kg) or 79:921 (Concentrate: 12.8 MJ/kg DM;  
138 920 g/kg). See Supplementary Table 1 and Duthie et al. (2017) for further details. The  
139 experimental design was reviewed and approved by SRUC's Animal Ethics Committee  
140 in accordance with UK Home Office guidelines.

141

## 142 *2.1 Animals and Management*

143 The steers were either homebred or purchased from Scottish farms and  
144 transported to the beef cattle research facility. In preparation for the trial, the steers  
145 were fed on a standard 50:50 forage:concentrate diet. They were transferred to 4 test  
146 pens at the start of the adaptation phase. These test pens were 18.4 x 9.9m. Feed was  
147 provided *ad libitum* from automatic feeders (HOKO, Insentec, Marknesse, The  
148 Netherlands), which recorded the start and stop weight of the feed alongside time of  
149 entry and exit from the individual feeder for each visit by each animal. Steers on the  
150 CONC diet were transitioned to the new concentrate levels gradually as part of the  
151 adaptation phase. There were 8 feeders per pen (2.5 animals/pen) and a water trough  
152 providing *ad libitum* access to water. Feed bins were refilled at approximately 8:00am  
153 each day. Each pen contained 20 animals and pens were balanced for breed and age,  
154 with starting weight balanced within breed. Animals were 3912±3. days of age and 471  
155 ± 62 kg bodyweight (BW) at the start of the experiment. Two pens were allocated to  
156 each of the 2 diets. Diets were fed in separate pens, as previous studies have shown  
157 that animals on less preferred diets could 'steal' feed from feed bins with the preferred  
158 diet which would bias the feed intake results (e.g. ; Ruuska et al., 2014; Tolcamp et al.,  
159 2000). This 'stealing' was noted in preliminary trials using this research facility, and  
160 subsequent studies have all used one feed per pen (e.g. Duthie et al., 2016; Llonch et  
161 al., in press). There is also a risk of acidosis in animals obtaining appreciable quantities

162 of a diet with a greater level of concentrate by stealing without an appropriate  
163 adaptation period.

164         There was a 4-week adaptation phase to allow the animals to adapt to the pens,  
165 the new social group and the automatic feeders, and to gradually introduce the test  
166 diets. The 56-day performance and feed efficiency testing phase started directly  
167 afterwards. Animals were weighed once a week on a calibrated weigh scale. Daily dry  
168 matter intake (DMI: kg/d) was recorded for each animal. Ultrasonic fat depth (FD) at  
169 the 12<sup>th</sup>/13<sup>th</sup> rib was taken for all steers at the end of the 56-day test period (see Duthie  
170 et al., 2017 for further details).

171

## 172 *2.2 Behavioural Measures*

173         Three major classes of behavioural variables were assessed: feeding behaviour,  
174 activity and dominance. These measures were all assessed during a performance test  
175 period, when feed efficiency and other traits were assessed.

176         Feeding behaviour was monitored automatically throughout the test period  
177 using the automatic feeders. Visits with negative intake values were excluded from the  
178 calculations. Feeding visits were not converted to meals, as suggested by Yeates et al.  
179 (2001), because this calculation allows short non-feeding intervals within an overall  
180 feeding period (or meal) to be identified and removed. However, an interval within a  
181 meal may be the result of an animal being displaced from the feeder by another animal.  
182 As the presence of these disruptions in feeding may be related to dominance rank, we  
183 wished to include these types of non-feeding intervals. Feeding data on days on which  
184 the animals were weighed (Mondays) were excluded, as time out of the pen would  
185 disturb normal feeding patterns. A number of parameters were calculated: mean  
186 number of feeding events/day (visits in which any quantity of feed was ingested:

187 nFeedVisit), total time spent feeding/day (FeedTime), average length of feeding visits  
188 (dFeedVisit) and standard deviation of the duration of the feed visits in a day  
189 (sdFeedVisit) as a measure of variability in the feeding visits. The daily fresh weight  
190 intake (Intake) was divided by FeedTime to calculate intake rate (IntakeRate).

191 Activity was assessed using activity monitors on Days 7 to 56 inclusive only  
192 due to limitations in data storage on the devices. Standing, lying, number of steps taken  
193 and summed overall motion was assessed using a tri-axial accelerometer-based activity  
194 monitor (IceTag Pro) and extracted from the device using IceManager 10 (IceRobotics,  
195 Queensferry, UK). An IceTag was attached to each animal above the fetlock joint.  
196 Lying bouts of less than 5 mins were eliminated as erroneous (as shown in Tolkamp et  
197 al., 2010). The amount of time spent standing/day (mins), the number of standing  
198 bouts, the average length of the standing bouts, the number of steps and the total  
199 motion index were extracted for each day. The motion index is absolute acceleration  
200 against gravity summed over the day, from which a step-count is derived. Any bout of  
201 behaviour that started before midnight and ended after midnight are not split across  
202 days, but are counted into the day in which it started. Weigh days and the first 3 days  
203 after initial tagging were excluded as not providing representative data (Mackay et al.,  
204 2012). The data were then summarised across all qualifying test days to give mean  
205 time standing/day (StandTime), mean number of standing bouts/day (nStandBout),  
206 mean duration of standing bouts (dStandBout), standard deviation of standing bout  
207 length (sdStandBout), mean number of steps/day (nSteps) and standard deviation of  
208 steps/day (sdSteps), mean daily motion index (MI) and standard deviation of motion  
209 index (sdMI). Battery failures meant that activity data was collected on 73 of the  
210 animals.

211 Dominance was assessed by analysing interactions at the feed bins. Although  
212 other work has shown that priority of access may vary according to the contested  
213 resource (e.g. Val-Laillet et al., 2008), priority of access to the feeders was considered  
214 the most relevant to feed efficiency. Two black and white CCTV infrared cameras  
215 were set up above the feeders in each pen. Animals were identified for video-recording  
216 purposes by unique numbers applied in spray-on stockmarker. The cameras were  
217 attached to a high storage capacity computer that used Geovision software to store and  
218 organise the digital video files (Version 8, Geovision Inc., Taipei, Taiwan). The view  
219 from the cameras allowed all interactions at the feeders to be observed. Previous  
220 research has shown that the majority of the aggressive interactions occur in the first  
221 two hours following fresh feed provision (MacKay et al., 2013). The first, third and  
222 fifth twenty-minute segments of video from the first two hours following feeding were  
223 analysed for one day per week for the first to fourth weeks of the performance  
224 recording period inclusive. The identity of any animal displacing another from the  
225 feeder (using a physical butt or push with the head or a threatening behavioural  
226 display) and the identity of the animal it displaced was recorded (see MacKay et al.,  
227 2013). Three observers analysed the video-recordings. Their observations were  
228 balanced across the four groups. To assess inter-observer reliability, each observer  
229 watched the same three 20min recordings and the count of displacements compared.  
230 The inter-observer reliability was 85%. The displacement index (DispIndex) was used  
231 as a measure of dominance and calculated as the no. of times the animal displaced  
232 another/(no. of times it displaced another + no. of times it was displaced) (Mendl et al.,  
233 1992; Galindo and Broom, 2000). There were no animals that had zero values.

234

235 *2.3 Growth and efficiency traits*

236 Details on the efficiency traits are shown in detail in Duthie et al. (2017).  
237 Briefly, growth was modelled by linear regression of BW against test date, to describe  
238 average daily gain (ADG), mid-test BW (BW) and mid-test metabolic BW  
239 ( $MBW=BW^{0.75}$ ). The dry matter contents of individual feed components were  
240 determined on duplicate samples twice weekly. Dry matter intake (DMI) was  
241 calculated by adjusting fresh weight values recorded by the automatic feeders with  
242 these dry matter content values. Daily DMI values were used to calculate average DMI  
243 over the 56-day period. Feed conversion ratio (FCR) was calculated as average DMI  
244 per day (DMI kg/day)/ADG. Residual feed intake (RFI) was calculated as the deviation  
245 of actual DMI (kg/day) from DMI predicted based on linear regression of actual DMI  
246 on ADG, MBW and fat depth at the 12/13<sup>th</sup> rib as suggested by Basarab et al., 2003.  
247 Conventionally, RFI is calculated on a breed and diet basis. However, an RFI value  
248 calculated over the whole group allows the animals to be ranked, and their behaviour  
249 patterns compared, even if the absolute value is not comparable to other studies.

250

#### 251 *2.4 Statistical analysis*

252 All variables were checked for normality. Fresh weight intake had a non-normal  
253 distribution, so was log-transformed.

254 There were two stages to the analysis. As it had been hypothesised that  
255 dominance would affect efficiency only indirectly via effects on feeding behaviour, the  
256 first step was to determine whether dominance affected feeding behaviour. This was  
257 done using Linear Mixed Models with REML to allow the major fixed effects (breed  
258 and diet) and random effects (pen) to be modelled. Each feeding behaviour variable  
259 was tested as the dependent variable, with breed, diet and DispIndex fitted as fixed  
260 effects. The random term had terms for both pen and animals nested within pens.

261 Pearson correlations were used to examine the relationships between the continuous  
262 variables and means examined for the categorical traits.

263 Secondly, Linear Mixed Models for ADG, FCR and RFI were run in which all  
264 feeding behaviour and activity variables, DispIndex, breed, diet and age were eligible  
265 as explanatory variables. Each explanatory variable was firstly tested alone as a  
266 univariate and became a candidate for the multivariable model if it had a P-value less  
267 than 0.2. The candidate variables were then added into a multivariate model in a  
268 forward-stepwise fashion, with the order of the variables determined by the Wald  
269 statistics. Candidate variables were kept in the model if they had significance levels of  
270  $P < 0.05$  (when all other explanatory variables in the models had been fitted). Akaike  
271 Information Criterion (AIC) values, as a measure of goodness-of-fit, were used to  
272 further guide the modelling process. Pearson correlations were used to examine the  
273 relationships between the continuous variables, and means used to determine the  
274 direction of effects for categorical variables. Feed intake and feed intake rate were not  
275 included in models for FCR and RFI to avoid circularity, as these are at least partly  
276 accounted for in the calculation of these measures. The random effect was pen and  
277 animal nested within pen. Genstat (Version 16: [www.genstat.co.uk](http://www.genstat.co.uk)) was used for all  
278 analyses. The numerator (ndf) and denominator (ddf) degrees of freedom are  
279 presented, and F statistics. Note that the ddf may not be a whole number due to the  
280 presence of missing data.

281 Data from two animals were excluded from the dataset and the analysis as they had  
282 very poor growth rates, suggesting an underlying health issue.

283

### 284 **3. Results**

285 Means and standard errors for behaviours are shown in Table 1. Effects of breed  
286 and diet on behaviour are shown in Table 2.

287

### 288 *3.1 Effects of diet and breed*

289 Steers on the MIXED diet had higher dry matter intakes (F=1786.91;  
290 ndf,ddf=1,1.9; P<0.001), higher nFeedVisit values (F=390.66; ndf,ddf=1,1.6; P=0.006)  
291 and higher daily feeding times than on the CONC diet (F=67.13; ndf,ddf=1,2;  
292 P=0.015). The CHx steers had greater intake rates than the Luing steers (F=5.54;  
293 ndf,ddf=1,72.1; P=0.021), but the Luing steers had longer FeedTime values (F=6.52;  
294 ndf,ddf=1,72.1; P=0.013). Overall, there was no difference in intake, number of  
295 feeding visits or length of feeding visit between the breeds (P>0.05). However, there  
296 was a tendency for CHx steers to have higher variation in their length of feeding visits  
297 (F=3.45; ndf,ddf=1,72.1; P=0.067). CHx steers had higher DispIndex scores than  
298 Luing steers (F=15.28; ndf,ddf=1,76; P<0.001). The CHx steers had higher BW at the  
299 mid-point of the trial than the Luing steers (F=30.94; ndf,ddf=1,73.9; P<0.001; mean  
300 and sem: CHx=550.3 ± 7.3 kg; Luing=476.4 ± 7.3 kg). However, there was no  
301 relationship between intake and mid-point BW (r=0.11, P=0.34). Effect of breed and  
302 diet on ADG, FCR and RFI is shown in Supplementary Table 2 (after Duthie et al.,  
303 2017).

304

### 305 *3.2 Relationship between dominance and feeding behaviour*

306 There were significant relationships between dominance and a number of  
307 aspects of feeding behaviour. Steers with higher DispIndex scores had higher DMI  
308 (F=10.55; ndf,ddf=1,72.5; P=0.002) and feeding rates (F=7.96; ndf,ddf=1,72.1;  
309 P=0.006). There was no relationship between DispIndex and the total time spent

310 feeding each day or the length or frequency of feeding bouts. However, there was a  
311 tendency for steers with higher DispIndex scores to have less variation in the duration  
312 of their feeding visits (F=3.47; ndf,ddf=1,67.3; P=0.07).

313

### 314 *3.3 Univariate and multivariate models*

315 The variables that showed associations with ADG, FCR and RFI in the  
316 univariate analysis with a P value of <0.2 are shown in Table 3. The final models are  
317 shown below with model R<sup>2</sup> values in brackets. Variance explained by addition of each  
318 variable to the model is shown in Supplementary Table 3.

319

320 ADG:  $\mu + \text{Diet} + \text{LogIntake} + \text{nStandBout}$  (0.33)

321

322 FCR:  $\mu + \text{AgeStartTest} + \text{nStandBout}$  (0.13)

323

324 RFI =  $\mu + \text{diet} + \text{Breed.sdFeedVisit}$  (0.36)

325

#### 326 *3.3.1 ADG*

327 Animals on the CONC diet had the highest ADG (F=17.78, ndf,ddf=1,48.6;  
328 P<0.001; mean±SEM (kg/day) (CONC: 1.7±0.3; MIXED: 1.5±0.4). Steers with higher  
329 ADG had more standing bouts (F=6.74; ndf,ddf=1,67.3, P=0.013; r=0.38, P<0.001)  
330 and higher intakes (F=15.16, ndf,ddf=1,67.7; P<0.001). A number of variables were  
331 significant at the univariate level including breed and DispIndex, but they were not  
332 significant in the overall model (Table 3).

333

#### 334 *3.3.2 FCR*

335           There was no effect of breed or diet on FCR ( $P < 0.05$ ). Animals that were  
336 younger at the start of the trial had lower (more favourable) FCR values ( $F = 6.70$ ,  
337  $ndf, ddf = 1, 66.3$ ;  $P = 0.011$ ;  $r = 0.24$ ,  $P = 0.04$ ). Steers that had more standing bouts had  
338 lower FCR values ( $F = 5.06$ ,  $ndf, ddf = 1, 66.8$ ,  $P = 0.028$ ;  $r = -0.22$ ,  $P = 0.06$ )

339

### 340 3.3.3 RFI

341           There was an interaction between breed and variation in the length of the feeding  
342 event ( $F = 9.71$ ,  $ndf, ddf = 1, 55.4$ ;  $P = 0.003$ ) suggested that for the Luings, efficiency (low  
343 RFI values) was associated with low variation in the length of feeder visits ( $r = 0.39$ ,  
344  $P = 0.02$ ). However, in the CHx steers, there was a tendency for the opposite association  
345 ( $r = -0.28$ ,  $P = 0.07$ ). There was an effect of diet in this model ( $F = 26.02$ ,  $ndf, ddf = 1, 2.1$ ;  
346  $P = 0.032$ ) suggesting that steers were more efficient on the MIXED diet (RFI values =  
347 0.28 vs -0.30 for CONC and MIXED diet respectively).

348

## 349 4. Discussion

350           In the present study, feed intake was affected by dominance, with steers with a  
351 greater ability to displace others achieving higher intakes. More dominant steers also  
352 tended to be heavier, and were more likely to be of the CHx breed. Fast-growing CHx  
353 steers have a higher growth potential than the hardier Luing steers and may simply  
354 have had a higher feed intake requirement. This would be a parsimonious explanation  
355 for the finding that the dominant animals had higher intakes. However, there was no  
356 relationship between liveweight and intake, which negates this explanation. The  
357 relationship between dominance and intake appears to be more than simply the effect  
358 of breed and weight, and it is likely to relate to other elements of the behaviour and  
359 temperament of the animals that were not assessed in this study. Ideally, a study would

360 be made with a single breed and diet, and more pens of animals, to provide further  
361 clarity on the effect of dominance per se, as we we not able to do in this experiment.  
362 However, the mixed breeds, and sometimes diets, used in this study is typical of those  
363 used in other feed efficiency trials (e.g. Basarab et al., 2003; Durunna et al. 2011;  
364 Fitzsimons et al., 2014; Llonch et al., in press).

365 This finding has potential implications for studies in which the growth rate of  
366 animals is assessed. If animals are tested in situations where there is not full access to  
367 feed simultaneously for all animals, low ranking animals may not achieve their full  
368 growth potential. Similar studies in situations where group-housed animals are fed  
369 from a limited number of bins have also shown that low-ranking animals have poorer  
370 access to feed (McPhee et al.. 1964; Stricklin and Gonyou, 1981) and lower weight  
371 gains (Brouns and Edwards, 1994). However, most recent studies in cattle have shown  
372 that despite dominant animals having greater access to the feeders, no difference was  
373 found in total daily intake between dominant and subordinate, or younger and older  
374 animals (beef cattle: Stricklin and Gonyou, 1981; dairy cattle: Hosseinkhani et al.,  
375 2008; Proudfoot et al., 2009; Collings et al., 2011). The variation in results across these  
376 studies suggest that the levels of displacement and its subsequent impact on feed intake  
377 are likely to be related to the space allowance at the feeders and also to the feeding  
378 motivation of the animals. The studies in dairy cattle mentioned above all had a  
379 bin:cow ratio of 1:2 in the ‘competitive’ situation and 1:1 in the ‘non-competitive’  
380 situation. The present study had a higher ratio of approximately 1:2.5, which may  
381 explain the greater impact on feed intake. Many studies investigating RFI in beef cattle  
382 had similar or higher bin:animal ratios (e.g. Golden et al., 2008: 1:5; Lancaster et al.,  
383 2009: 1:6-8).

384 The average FeedTime per animal in this study was 133.4 mins/day. With an  
385 average of 2.5 animals/bin this means that each bin may have only been occupied for  
386 5.5h/day. This suggests that there was no real time constraint on access to the feeder,  
387 and yet observations of high levels of interactions at the feeder in this and similar  
388 studies in the period just after food delivery suggest that steers are strongly motivated  
389 to access the feeder when fresh feed is delivered (e.g. Mackay et al., 2013). There are a  
390 number of reasons for this. Fresh feed may be attractive to cattle and the bins may be  
391 easier to feed from when they are full. Cattle are also a social species, and are  
392 motivated to feed together (e.g. O'Connell et al., 1989), providing further motivation  
393 for animals to join the influx of animals to the feeders when feed is first delivered.  
394 Dairy cattle have also been shown to 'sort' fresh feed to preferentially select the larger  
395 concentrate particles of the feed (De Vries et al., 2008). It is possible that beef cattle on  
396 mixed rations in studies such as this one may also sort feed, which means that the  
397 quality of the ration declines over the day.

398 Feeding rate was also influenced by dominance, with higher intake rates shown by  
399 steers of higher DispIndex scores. In other studies with dairy cattle, increased feeding  
400 rates have been shown in situations of competition compared to non-competitive  
401 situations (Hosseinkhani et al., 2008; Collings et al., 2011), and so it might have been  
402 expected that intake rate would be higher in subordinate animals. As suggested above,  
403 there was no real time restriction on feeding time, and so no need for subordinate  
404 animals to eat faster. Additionally, as it was the larger animals that had the higher  
405 DispIndex scores, their greater size may have allowed them to eat faster. The  
406 indication of a slightly lower variation in feeding visit length for dominant animals  
407 suggests that these animals were being disturbed less by other animals or events

408 compared to subordinate animals. This greater consistency in feeding visit length in  
409 dominant animals has been shown elsewhere (e.g. Post et al., 1980).

410 Despite DispIndex showing a weak association with ADG and being a candidate  
411 variable for the full model of ADG (Table 2), DispIndex did not appear in the final  
412 model. This suggests that subordinate animals are still able to access sufficient feed to  
413 support growth. However, ADG was affected by intake, so there may be an indirect  
414 effect of dominance on ADG through its association with intake. Additionally,  
415 DispIndex was not associated with FCR or RFI. However, the lower feed intake seen  
416 in subordinate animals suggests that these animals are not able to fully express their  
417 potential for growth or efficiency. This may be the case in studies in which there is less  
418 than a 1:1 ratio between feeders and animals, or sufficient space at an open feed-trough  
419 for all animals to feed simultaneously. It is probable that ADG values, and possibly  
420 also FCR and RFI measures, for subordinate animals will depend on the level of access  
421 to feed. Additionally, it means that FCR values may not be comparable across studies,  
422 as the level of feed competition imposed in the trial may affect recorded values. This  
423 argument is not relevant for RFI values, as RFI values are a ranking of animals relative  
424 to the group mean.

425 Genetic selection for highly efficient animals is seen as an important way of  
426 improving the overall efficiency of beef production (Archer et al., 1999; Robinson and  
427 Oddy, 2004). Although there is no direct effect of dominance on efficiency, the use of  
428 feed intakes in any genetic selection programme may be inadvertently selecting for  
429 increased aggression in animals. Selection for productivity traits in isolation has been  
430 shown to have adverse effects on animal health and welfare (Rauw, 1998), and there  
431 may also be an issue in this situation. In practical terms, however, increasing access to

432 feed by increasing the length of feed trough per animal may improve intake and ADG  
433 for all animals in the group.

434 It has been found previously that higher activity is associated with poorer  
435 efficiency in beef cattle (Herd et al., 2004, Llonch et al., (in press)) as shown by the  
436 number of steps taken. No relationship between efficiency and activity, expressed in  
437 the step count, MI and total standing time, was found in the present study. The results  
438 show that there was an association between lower (better) FCR values and a higher  
439 number of standing bouts. Animals may be standing to access feed and water, or to  
440 perform other behaviours as required, in short bouts, with no overall effect on standing  
441 time. Steers with lower RFI scores also had more consistent lengths of standing bouts.  
442 This consistency suggests that the animal is able to voluntarily choose the length of  
443 standing bout, rather than it being influenced by other animals or the husbandry  
444 procedures. In group housing situations, where animals must walk to get feed and  
445 water, and interactions with other animals are likely to be frequent, all animals must be  
446 reasonably active, and distinguishing between active and inactive genotypes is  
447 difficult. Additionally, there has likely been direct or indirect selection against animals  
448 that are over-reactive to group housing, also reducing the likelihood of there being an  
449 overt influence of activity on efficiency.

450 Overall, some associations between feeding behaviour and efficiency were evident  
451 in the modelling of factors affecting FCR and RFI, contrary to what has been shown in  
452 other studies (Basarab et al., 2007; Nkrumah et al., 2007a; Golden et al, 2008;  
453 Lancaster et al 2009; Kelly et al., 2010; Durunna et al., 2011). Low variation in the  
454 length of the feeder visits was associated with lower RFI values for the Luing steers. A  
455 consistent length of feeder visits suggests that these animals maintained a consistent  
456 feeding strategy across days or were not disturbed during feeding. This strategy clearly

457 allowed these animals to maximise feed efficiency and also corresponds to the  
458 relationship between consistency of standing bouts and efficiency. However, there was  
459 a non-significant association in the opposite direction for the CHx steers, suggesting  
460 that the most effective feeding strategies depend on the animal and the situation.  
461 Relationships between feeding traits and RFI are typically analysed by dividing  
462 animals into groups (e.g. low and high, or low, medium and high) and modelling the  
463 effect of feeding traits (e.g. Golden et al., 2008; Fitzsimons et al., 2014) rather than  
464 using individual animal RFI value as a continuous trait in a model which considered all  
465 possible influencing factors. The results of this study suggest that individual animal  
466 characteristics affect feed intake and feeding behaviour, which suggests that RFI and  
467 other traits should be modelled as continuous traits that allow these characteristics to  
468 be taken into account. Further confirmation is needed, but these results suggest that  
469 individual animals adopt particular behavioural strategies dependent upon their  
470 genotype and diet. The concept that animals will adapt their feeding behaviour and  
471 activity in response to the social context and resource availability, and that this may  
472 affect their growth and efficiency is not considered in the field of feed efficiency in  
473 beef cattle. By providing more feeder space per animal and/or lower stocking density,  
474 overall efficiency in groups of animals may be improved.

475

## 476 **5. Conclusion**

477 In conclusion, the results suggest that feed intake and feeding rate were affected by  
478 dominance rank in the experimental conditions that are typically used to estimate feed  
479 efficiency. This may indirectly affect ADG at the level of the individual animal. While  
480 dominance did not directly affect RFI or FCR, the results suggest that situations in  
481 which animals must compete for feed may impair their ability to achieve optimal

482 growth. Behavioural traits influence efficiency as efficient animals have more  
483 consistent standing bout and feeder visit lengths.

484

#### 485 **Conflicts of interest**

486 The authors declare that they have no conflicts of interest

487

#### 488 **Acknowledgements**

489 The authors are grateful for the support of Mhairi Jack, Jo Donbavand, Lesley Deans  
490 and Laura Nicoll and for the technical support and animal care of the team at the Beef  
491 and Sheep Research Centre, and for the advice from Ian Nevison of Biological  
492 Statistics Scotland (BioSS). SRUC receives funding from Scottish Government's Rural  
493 and Environmental Science and Analytical Services Division. The research was funded  
494 by the UK Department for Environment, Food and Rural Affairs (Defra) and the  
495 devolved administrations (Scotland, Wales, Northern Ireland) through the UK  
496 Agricultural Greenhouse Gas Inventory Research Platform  
497 (<http://www.ghgplatform.org.uk>). The Scottish Government provides directly core-  
498 funding to SRUC.

499

500

#### 501 **References**

502

503 Archer, J.A., Richardson, E.C., Herd, R.M., Arthur, P.F., 1999. Potential for selection  
504 to improve efficiency of feed use in beef cattle: a review. *Aust. J. Agric. Res.* 50, 147-  
505 161.

506

507 Arthur, P.F., Archer, J.A., Herd, R.M., 2004. Feed intake and efficiency in beef cattle:  
508 overview of recent Australian research and challenges for the future. *Aust. J. Exp.*  
509 *Agric.* 44, 361-369.

510

511 Basarab, J.A., Price, M.A., Aalhus, J.L., Okine, E.K., Snelling, W.M., Lyle, K.L.,  
512 2003. Residual feed intake and body composition in young growing cattle. *Can. J.*  
513 *Anim. Sci.* 83, 189-204.

514  
515 Basarab, J.A., McCartney, D., Okine, E.K., Baron, V.S., 2007. Relationships between  
516 progeny residual feed intake and dam productivity traits. *Can. J. Anim. Sci.* 87, 489–  
517 502.  
518  
519 Brouns, F. and Edwards, S.A., 1994. Social rank and feeding behaviour of group-  
520 housed sows fed competitively or ad libitum. *Appl. Anim. Behav. Sci.* 39, 225-235.  
521  
522 Collings, L.K.M., Weary, D.M., Chapinal, N., von Keyserlingk, M.A.G., 2011.  
523 Temporal feed restriction and overstocking increase competition for feed by dairy  
524 cattle. *J. Dairy Sci.* 94, 5480–5486.  
525  
526 DeVries, T.J., Dohme, F., Beauchemin, K.A., 2008. Repeated ruminal acidosis  
527 challenges in lactating dairy cows at high and low risk for developing acidosis: feed  
528 sorting. *J. Dairy Sci.* 91, 3958–3967.  
529  
530 Durunna, O.N., Wang, Z., Basarab, J.A., Okine, E.K., Moore, S.S., 2011. Phenotypic  
531 and genetic relationships among feeding behaviour traits, feed intake, and residual feed  
532 intake in steers fed grower and finisher diets. *J. Anim. Sci.* 89, :3401-3409.  
533  
534 Duthie, C-A., Rooke, J. A. Troy S., Hyslop, J. J. Ross, D. W. Waterhouse, A., Roehle  
535 R., 2016. Impact of adding nitrate or increasing the lipid content of two contrasting  
536 diets on blood methaemoglobin and performance of two breeds of finishing beef steers.  
537 *Animal* 10, 786-795.  
538  
539 Duthie, C-A., Haskell, M.J., Hyslop, J.J., Waterhouse, A., Wallace, R.J., Roehle, R.,  
540 Rooke, J.A., 2017. Breed and diet of finishing beef steers have different effects on  
541 performance, methane emissions and rumen characteristics. *Animal*. 11, 1762-1771.  
542  
543 Fitzsimons, C., Kenny, D. A., Fahey, A.G., McGee, M., 2014. Feeding behaviour,  
544 ruminal fermentation, and performance of pregnant beef cows differing in phenotypic  
545 residual feed intake offered grass silage. *J. Anim. Sci.* 92, 2170-2181.  
546  
547 Galindo, F. and Broom, D.M., 2000. The relationships between social behaviour of  
548 dairy cows and the occurrence of lameness in three herds. *Res. Vet. Sci.* 69, 75-79.  
549  
550 Gibbons, J.M., Lawrence, A.B., Haskell, M.J., 2009. Consistency of aggressive feeding  
551 behaviour in dairy cows. *Appl. Anim. Behav. Sci.* 121, 1-7.  
552  
553 Golden, J.W., Kerley, M.S., Kolath, W.H., 2008. The relationship of feeding behaviour  
554 to residual feed intake in crossbred Angus steers fed traditional and no-roughage diets.  
555 *J. Anim. Sci.* 86, 180-186.  
556  
557 Hafla, A.N., Carstens, G.E., Forbes, T.D.A., Tedeschi, L.O., Bailey, J.C., Walter, J.T.,  
558 Johnson, J.R., 2013. Relationships between postweaning residual feed intake in heifers  
559 and forage use, body composition, feeding behaviour, physical activity, and heart rate  
560 of pregnant beef females. *J. Anim. Sci.* 91, 5353-5365.  
561

562 Herd, R.M., Oddy, V.H., Richardson, E.C., 2004. Biological basis for variation in  
563 residual feed intake in beef cattle. 1. Review of potential mechanisms. *Aust. J. Exp.*  
564 *Agric.* 44, 423-430.  
565

566 Hosseinkhani, A., DeVries T.J., Proudfoot, K.L., Valizadeh, R., Veira, D.M.,  
567 Keyserlingk, M.A.G., 2008. The effects of feed bunk competition on the feed sorting  
568 behavior of close-up dry cows. *J. Dairy Sci.*, 91, 1115–1121.  
569

570 Huzzey, J.M., DeVries T.J., Valois, P., von Keyserlingk, M.A.G., 2006. Stocking  
571 density and feed barrier design affect the feeding and social behavior of dairy cattle . *J.*  
572 *Dairy Sci.* 89, 126–133.  
573

574 Hyslop, J.J., Duthie, C-A., Ross, D.W., Rooke, J.A., Roehe, R., 2012. An assessment  
575 of alternative test length periods when measuring liveweight change in finishing cattle  
576 during feed efficiency studies. *Proceedings of the British Society of Animal Science*  
577 *and the Association of Veterinary Teaching and Research Work, April 2012, Vol 3;*  
578 *Part 1. Paper 46.*  
579

580 Kelly, A.K., McGee, M., Crews, D.H. Jr., Fahey, A.G., Wylie, A.R., Kenny, D.A.,  
581 2010. Effect of divergence in residual feed intake on feeding behaviour, blood  
582 metabolic variables, and body composition traits in growing beef heifers. *J. Anim. Sci.*  
583 88, 109-123.  
584

585 Koch, R.M., Swiger, L.A., Chambers, D., Gregory, K.E., 1963. Efficiency of feed use  
586 in beef cattle. *J. Anim. Sci.* 22, 486-494.  
587

588 Lancaster, P.A., Carstens, G.E., Ribeiro, F.R.B., Tedeschi, L.O., Crews, D.H., Jr.,  
589 2009. Characterization of feed efficiency traits and relationships with feeding  
590 behaviour and ultrasound carcass traits in growing bulls. *J. Anim. Sci.* 87, 1528-1539.  
591

592 Lawrence, P., Kenny, D.A., Earley, B., Crews, D.H., Jr., McGee, M., 2011. Grass  
593 silage intake, rumen and blood variables, ultrasonic and body measurements, feeding  
594 behaviour, and activity in pregnant beef heifers differing in phenotypic residual feed  
595 intake. *J. Anim. Sci.* 89, 3248-3261.  
596

597 Llonch P., Somarriba, M., Duthie, C.A., Troy, S., Roehe R., Rooke, J.A., Haskell M.  
598 J., Turner, S. P. (in press). Temperament and dominance relate to feeding behaviour  
599 and activity in beef cattle: implications for performance and methane emissions.  
600 *Animal.*  
601

602 Luiting, P., Urff, E.M., Verstegen, M.W.A., 1994. Between-animal variation in  
603 biological efficiency as related to residual feed consumption. *Neth. J. Agric Sci.* 42,  
604 59-67.  
605

606 MacKay, J.R.D., Deag, J.M., Haskell, M.J., 2012. Establishing the extent of  
607 behavioural reactions in dairy cattle to a leg mounted activity monitor. *Appl. Anim.*  
608 *Behav. Sci.* 139, 35-41.  
609

610 MacKay, J.R.D., Turner, S.P., Hyslop, J., Deag, J. M., Haskell, M. J., 2013. Short term  
611 temperament tests in beef cattle relate to long term measures of behaviour recorded in  
612 the home pen. *J. Anim. Sci.* 91, 4917-4924.  
613

614 McPhee, C.P. McBride, G., James, J.W., 1964. Social behaviour of domestic animals  
615 III. Steers in small yards. *Anim. Sci.* 6, 9-15.  
616

617 Mendl, M., Zanella, A. J., Broom, D. M., 1992. Physiological and reproductive  
618 correlates of behavioural strategies in female domestic pigs. *Anim. Behav.* 44, 1107–  
619 1121.  
620

621 Nkrumah, J.D., Crews, D.H., Jr, Basarab, J.A., Price, M.A., Okine, E.K., Wang, Z., Li,  
622 C., Moore, S.S., 2007. Genetic and phenotypic relationships of feeding behaviour and  
623 temperament with performance, feed efficiency, ultrasound and carcass merit of beef  
624 cattle. *J. Anim. Sci.* 85, 2382-2390.  
625

626 O'Connell, J., Giller, P., Meaney, W., 1989. A Comparison of Dairy Cattle  
627 Behavioural Patterns at Pasture and during Confinement. *Irish. J. Agric.Res.* 28, 65-72  
628

629 Post D.G., Hausfater G., McCuskey, S.A., 1980. Feeding behavior of yellow baboons  
630 (*Papio cynocephalus*): Relationship to age, gender and dominance rank. *Folia Primatol.*  
631 34, 170–195.  
632

633 Proudfoot, K.L., Veira, D.M., Weary, D.M., von Keyserlingk, M.A.G., 2009.  
634 Competition at the feed bunk changes the feeding, standing and social behavior of  
635 transition dairy cows. *J. Dairy Sci.* 92, 3116-3123.  
636

637 Rauw, W.M., Kanis, E., Noordhuizen-Stassen, E.N., Grommers, F.J., 1998.  
638 Undesirable side effects of selection for high production efficiency in farm animals: a  
639 review. *Livest. Prod. Sci.* 56, 15-33.  
640

641 Robinson, D.L. and Oddy, V.H., 2004. Genetic parameters for feed efficiency, fatness,  
642 muscle area and feeding behaviour of feedlot finished beef cattle. *Livest. Sci.* 90, 255–  
643 270.  
644

645 Richardson, E.C., Herd, R.M., Colditz, I.G., Archer, J.A., Arthur, P.F., 2002. Blood  
646 cell profiles of steer progeny from parents selected for and against residual feed intake.  
647 *Aust. J. Exp. Agric.* 42, 901-908.  
648

649 Richardson, E.C., Herd, R.M., Oddy, V.H., 2000. Variation in body composition,  
650 activity and other physiological processes and their associations with feed efficiency.  
651 In 'Feed efficiency in beef cattle. Proceedings of the Feed Efficiency Workshop'. Eds:  
652 J.A. Archer, R.M. Herd and P.F. Arthur, pp 46-50. University of New England,  
653 Armidale, NSW.  
654

655 Ruuska, S., Hämäläinen, W., Sairanen, A., Juutinen, E., Tuomisto, L., Järvinen, M.,  
656 Mononen, J., 2014. Can stealing cows distort the results of feeding trials? An  
657 experiment for quantification and prevention of stealing feed by dairy cows from  
658 roughage intake control feeders. *Appl. Anim. Behav. Sci.* 159, 1-8.  
659

660 Stricklin, W.R. and Gonyou, H.W., 1981. Dominance and eating behavior of beef  
661 cattle fed from a single stall. *Appl. Anim. Ethol.* 7, 135-140.  
662  
663 Syme, G.J., 1974. Competitive orders as measures of social dominance. *Anim. Behav.*  
664 22, 931-940.  
665  
666 Tolkamp, B.J., Schweitzer, D.P.N., Kyriazakis, I., 2000. The biologically relevant unit  
667 for the analysis of short-term feeding behaviour of dairy cows. *J. Dairy Sci.* 83, 2057-  
668 2068.  
669  
670 Tolkamp, B.J., Haskell, M.J., Langford, F.M., Roberts, D.J., Morgan, C.A., 2010. Are  
671 cows more likely to lie down the longer they stand? *Appl. Anim. Behav. Sci.* 124, 1-  
672 10.  
673  
674 Val-Laillet, D., Viera, D.M., Von Keyserlingk, M.A.G., 2008. Short communication:  
675 dominance in free-stall-housed dairy cattle is dependent upon resource. *J. Dairy Sci.*  
676 91, 3922-3926  
677  
678 Yeates, M.P., Tolkamp, B.J., Allcroft, D.J., Kyriazakis, I., 2001. The use of mixed  
679 distribution models to determine bout criteria for analysis of animal behaviour. *J.*  
680 *Theor. Biol.* 213, 413-425.  
681