Suckler Cow Efficiency – Breed by Environment Interactions in Commercial Herds under Various Natural Production Conditions

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The significance of breed by environment interaction on suckler cow efficiency traits was investigated, using production data from the Norwegian Beef Cattle Recording System and data collected (feed regimes, etc.) from 27 suckler cow herds. Two statistical approaches were used; mean breed performance in extensive/intensive environments (mixed models), or as within breed regressions of cow performance on individual cow feed intake. Aberdeen Angus produced higher weaning weight than Hereford below 12 000 MJ NE (241 kg) and Charolais below 13 000 MJ NE (244 kg) cow feed intake in the suckler period, after which the breeds re-ranked. The corresponding re-rank between Hereford and Charolais was at 14 500 MJ NE (263 kg) cow feed intake. Overall, breed by environment interactions were observed for calving interval, number/kg calves weaned/mated cow/year and feed efficiency, which emphasise that choice of cow breed should be dependent of the natural production resources available.

Keywords: extensive; intensive; feed intake; Aberdeen Angus; Hereford; Charolais

1.0 Introduction

Growth traits have been assumed to be the most important traits for the farm economy in suckler cow production (Michalickova et al., 2015). However, suckler cow efficiency, including maternal and reproductive traits, are also highly important for the economy on beef cattle farms. Among maternal traits, milk yield and pre-weaning gain are important (Meyer et al., 1994; Murphy et al., 2008). Furthermore, reproduction/survival traits such as calving interval, age at first calving, percentage stillbirths and calf losses are also important to optimise beef cattle production efficiency (Åby et al., 2012).

Genotype by environment (GxE) interactions are defined as unique genetic expressions of genotypes in different environments, often observed in traits such as growth, mature size and milk potential (Ferrell & Jenkins, 1985). Recently, GxE

interactions have been reported for beef breeds located in different countries or regions with unique climatic and geographical conditions (Toral et al., 2004; Cardoso et al., 2011; Santana et al., 2012; Williams et al., 2012; Espasandin et al., 2013).

The variation in feed requirements between breeds will influence their suitability to different types of pasture, especially affected by variation in altitudes and temperature (Petit et al., 1992). In Europe, beef cattle are managed and bred under a wide variety of production systems and with large variation in geographical and climatic conditions. The herd environments vary on a wide scale from harsh (extensive) to highly cultivated (intensive) agricultural areas. Often, British breed types (e.g. Aberdeen Angus and Hereford) are preferred in the extensive systems, while continental breed types (e.g. Charolais, Simmental and Limousin) are preferred in the intensive systems (Åby et al., 2012). If GxE is present, farmers should select breeds that are well adapted to their actual production conditions. Investigation of environmental factors important for GxE interactions and identification of breeds best suited for a given environment will help farmers in making optimal decisions (Wakchaure et al., 2016).

Earlier, GxE studies focusing on variation in nutritional environmental conditions have mainly been performed in controlled experiments (e.g. Mezzadra et al., 1992; Nugent et al., 1993; Jenkins & Ferrell, 1994; Baker et al., 2002; Durunna et al., 2011; McGregor et al., 2012). However, to investigate effects of GxE under commercial conditions, production results from commercial farms will have to be analysed. A pilot study (Aass & Vangen, 1999) indicated that GxE interaction might be present for beef breeds when exposed to highly varying commercial production conditions. The aim of the present study was to investigate the significance of breed by environment interaction (from now on called GxE) on suckler cow efficiency traits (e.g. age at first calving, calving interval, no. weaned calves/mated cow/year, weaning

weight, kg calves/mated cow/year, kg calves/100 kg wt$^{.75}$ mated cow/year and gram calf/MJ NE cow feed intake) involving British and Continental beef cattle breeds in commercial herds with large variation in the natural resource base.

2.0 Material and methods

2.1 Herds

Suckler cow herds with Aberdeen Angus (AA), Hereford (HE) and Charolais (CH), and with data recorded in the Norwegian Beef Cattle Recording System (NBS) in the period 2010-2014, were selected for this study. The NBS database contains individual information on birth date, sex, breed, herd, ancestry, health, natural mating/AI, calving difficulties, stillbirths, calf deaths before weaning, weights at birth, 200 (weaning) and 365 days of age and carcass data. The initial selection criteria were a minimum of 70 % registrations of weaning weights, and a minimum of 10 purebred cows per herd. These requirements were met by 188 herds. From those, 27 herds (nine of each of the three breeds) were finally selected for the study (average 42 cows/herd; range 16-132 cows/herd), based on a largest possible variation in geographical location (longitude, meter above sea level and climatic zone) within breed (Figure 1). Calving intervals (CI) shorter than 280 days and age at first calving (AFC) lower than 20 months or higher than 3.2 years were omitted. Additionally, only purebred calves born in the period January-July (93 % of the total no. of calvings) were included in the study.

2.2 Categorisation of herds

In order to categorise herds as extensive (EXT) or intensive (INT) and estimate animal feed intake, additional data were collected through personal visits on all farms. Detailed data were registered including management system, annual feeding regimes for the cows, heifers and calves, harvesting time of roughages (early, medium or late),

type/amounts of concentrates, type of pastures and the pasture/grazing management.

Three typical pastures were used; outfields (mountain/forest), uncultivated (unfertilised natural grassland) and cultivated (cultured and fertilised) pastures. Corresponding to normal practice in Norwegian suckler cow production, the calving season was mainly in the spring and lasted 2-3 months before the grazing period (May/June-September/October). Some herds (AA/HE herds, n=11; CH herds, n=4) utilised outfields from June/July to August/September, with a period on cultivated/uncultivated pasture before and after the outfield period. Calves were weaned at about 6-8 months of age in the end of the grazing season. The rest of the year, all animals were feed and kept indoor.

Initially, the herds were categorised after climatic zone (3-5=INT and 6-8=EXT). However, if the main pasture and feed management in the suckler period implied that herds should be categorised otherwise, some exceptions were necessary. If a considerable number of days (60-100%) of the grazing period was in outfields and/or uncultivated pastures, the herd were categorised as EXT. Likewise, if 60-100% of the grazing period were in cultivated pastures, the herds were categorised as INT. Overall, the grazing period constituted the main part of the suckler period (mean 60%; range 33-100%). However, if the indoor suckler period before the pasture season included concentrate feeding and comprised more than 60% of the total suckler period, the herd was categorised as INT (n=2).

The final number of herds, cows and calvings, unsuccessful matings and number of bull and heifer calves within breeds and environment are shown in Table 1. The dataset had an approx. 50:50 distribution of primiparous (n=1294) and multiparous (n=1378) cows, which were separated and analysed in two subsets to avoid confounding of their production results. From the group of primiparous cows, 635 cows had

subsequent parities in the multiparous group of cows. As shown in Table 1, the calving data (n=4070) had an acceptable distribution between the three breeds and the EXT and INT herds. Calves missing data on sex (n=75) were excluded in all analyses, which included the fixed effect of sex.

2.3 Estimations of feed intake

The on-farm collected data with detailed annual feed managements constituted a basis for estimations of individual feed intake for calves, young heifers, pregnant heifers, primiparous and multiparous cows in various periods (separated in suckler and dry period for cows) during the production year, measured in MJ NE. The feed intake by the cow and the calf (from parturition until weaning), subtracted the energy from cow milk, was defined as a cow/calf unit. Milk yield was set to 1000 litres (1624 MJ NE) and 1200litres (1930 MJ NE) from birth until weaning for AA and HE/CH, respectively (90% milk yield per calf if twins) (e.g. Andersen, 1990; Jenkins & Ferrell, 1992; McGee et al., 2005; Rodrigues et al., 2014). The total primiparous cow feed intake was defined as the feed energy (MJ NE) consumed from birth of the heifer until weaning of her first calf, while the total multiparous cows feed intake was defined as the feed energy (MJ NE) consumed from weaning of last calf until weaning of next calf. The total feed intake was in also separated into the suckler period and the rearing/dry period.

In the absence of data on individual cow mature weights, actual cow carcass weights in each herd (2010-2014) were used to approximate average cow live weights, corrected for dressing % within EUROP conformation score (scale 1-15; Animalia, 2011). The approximated mature weights were set to 600, 650 and 750 kg for AA, HE and CH, respectively, showing high compliance with the breed-specific national statistics (n=3886; calculations not shown; Animalia, 2017). At mating/calving, heifer

weights were set to 60/80 % of their mature weight. The calf feed requirement based on individual weaning weight were assumed met using estimates from Andersen (1990).

Roughage analyses were provided from five farms. For the other farms, roughage quality was set based on roughage analyses from other farms within the same municipalities and years (2010-2014; n=3961), provided by Eurofins, the national centre for such analyses. If the farmers fed concentrate, a substitution effect of 0.33 for low (5.3-5.8 MJ NE/kg DM) and moderate (5.9-6.1 MJ NE/kg DM) quality roughages, and 0.63 for high (6.2-6.4 MJ NE/kg DM) quality roughages were used (Randby et al., 2012). Ammonium treated/dry straw was fed at 12 farms, and energy content set to 4.95 MJ NE/kg DM/2.12 MJ NE/kg DM (Norwegian university of life Sciences: Department of Animal and Aquacultural Sciences & Norwegian Food Safety Authority, 2008).

Indoor and pasture feed intake were calculated to estimate feed efficiency. Amounts of roughage fed (kg) and DM content was provided in herds with restrictive roughage feeding during the indoor period (n=5). If roughage were fed *ad libitum*, indoor feed intake was calculated with the Danish fill unit system for suckler cows (Andersen, 1990). Andersen (1990) did not discuss roughage intake potential for weaned calves, thus for heifers, the estimates from Wilkinson (1985) were used.

As Norwegian farmers receive subsidies per hectare and number of animals at pasture, these data were provided from the study herds. For both uncultivated/cultivated types of pastures, stocking rate was well within carrying capacity, indicating that pasture availability was not a limiting factor. Feed intake on these pastures was set to 84.9 MJ NE/day in the early summer (before July 15th), 70.8 MJ NE/day in the late summer (July15th – Aug. 30th) and 56.6 MJ NE/day in the autumn (later than Aug.30th) for all cows independent of breed, based on documentation from the Norsk landbruksrådgiving (2015). For herds using outfield pastures, the feed quality was

evaluated by experts during 2016/2017, using animal GPS tracking data as an aid to localise the areas actually grazed (Rekdal et al., 2018). Despite the variation in outfield localities, all herds were classified with pasture qualities varying from 'good' to 'very good'. Additionally, stocking rate was low on all outfield pastures (mean:41.1; range:1.0-128.6 hectare/cow/calf unit). A medium-sized suckler cow can have a daily feed intake of 60.1 MJ NE in outfield pastures Rekdal (2006). This choice of estimate is supported by a large cattle study in Norwegian outfields (Bjor & Graffer, 1963) and thus the best reasonable average for all suckler cow breeds based on the existing literature. Implications of this estimate for the large-sized breed CH is further discussed in Section 4.2.

2.4 Cow efficiency traits

Cow efficiency traits analysed were age at first calving (AFC), calving interval (CI), number of calves weaned per mated cow per year (NC), birth weight (BW), 200 days weaning weight (WW), kg calf weaned per mated cow per year (KC) and kg calf weaned per 100 kg metabolic weight of mated cow per year (KCwt$^{.75}$). Metabolic cow weight (in KCwt$^{.75}$) was calculated as mature weight$^{.75}$ (Keiber, 1932). Feed efficiency traits were measured as gram calves weaned/MJ NE feed intake for the cow/calf unit in the suckler period (GMJs) and gram calves weaned/MJ NE feed intake for the cow/calf unit in the total period (suckler period + rearing/dry period) (GMJt). Cows that did not conceive during the mating season were included when analysing traits measured per mated cow. Calf weights were adjusted to 200 days weight based on individual growth rate from date of birth to date of weighing (150-275 days of age).

2.5 Statistical analyses

All data editing and analyses were performed using various statistical procedures in SAS (SAS Version 9.4; SAS Software Institute INC). The results were considered significant if $p<0.05$. Initially, statistical analyses (PROC GLM; SAS) of the cow/calf feed intake in the suckler, rearing/dry and total period (defined in Section 2.3) were performed (Model 1), including the fixed effect of breed, environment, breed by environment interaction, twin, sex and herd within breed and environment.

To investigate the presence of GxE, the data were analysed using two approaches (Falconer & Mackay, 1996). The first analysis (Model 2) estimated GxE based on mean breed performance in the two discrete environments, EXT and INT. The second approach (Model 3) investigate the environmental sensitivity of the breeds interpreted as linear regressions of individual cow performance on the cow feed intake.

In the first approach (Model 2), the data were analysed using mixed models (PROC MIXED; method MIVQUE0). Initially, an animal model with pedigree was considered to correct for possible genetic relationships. An examination of the pedigree revealed that the genetic relationship between herds were negligible, because a high number of unique sires within breed was present (AA, n=126; HE, n=96; CH, n=198), combined with about the same number of unique paternal grandsires. In addition, the sires/grandsires used were not confounded with the EXT and INT herd groups, i.e. the genetic basis was almost similar and randomly distributed among the two groups of herds. Furthermore, control analyses with each herd successively left out were performed, revealing that no herd had an unproportionally large impact on the results in the EXT and INT groups. Model 2 was defined as:

$$Y = \mu + B_i + E_j + BE_{ij} + HY_k(BE_{ij}) + T_l + S_m + CM_n + CA_o + cow_p(HY_kBE_{ij}) + e_{ijklmnop}$$

Were Y was the studied suckler cow efficiency traits, μ was the overall mean, B_i was the fixed effect of breed (i=1,2,3), E_j was the fixed effect of environment (j=1,2), BE_{ij} was the fixed effect of interaction between breed and environment (ij=1,...,6), HY_k was the fixed effect of herd times year within BE_{ij} (k=1,.....134; 27 herds times 5 years), T_l was the fixed effects of twin (l=1,2), S_m was the fixed effects of sex of the calf (m=1,2), CM_n was the fixed effect of calving month (n=1,...,7), CA_o was the fixed effect of cow age (o=1,...,7), $cow_p(HY_kBE_{ij})$ was the random effect of cow within herd, year, environment and breed and $e_{ijklmnop}$ was the random error term. Cow age varied (primiparous 2-3 years; multiparous 3-17 years). Thus, the cows were grouped in age groups 1-7 with one-year intervals from 20 months ($\approx$1.5 years) of age up to age group $7 \geq 8.5$ years of age. In age group 1, 96 % of the primiparous cows were included, while the distribution of multiparous cows varied from 24 % (group 3) to 13 % (group 7).

BW and WW were analysed using the full model (Model 2), while some of the fixed effects (sex, twin, age of cow) were non-significant and thus omitted from the models for AFC and CI. For the traits NC, KC and KCwt$^{.75}$, the fixed effect of calving month was additionally excluded from the full model, as these traits were calculated as mean calf production per year. The fixed effect of cow age was excluded in the feed efficiency models (GMJs and GMJt), as feed intake was independent of age within the groups of primiparous and multiparous cows.

To investigate the significance of GxE interactions, pairwise t-tests were performed for each trait, which tested if the differences in absolute mean performance between breeds within one (EXT) environment, were sign. different to the absolute mean differences between the breeds in the second (INT) environment (((AA_{EXT}-HE_{EXT}) vs (AA_{INT}-HE_{INT})), ((AA_{EXT}-CH_{EXT}) vs ((AA_{INT}-CH_{INT})) and ((HE_{EXT}-CH_{EXT}) vs (HE_{INT}-CH_{INT}))).

In the second approach, individual cow production records (AFC, CI, NC, BW, WW, KC and KCwt.75) were pre-corrected for the same effects as described under Model 2 (except breed, environmental group, herd and cow), prior to the regression analyses. The general regression model (Model 3) was:

$$Y_{PCT} = \mu + B_i + \beta_0 FI + \beta_i FI(B_i) + e_{(j)i}$$

where Y_{PTC} is the precorrected cow efficiency trait (AFC, CI, NC, BW, WW, KC and KCwt.75), μ is the overall mean, B_i is the fixed effect of breed (i=1,2,3), $\beta_0 FI$ is the general regression of Y_{PTC} on cow feed intake, $\beta_i FI(B_i)$ is the regression of cow feed intake within breed and $e_{j(i)}$ is the random error term associated with the jth observation of cow feed intake within breed.

The regression analyses were performed on cow feed intake (x-axis) in the dry period previous calving for BW and the corresponding suckler period for WW. For the regressions involving CI, the x-axis variable was either cow feed intake in the suckler, dry or total period belonging to the previous cow/calf event. For AFC, the x-axis variable was the mean feed intake per year in the rearing period. Finally, the regressions for the fertility traits NC, KC and KCwt.75 were based on the cow mean feed intake per year in the 'total period' (Section. 2.3) for both primiparous and multiparous cows. For cows that did not conceive during one or more of the study years (n=347), the total period was defined as the retention time for the non-pregnant cow in the herd.

3.0 Results

3.1 Feed intake

The estimated feed intake in the suckler period was significantly higher in the INT than in the EXT environment for both primiparous and multiparous cows within all three breeds (Table 2).

3.2. GxE estimates based on mean breed performance

Overall breed estimates and the results from the GxE analyses based on mean breed performance in the EXT and INT environments (model 2) are presented in Table 3. In general, the performance results for calf production from the primiparous cows did not reveal important GxE interactions (i.e. AFC, NC, BW and WW, Table 3). CH had a superior yearly kg calf production (KC) in the EXT environment compared to AA and HE, but breed differences were offset in the INT group, and a significant GxE interaction was revealed ($p \leq 0.05$). Additionally, when adjusting for metabolic cow size ($KCwt^{.75}$), the breed differences in kg calf production were considerably reduced and non-significant within both environmental groups. Still, the interaction involving HE and CH was significant ($p \leq 0.05$). Furthermore, for GMJs, highly significant GxE interactions were observed ($p \leq 0.001$) in primiparous cows. AA was the superior breed in both environments. While AA improved the feed efficiency significantly in the INT compared to the EXT environment, HE and CH cows reduced their feed efficiency at the same rate.

In contrast to the primiparous cows, the elder HE and CH cows responded with increased fertility when exposed to the INT environment (Table 3), which contributed to highly significant GxE interactions between breeds for NC. For the HE cows, this was particularly noticeable for NC (+0.15, $p \leq 0.001$), while the CH cows excelled with

lowered CI (-13 days, P≤0.001). The multiparous AA cows did not respond

correspondingly.

The breeds responded very differently in KC and KCwt$^{.75}$ when exposed to

higher feed intakes. While the multiparous AA cows showed no significant differences

in performance, the response was considerable in both traits for CH cows, and even

higher for the HE cows (Table 3). Significant GxE interactions were observable for both

traits, including a re-ranking between AA and HE. As for the primiparous cows, breed

differences were considerably reduced when calf weights were adjusted to metabolic

cow size (KCwt$^{.75}$).

The multiparous AA and HE cows performed similar and had significantly

higher feed efficiency in the suckler period (GMJs) compared to CH cows in the EXT

herd group. Higher feed intake in the INT group did not influence the performance of

AA cows, while feed efficiency decreased for CH and HE cows. Although no re-

ranking occurred, the highly significant GxE interactions involved all three breeds

(Table 3).

3.3. GxE estimates based on regression analysis

Regression coefficients (Model 3) and the 5 and 95 % quantiles for the observed

individual cow feed intake within breed are presented in Table 4. Below or above 5 and

95 % quantiles, the regressions were uncertain due to few observations. In primiparous

cows, yearly feed intake from birth to first calving did not influence AFC. However,

when analysing the effect of increased yearly feed intake (from birth of the cow until

weaning of the 1st calf) on NC, results revealed a positive response in HE (highest

response) and AA (Table 4).

The regression analysis of WW on primiparous cow feed intake in the suckler

period revealed GxE interactions were CH showed the highest response, followed by

HE and then AA (horizontal slope) (Figure 2). This caused a re-ranking between AA and HE at 10 500 MJ NE, AA and CH at approx. 13 000 MJ NE and between HE and CH at 14 000 MJ NE feed intake in the suckler period.

As for WW, the sum of yearly calf weights per mated heifer (KC) showed a significant increase in all breeds following higher feed intake (Table 4). The KC slopes for HE and CH were parallel (p=0.10) and steeper than the slope for AA cows. AA cows were superior to HE cows at lower feed intakes. However, a re-ranking in KC occurred at approx. 15 500 MJ NE/year. When adjusting for metabolic cow weight (KCwt$^{.75}$), the gradients of the slopes were reduced for all breeds. Still, the highest b-value was observed for HE, significantly different from AA (p<0.001) and CH (p<0.01).

Cow feed intake in the suckler period did not influence the subsequent CI (b-values ns.; Table 4). However, cow feed intake in the dry period prior to mating influenced CI (b-values≠ 0). While AA had the largest reduction in CI, followed by HE, the opposite was the case for CH cows. Significant interactions were present, involving AA versus CH (p≤0.001) and HE (p≤0.05). The regression of CI on feed intake the total period (suckler + dry) prior to mating showed approximately the same pattern.

For multiparous cows, the regression analysis of WW on cow feed intake in the corresponding suckler period showed similar patterns as for the primiparous cows (Figure 3). AA cows produced higher weaning weights than HE and CH cows below 12 000 MJ NE and 13 000 MJ NE cow feed intake in the suckler period, respectively, after which the ranks interchanged. The corresponding change in rank between HE and CH cows occurred at 14 500 MJ NE.

AA and CH responded with a higher yearly production of kg weaned calf (KC) with increased yearly cow feed intake (Table 4). Additionally, the regression

coefficients for AA and CH cows were significantly different and revealed a GxE interaction. AA cows had a higher KC production than CH cows up to approx. 23 500 MJ NE annual cow feed intake before they re-ranked. As for primiparous cows, when adjusting KC for metabolic cow weight ($KCwt^{.75}$), the gradients of the slopes were reduced for all breeds (Table 4).

4.0 Discussion

4.1 The data

The data showed a considerable variation in production results and feed regimes, but within the breed population ranges of production averages in the NBS. A high number of unrelated sires were present over herds within breeds, which confirmed that broad genetic bases and similar genetic levels within breed were present. Thus, it is reasonable to regard the farms as representatives of the populations of the three breeds in domestic, commercial suckler cow production.

Reliable registrations of mature cow weights in sufficient quantities are seldom available from commercial farms. Using data on cow carcass weights in the herds was the best available alternative.

Feed intake estimates are encumbered with some uncertainty, due to both breed level cow mature weights and dry matter intake capacity assumptions. However, the prerequisites were the same for all herds within breed. Roughage quality normally shows large variation between geographical locations, production year and stage of maturity at the time of harvest. The data from Eurofins, the national centre for roughage analyses accounted to a large extent for these sources of variation.

Measuring pasture feed intake is challenging (Cottle, 2013), and was not applicable in the present project. Thus, the same pasture intake was set within pasture

type (outfield/uncultivated/cultivated) for all herds/breeds (Section 2.3). Even though pasture availability was not limited, pasture intake was not necessarily enough to meet requirements for all the breeds (further discussed in Section 4.2). According to Norwegian advisory services, the suckler cow/calf feed intake used were within an expected range (Nortura SA, 2019). In addition, the significant differences between the EXT and INT herds demonstrated that the feed intake estimations are reliable.

4.2 Suckler cow efficiency traits

Feed intake is a major regulator of reproductive performance in suckler cow production (Wettemann et al., 2003; Funston, 2004; Diskin & Kenny, 2014). In contrast to the present study, GxE interaction in AFC has been observed (Chiaia et al., 2015), which may be explained by lowered age at puberty onset, as a result of higher feed intake (Review; Randel & Welsh, 2013). CI was reduced in AA cows with higher annual feed intake (Table 4), which were in accordance with Nugent et al. (1993). However, in the present study, the CI regression coefficients for HE and CH were low and diverging. For these breeds, the results may be explained by the partition of the annual feed volume, i.e. the EXT herds practised a higher feed intake in the dry period than the INT herds (and vice versa in the suckler period; Table 2), probably to compensate for insufficient feed availability during the suckler/pasture period. The substantially lower CI in the INT CH herds (Table 3) supports this interpretation and demonstrates the importance of sufficient access of energy for the suckler cow during the calf period.

Apparently, no effects of environment were present on the observed number of weaned calves (NC) from primiparous cows (Table 3). However, results from the regression analyses (Table 4) suggest that the herds with the lowest annual heifer feed intake in the rearing and 1st suckler period were suboptimal for AA and HE. Additional analysis clarifies that the superior NC of multiparous CH cows was caused by a higher

pregnancy rate (results not shown), although higher twin frequency was present in CH than the other two breeds (6 % vs 2%; P<0.001). Furthermore, the GxE interactions in NC observed as a considerably poorer performance of multiparous HE cows in the EXT environment relative to AA and CH (Table 3), was due to lower pregnancy rate. The corresponding substantial positive effect of increased feed intake on this trait in the INT herds (Table 2) was not supported by the HE regression analysis of NC on MFIY (b-value ns.; Table 4; multiparous cows). However, considering the results for both primiparous and multiparous cows, this could indicate that negative effects of the suboptimal heifer feed intake on NC propagates to subsequent parities. In addition, the relatively lower annual feed intake level offered HE multiparous cows in the EXT herds compared to the INT herds (approx. 3000 MJ NE) might be the primary cause (Table 2). Ciccioli et al. (2003) also found increased pregnancy rate with higher feed intake in the postpartum period for Aberdeen Angus and Hereford heifer crosses.

Weaning weight breed differences were in agreement with other studies (e.g. Marston et al., 1992; Bullock et al., 1993; Aass & Vangen, 1999; Duangjinda et al., 2001; Estermann et al., 2002). Furthermore, in accordance with other studies (e.g. Cafe et al., 2006; Martin et al., 2007; Bohnert et al., 2013), WW improved with increased cow feed intake.

Variation in climatic zones and longitudes/latitudes have been observed to cause of GxE interactions (Espasandin et al., 2013; Santana et al., 2013). Although no GxE interaction in WW were observed between EXT and INT environments in the present study (Table 3), regressions of WW on cow feed intake in the suckler period identified significant interactions (Table 4). The results (Fig. 1 and Fig. 2) suggested superiority of AA in WW to the other breeds at lower feed levels (10 500 – 12 000 MJ NE) in the suckler period, while CH cows exceeded HE cows at higher feed levels (>14 000 MJ

NE). Jenkins & Ferrell (1994) found that AA cows were superior to CH cows in weaning weights with a lowered annual feed intake (re-ranking at 5000 kg DMI/year, approx. 29 300 NE MJ/year). Although this was a controlled experiment with the breeds exposed to a wider feed intake range than the present study, the results interestingly demonstrate similar patterns.

Cow milk production and WW are positively correlated (e.g. McGee et al., 2005; Murphy et al., 2008; Mummed, 2013; Espasandin et al., 2016). Thus, the lower regression coefficients of WW on cow feed intake for AA and HE cows can indicate lower response in milk production compared to CH cows. This is in accordance with Jenkins & Ferrell (1992), who found that CH had the largest response in milk production compared to AA and HE cows when exposed to a higher feed intake. Additionally, AA is observed to allocate higher energy intake to increased body weight rather than milk (Brauner et al., 2011) or calf production (Jenkins & Ferrell, 1994).

HE had the largest response in KC and KCwt$^{.75}$, followed by CH. These were reasonable results due to higher pregnancy rates and caused significant GxE interactions (Table 3). CH was no longer superior in kg calf production when KC was adjusted to metabolic cow weight (KCwt$^{.75}$). This lack of breed differences in calf production relative to cow size, indicate that CH did not had a more efficient production in a biological sense, even though the calf production volume was higher. Morris et al. (1993) found that HE and AA had higher kg calf production relative to cow size than CH in three locations differing in harshness. Additionally, Scasta et al. (2015) observed similar results in cows with different mature weights (453-634kg). The lower maintenance requirement by the small-sized cows were an explanation of higher efficiency, which were even more important when environmental conditions were challenging because of drought. In a review, Arango & Van Vleck (2002) conclude that

cow size may influence beef production efficiency and that optimal cow size may vary between environments.

Variation in feed efficiency has been observed for both growing and adult beef cattle (review; Archer et al., 1999). All breeds responded positively in annual feed efficiency (GMJt), which is in accordance to Jenkins & Ferrell (1994). However, Jenkins & Ferrell (1994) observed that AA and HE decreased in feed efficiency above 4000 kg DMI/year (approx. 23 400 NE MJ/year). The exposure to a wider range in feed availability created a clearer biological response in the cited study.

Although there was little difference in annual feed intake between EXT and INT CH herds (multiparous cows; Table 2), the INT herds were superior in annual feed efficiency (GMJt; Table 3). The different partition of annual feed intake in the EXT CH herds (Table 2) was probably the cause, affecting feed efficiency negatively. The overall superior feed efficiency in AA compared to HE and CH, may be explained by smaller mature size and maintenance requirement (Parnell, 1994).

The patterns of GxE interactions in the regressions of WW on cow feed intake (Table 4), and the clear response in WW gained for HE and in particular CH cows, could be retrieved in the level of breed responses in GMJt. Combining these results, the lowered cow feed availability performed in the EXT HE and CH herds during the suckler period, presumably led to reduced weaning weights. For CH cows, it also resulted in lowered annual feed efficiency. The high proportion of harsh pastures (outfield/uncultivated) may not have met the feed requirements in those breeds, as varying altitudes and temperatures may affect larger sized breeds to a larger extent (Petit et al., 1992). The results were opposite in the INT herds of the two breeds, as well as for AA. These effects of suckler vs dry period feeding regimes also had effects on number (NC) and weights (KC) of weaned calves per mated cow.

5.0 Conclusion

The study revealed significant GxE interactions under commercial production conditions with varying feed intakes for essential suckler cow efficiency traits like calving interval, number of weaned calves/mated cow/year, weaning weight, kg calves/mated cow/year, kg calves/100 kg wt$^{.75}$ mated cow/year and gram calf/MJ NE suckler period feed intake. The feed intake in the AA and HE herds, were within the same range. Still, production performance diverged and demonstrated that AA had higher production than HE in the extensive feed regimes. CH cows clearly needed the most intensive feed regimes in the suckler period to reach their production potential. Feed level in the suckler period was crucial for the annual production and feed efficiency. Even though CH had the largest production volume, the production efficiency relative to the mature cow weight were equal in AA and CH, and relative to feed intake was highest in AA, followed by HE.

6.0 Acknowledgments

7.0 References

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Table 1. Number of herds, primiparous (parity=1) and multiparous (parity > 1) cows, calvings, unsuccessful matings and calves (within sex) within breed (AA, HE and CH) and environment (EXT and INT) from 2010-2014.

	Number of observations						
Breed[1]		EXT			INT		Total
Environment[2]	AA	HE	CH	AA	HE	CH	
Herds	5	5	3	4	4	6	27
Primiparous cows	210	283	228	227	149	197	1294
Calvings	170	217	197	193	146	181	1104
Multiparous cows	249	267	245	241	149	227	1378
Calvings	554	465	573	478	287	609	2966
Mated cows, n.c.[3]	142	241	140	151	63	103	842
Bull calves	379	319	404	323	209	403	2037
Heifer calves	339	345	343	342	212	377	1958
Calves, u.s.[4]	6	18	23	6	12	10	75

[1]AA=Aberdeen Angus, HE=Hereford, CH=Charolais.

[2] EXT=extensive feed regimes and INT=intensive feed regimes.

[3]Mated cows that did not conceive during the mating season.

[4]Calves with unknown sex.

Table 2. Estimated least square means with (STD) for feed intake (MJ NE) for the cow/calf unit within breed (AA, HE and CH) and environment (EXT and INT) in different periods.

Feed intake within breed and environment						
Breed[1]		EXT			INT	
Environment[2]	AA	HE	CH	AA	HE	CH
Primiparous cows						
Rearing period[3]	24 950 a (250)	27 100 b (250)	34 000 c (250)	25 650 d (250)	27 700 b (300)	33 650 c (250)
Suckler period[4]	16 350 a (300)	16 800 b (300)	19 850 c (300)	17 650 d (300)	19 800 c (350)	23 100 e (300)
Total period[6]	41 200 a (700)	43 800 b (700)	53 750 c (650)	43 250 b (650)	47 400 d (700)	56 600 e (700)
Multiparous cows:						
Dry period[5]	7800 a (150)	8750 b (150)	10 650 c (200)	7850 a (150)	7500 a (200)	8700 b (150)
Suckler period[4]	19 400 a (150)	19 300 a (150)	23 500 c (150)	20 700 b (150)	23 350 c (150)	26 600 d (100)
Total period[6]	27 100 a (250)	27 900 b (250)	34 000 c (300)	28 400 b (250)	30 800 d (300)	35 200 e (250)

[1]AA=Aberdeen Angus, HE=Hereford, CH=Charolais.

[2] EXT=extensive feed regimes and INT=intensive feed regimes.

[3]Rearing period: From birth of the heifer calf until weaning of her first calf.

[4]Suckler period: From birth to weaning of the calf.

[5]Dry period: Form weaning to birth of the next calf.

[6]Total period: Suckler + Rearing/Dry period.

[7] Least square means rounded off. Different letters (a-e) shows least square means significantly different from each other (P<0.001-0.035).

Table 3. Estimated least square means for the overall breed effects (AA, HE and CH), breed effects within environments and significance of breed by environment interactions (GxE) on suckler cow efficiency traits[1] for a cow/calf unit based on mean breed performance in two environments (EXT and INT).

	GxE based on mean breed performance											
	Overall breed effects[4]			Breed effects within environment[5]						Sign. of G x E[6]		
Environment[2]				EXT			INT					
Breed[3]	AA	HE	CH	AA	HE	CH	AA	HE	CH	AA-HE	HE-CH	AA-CH
Primiparous cows:												
AFC (days)	772 a	778 a	783 a	768 a	768 a	778 a	776 a	787 a	788 a	ns	ns	ns
NC (no.)	0.30 a	0.31 a	0.32 a	0.29 a	0.29a	0.34 a	0.31 a	0.34 a	0.31 a	ns	*	ns
BW (kg)	32 a	34 b	38 c	32 a	34 b	38 c	32 a	33 b	38 c	ns	ns	ns
WW (kg)	199 a	210 b	235 c	187 a	194 a	222 b	212 b	225 b	248 c	ns	ns	ns
KC (kg)	68 a	75 ab	84 b	62 a	64 a	83 b	74 ab	86 b	86 b	ns	*	ns
KCwt.75 (kg)	56 a	58 a	59 a	51 a	49 a	58 ab	61 ab	66 b	60 ab	ns	*	ns
GMJt	7.0 a	6.8 b	6.4 c	6.8 ad	6.7 ad	6.3 c	7.3 b	6.9 a	6.6 cd	ns	ns	ns
GMJs	17.6 a	17.2 b	16.6 c	17.3 ac	17.5 ab	16.9 c	18.0 b	16.9 c	16.2 d	***	ns	***
Multiparous cows:												
CI (days)	373 a	368 a	380 b	374 a	370 a	387 b	373 a	367 a	374 a	ns	ns	*
NC (no.)	0.89 a	0.86 a	0.95 b	0.90 a	0.78 b	0.93 c	0.88 a	0.93 ac	0.97 c	***	***	*
BW (kg)	35 a	36 b	42 c	35 ab	36 ab	43 c	35 a	36 b	42 c	ns	**	ns
WW (kg)	230 a	238 b	272 c	218 a	223 a	263 b	254 c	244 bc	282 d	ns	0.06	ns
KC (kg)	221 a	224 a	272 b	216 a	192 b	251 c	227 a	256 c	293 d	***	*	***
KCwt.75 (kg)	183 a	174 b	190 a	178 a	149 c	176 a	188 ab	198 bd	205 d	***	**	**
GMJt	12.4 a	11.9 b	11.5 c	12.2 a	11.8 b	11.2 c	12.5 d	12.0 ab	11.8 b	ns	0.06	ns
GMJs	17.4 a	16.6 b	16.1 c	17.3 ab	17.1 b	16.4 c	17.5 a	16.2 c	15.9 d	***	**	***

[1]AFC: Age at first calving, NC: No. weaned calves/mated cow/year, BW: Birth Weight, WW: Weaning Weight, KC: Kg calves/mated cow/year, KCwt$^{.75}$: Kg calves/100 kg wt$^{.75}$ mated cow/year, GMJt: Gram calf/MJ NE total period, GMJs: Gram calf/MJ NE suckler period, CI: Calving interval.

[2]EXT=extensive feed regimes and INT=intensive feed regimes.

[3]AA=Aberdeen Angus, HE=Hereford and CH=Charolais.

[4,5] Different letters (a-d) shows least square means significantly different from each other (P<0.001-0.053).

[6]Significans of estimated GxE interactions:

(((AA_{EXT}-HE_{EXT}) vs (AA_{INT}-HE_{INT})), ((HE_{EXT}-CH_{EXT}) vs ((HE_{INT}-CH_{INT})) and ((AA_{EXT}-CH_{EXT}) vs (AA_{INT}-CH_{INT}))).

Table 4. Breed by environment interactions (GxE) based on regressions of suckler cow efficiency[1] for the cow/calf unit on the cow feed intake in different periods and the data range (5 and 95 % quantiles) of individual cow feed intake (MJ NE).

	GxE based on regressions									
	Regression coefficients for the suckler cow efficiency[3]				5 and 95 % quantile for the cow feed intake[5]					
Breed[2]	AA	HE	CH	Feed intake[6]	AA		HE		CH	
					Q5%	Q95%	Q5%	Q95%	Q5%	Q95%
Primiparous cows:										
AFC	-0.0040 ab	0.0016 a	-0.0075 b	MFIYRP	9 800	14 250	12 150	15 150	14 300	18 000
NC (no.)	0.000048 a***	0.000069 b***	0.000055 a	MFIY	10 650	16 100	12 200	17 000	14 950	20 350
BW (kg)	0.000142 a*	0.000012 a	0.000172 a	RP	20 450	31 150	24 000	35 300	29 100	39 600
WW (kg)	-0.0001 a	0.0057 b*	0.0179 c***	SP	10 450	13 400	9 850	14 600	13 300	16 900
KC (kg)	0.0119 a***	0.0182 b***	0.0158 b**	MFIY	10 650	16 100	12 200	17 000	14 950	20 350
KCwt.75 (kg)	0.0098 a***	0.0141 b***	0.0110 a	MFIY	10 650	16 100	12 200	17 000	14 950	20 350
Multiparous cows:										
CI (days)	-0.0001 a	0.0030 a	0.0014 a	SPpre	10 750	14 950	11 000	15 200	14 600	18 300
CI (days)	-0.0029 a***	-0.0008 b*	0.0007 b***	DPpre	5 050	12 100	5 150	11 500	5 250	15 550
CI (days)	-0.0023a***	-0.0001 b*	0.0007 b***	TPpre	16 700	24 650	16 850	25 100	21 100	32 300
NC (no.)	0.000046 a***	0.000053 a	0.000053 a	MFIY	17 650	23 000	17 200	24 000	20 950	27 500
BW (kg)	-0.000019 a	-0.000074 a	0.000172 b**	DP	5 200	11 200	5 100	11 450	5 450	16 850
WW (kg)	0.0023 a*	0.0087 b***	0.0130 c***	SP	11 050	14 800	11 000	15 200	13 300	18 350
KC (kg)	0.0116 a***	0.0154 ab	0.0180 b**	MFIY	17 650	23 000	17 200	24 000	20 950	27 500
KCwt.75 (kg)	0.0095 a***	0.0120 ab	0.0126 b*	MFIY	17 650	23 000	17 200	24 000	20 950	27 500

[1]AFC: Age at first calving, NC: No. weaned calves/mated cow/year, BW: Birth Weight, WW: Weaning Weight, KC: Kg calves/mated cow/year, KCwt.75: Kg calves/100 kg wt.75 mated cow/year, CI: Calving interval.

[2]AA=Aberdeen Angus, HE=Hereford, CH=Charolais.

[3] Different letters (a-c) shows regression coefficients significantly different between breeds (P<0.001-0.053). Stars indicate significant regression coefficients, not equal zero.

[4]MFIYRP: Mean feed intake/year in the Rearing period (from birth of the heifer calf until weaning of her first calf), MFIY: Mean feed intake/year in the Total period (Suckler period, from birth to weaning of the calf + Rearing/Dry period, form weaning to birth of the next calf.), RP: Rearing period, SP: Suckler period, SPpre: Suckler period, previous calf, DPpre: Dry period, previous calf, TPpre: Total period, previous calf, DP: Dry period.

[5]The 5 and 95 % quantile shows the valid range in cow feed intake within breed. Numbers rounded off.

Figure 1. Location of herds.

Figure 2. Regression of WW – primiparous cows.
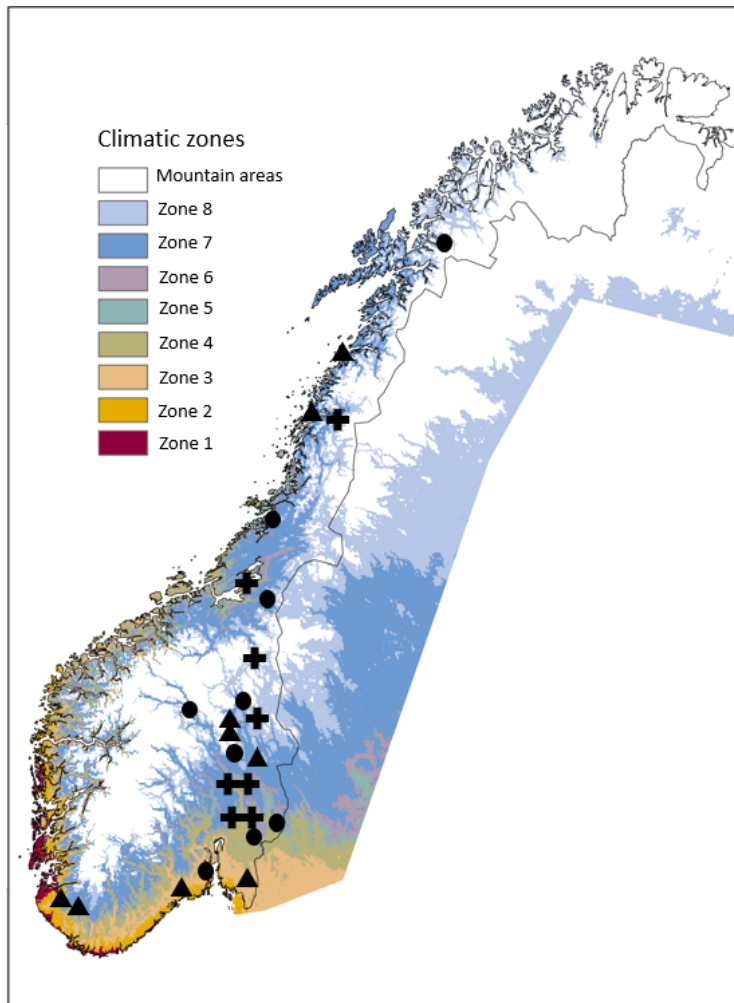
Figure 3. Regression of WW – multiparous cows.

Figure 1. Official scale of climatic zones in Norway compiled by Det norske hageselskap (the Norwegian Garden Company) in cooperation with the Norwegian Meteorological Institute in 2006 (reproduced with permission). Location of herds from the South (Rogaland; Longitude=58.6) to the North (Troms; Longitude=68.9), with altitudes varying from 0 to 1100 metres above sea level and climatic zones ranging from 3 (good) to 8 (harsh). Triangle=Hereford, Cross=Aberdeen Angus and Circle=Charolais.
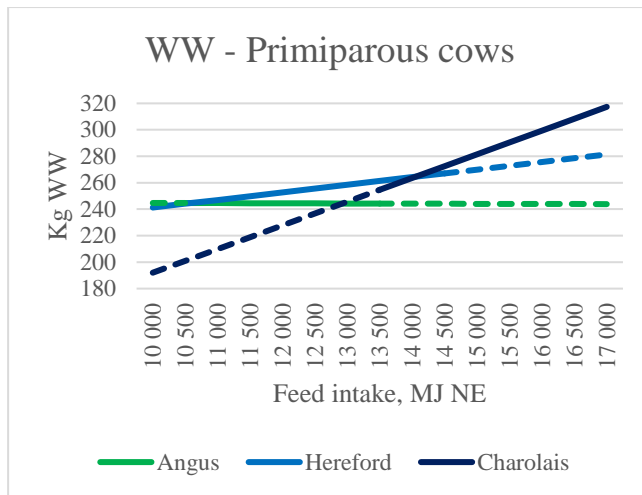
Figure 2. Regression of WW (weaning weight) on cow feed intake in suckler period for primiparous cows. Extrapolation with dashed lines.
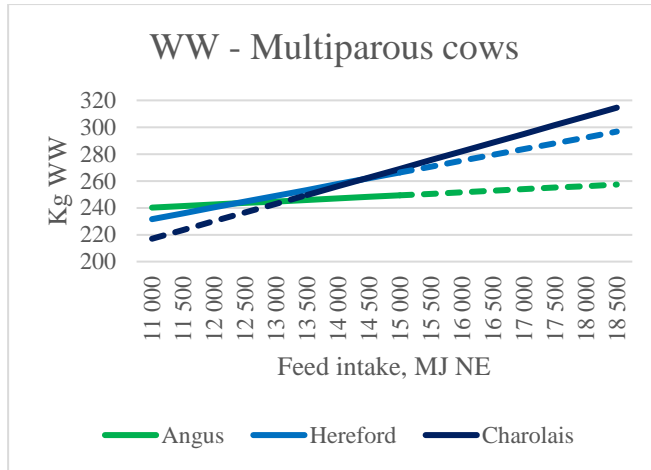
Figure 3. Regression of WW (weaning weight) on cow feed intake in suckler period for multiparous cows. Extrapolation with dashed lines.