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

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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 Luings (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 Luings 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

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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 Luining steers (n=39). This design contrasted the fast-
134 growing Charolais with the hardier Scottish Luining 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 12th/13th 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 12/13th 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) 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 R² 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

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499

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