Estimation of breed and heterosis effects for cow productivity, carcass traits and income in beef x beef and dairy x beef crosses in commercial suckler cow production

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This study aims to investigate calving difficulties, birth-, weaning- and carcass weight, herd life of cow, age at slaughter, average daily carcass gain, carcass conformation, carcass fatness and carcass income per carcass, kg or day, in Aberdeen Angus (A), Hereford (H), Charolais (C), Limousin (L), Simmental (S), Norwegian red (N) and their crosses, in order to evaluate crossbreeding strategies. Direct and maternal breed additive and heterosis effects and predicted phenotypic means were estimated with multiple regression using SAS. Crosses with N resulted in higher weaning weight and less calving difficulties than beef purebreds. Due to favourable maternal additive effects of N on carcass weight and -income, crosses with British breeds had higher performance than the purebreds. (AxC)xC had overall high performance due to beneficial maternal heterosis effects on calving difficulties and carcass weight. In conclusion, utilising profitable heterosis effects have potential in commercial production, but are dependent on production systems.

Keywords: birth weight; weaning weight; calving difficulties; carcass weight; carcass grading

1.0 Introduction

Crossbreeding has been widely used in beef cattle production for several decades (Sorensen et al., 2008), and it is established that heterosis effects increase productivity (Damon et al., 1961; Nelson et al., 1982; Gregory et al., 1991; Gregory et al., 1995). Heterosis effects in birth weight, weaning weight and carcass traits are observed within and between crosses of small (British) and large (Continental) beef breeds (Williams et al., 2010). The large breeds produce calves with high growth rates and favourable carcass classification (Bullock et al., 1993; Schiermiester et al., 2015). However, breeds selected for growth also increase the proportion of calving difficulties (Bennett & Gregory, 2001). This may reduce animal welfare, production efficiency and economic output. When evaluating crossbreeding strategies in suckler cow production, both cow productivity and carcass traits should be included.

Cows in dairy production that are not needed to produce dairy replacement heifers have the potential to produce beef x dairy crosses. This breeding strategy provides both male crosses with high growth potential for fattening and dairy x beef replacement heifers with potentially reduced proportions of calving difficulties and higher calf weaning weights (Wolfová et al., 2007; McCabe et al., 2019).

Crossbreeding effects of beef x beef and dairy x beef cattle are well documented in the literature. However, the focus has primarily been on growth (e.g. Gregory et al., 1991; Hearnshaw et al., 1995; Dadi et al., 2002; Schiermiester et al., 2015) or carcass traits (e.g. Gregory et al., 1994; Aass & Vangen, 1998; Müller et al., 2015; Huuskonen & Pesonen, 2017), not considering the associated proportions of calving difficulties or calf losses. Additionally, studies with controlled experiments are common (Gregory et al., 1991; Gregory et al., 1994; Gregory et al., 1995; Hearnshaw et al., 1995), which may reflect neither management variabilities nor actual production results in commercial herds. Firstly, the current study aimed to estimate direct and maternal breed additive effects, direct and maternal heterosis effects, in addition to predicted phenotypic means for cow productivity traits, carcass traits and carcass income measures in Aberdeen Angus and Hereford (British breeds), Charolais, Limousin and Simmental (Continental breeds), Norwegian Red (dairy breed) and their crosses in commercial suckler cow production. The traits studied were calving difficulty score (CDS), birth weight (BW), weaning weight (WW) and herd life of cow (HCL); carcass weight (CW), age at slaughter for bulls (AS_b), average daily carcass gain for bulls ($ADCG_b$), EUROP conformation score (ECS) and EUROP fat score (EFS); and total carcass income (CINC), carcass income per kg (CINC/kg) and carcass income per day for bulls ($CINC/d_b$) for the three groups of traits, respectively. Secondly, the aim was to evaluate which crossbreeding strategies might be favourable when results for all traits were considered simultaneously. The hypothesis was that Continental breeds and crosses have superior growth and carcass production traits, but also higher proportions of calving difficulties than British breeds in a crossbreeding system. A second hypothesis was that Norwegian Red x beef suckler cows produce offspring with higher weaning weights and lowered proportions of calving difficulties, but also less favourable carcass production (lower carcass weight and conformation scores).

2.0 Material and methods

2.1 Data material

Data from the Norwegian Beef Cattle Recording System (NBS) recorded from January 2010 until May 2017 was used to estimate direct and maternal breed additive effects, direct and maternal heterosis effects and predicted phenotypic means for cow productivity traits, carcass traits and carcass income in beef and dairy crossbreds. The data included six purebred groups: 100% purebred Aberdeen Angus (A), Hereford (H), Charolais (C), Limousin (L), Simmental (S) and Norwegian Red (N). Furthermore, all data of possible combinations of two-breed crosses (50+50%), three-breed crosses (25+25+50%) and backcrosses (25+75%) between those breeds (crossed with 100% purebred sire) available in the NBS were included.

Data from the NBS included information on animal identification, herd, percentage of dam and sire breed, sex, twin, birth-, weaning- and slaughter date, abattoir, CDS, BW, WW, CW, ECS and EFS. The calves were weaned between 150 and 275 days of age and the WW adjusted to 200 days weight (BW + (growth rate between birth and weaning * 200 days)). Calving difficulties were assessed by the farmer on a scale from 1–3 (1=no assistance, 2=some assistance by farmer and 3=major assistance by farmer and/or veterinarian). ECS was measured with the EUROP grading scheme, including 15 classes (i.e. P-, P, P+,…, E-, E, E+)

and correspondingly, EFS measured in 15 classes (i.e. 1-, 1, 1+,…,5-, 5, 5+). Carcass income (CINC) was calculated in NOK with the current Norwegian market prices of October 2019 (Nortura SA, 2019), based on the individual CW, ECS and EFS (Appendix 1).

Data on carcass traits for heifers were excluded, as they constituted only a small part (approximately 10%) of the data. Thus, young bulls (AS between 301–730 days), young cows (AS between 731–1460 days) and cows (AS above 1461 days) classified in age/sex groups according to the Norwegian grading scheme, were investigated (hereafter, “cows” includes both young cows and cows). Average daily carcass gain was only calculated for bulls ((CW-(BW*0.5))/AS). As only 14% of the slaughtered animals had BW recordings, an average birth weight within breed group was used. BW, WW, CW and $ADCG_b$ data below or above three STD from the mean were considered as illogical and deleted. Approximately 100% of the N purebred calves were purchased from dairy production (not reared as suckler calves) and thus omitted from the analyses of WW. The purebreds constituted from 70 to 87% of the data material on CDS (n=162223), BW (n=83562), WW (n=26714), carcass traits for bulls (n=115006) and carcass traits for cows (n=35607) (Appendix 2).

2.2 Calculation of heterozygosity

Heterosis is defined as the deviation from the expected mean between two breeds (Falconer & Mackay, 1996). Direct and maternal heterosis was assumed proportional to the expected heterozygosity between the dam and sire breed (maternal heterosis; first and second dam breed), calculated based on the percentage of different breeds (A, HE, C, L, S or N) in the dam and the sire. The following equation was used to calculate the heterozygosity between to breeds (Dickerson, 1973):

$$H_{12}=1-(pD_1*pS_1 + pD_2*pS_2) \text{ (equation 1)}$$

where H_{12} is the expected heterosis between the first and the second breed (N-A, N-HE, N-C, N-L, N-S, A-HE, A-C, A-L, A-S, HE-C, HE-L, HE-S, C-L, C-S or L-S); pD_1 is the percentage of first dam breed; pS_1 is the percentage of the first sire breed; pD_2 is the percentage of the second dam breed; and pS_2 is the percentage of the second sire breed (the sire in the present study was always purebred, i.e. $pS_2=0$). The number of heterozygote crosses within breed combinations are presented in Appendix 3.

2.3 Statistical analyses

To estimate direct and maternal breed additive and heterosis effects on the traits studied, multiple regression models were performed with the procedure PROC MIXED (SAS Software Institute INC).

2.3.1 Cow productivity traits

To estimate the direct and maternal breed additive and heterosis effects on cow productivity traits (except herd life of cow), the following model (Model 1) was used:

$$Y= \mu + S_i + T_j + YS_k + \beta_0 CA + \beta_0 B_m + \beta_0 M_n + \beta_0 Hd_o + \beta_0 Hm_p + Cow_q + e_{ijkmnopq} \text{ (Model 1)}$$

where Y is BW, WW or CDS; μ is the overall mean; S_i is the fixed effect of sex (i=1,2); T_j is the fixed effect of twins (j=1,2); YS_k is the fixed effect of season within birth year (k=1,…,15); $\beta_0 CA$ is the overall regression of cow age; $\beta_0 B_m$ is the partial regression of the direct additive effect of breed (proportion of germplasm from breed m; m=1,…,6); $\beta_0 M_n$ is the partital regression of the maternal additive effect of dam breed n (proportion of germplasm from dam breed n; n=1,…,6); $\beta_0 Hd_o$ is the partial regression of direct heterosis expressed for the breed combinations of the six breeds (proportion of heterozygote loci with one gene from the dam breed and one gene from the sire breed; o=1,…15,); $\beta_0 Hm_p$ is the partial regression of maternal heterosis expressed for the breed combinations of the six breeds (proportion of heterozygote loci with one gene from the first dam breed and one gene from the second dam breed; p=1,…15,); Cow_q is the random effect of cow; and $e_{ijkmnoq}$ is the random error term. Calving season was divided into spring (January–June) and autumn (July–December), giving two seasons within seven years (except autumn 2017). Approximately 80% of the calves were born in spring. Due to few observations on WW, direct and maternal heterosis effects were not estimable.

Some restrictions were necessary to remove singularity. Thus, direct and maternal breed additive effects of Angus were set to zero, and the other direct and maternal breed additive effects are expressed as deviations from the respective effects for Angus. Contrasts of the estimated genetic effects were used to investigated differences among the breed groups. Furthermore, phenotypic means for selected two-, three- and backcrosses were predicted using the ESTIMATE option in PROC MIXED (Littell et al., 1996). The following equation, e.g., was used to predict phenotypic means for a three-breed cross:

$$P=D_1*0.25 + D_2*0.25 + D_3*0.5 + M_1*0.5 + M_2*0.5 + Hd_{13}*0.5 + Hd_{23}*0.5 + Hm_{12}*1$$

(equation 2)

where P is the predicted phenotypic mean (CDS, BW or WW) for a three-breed cross; D_1 is the direct additive effect of the first dam breed; D_2 is the direct additive effect of the second dam breed; D_3 is the direct additive effect of the sire breed; M_1 is the maternal additive effects of the first dam breed; M_2 is the maternal additive effects of the second dam breed; Hd_{13} is the direct heterosis effect between breed first dam breed and sire breed; Hd_{23} is the direct heterosis effect between breed second dam breed and sire breed; and Hm_{12} is the maternal heterosis effect between first and second dam breed.

2.3.2 Carcass traits and carcass income

To estimate the direct and maternal breed additive and heterosis effects on carcass traits, carcass income and herd life of cow, the following model (Model 2) was used:

$$Y = \mu + CL_i + AYS_j + \beta_0 B_m + \beta_0 M_n + \beta_0 Hd_o + \beta_0 Hm_p + e_{ijmnop} \text{ (Model 2)}$$

where Y is CW, AS_b, $ADCG_b$, ECS, EFS, CINC, CINC/kg, $CINC/d_b$ or HLC; μ is the overall mean; CL_i is the fixed effect of age/sex group (i=1,…,3; young bulls, young cows and cows); AYS_j is the fixed effect of slaughter year and season within abattoir (j=1,…,728); $\beta_0 B_m$ is the partial regression of the direct additive effect of breed (proportion of germplasm from breed m; m=1,…,6); $\beta_0 M_n$ is the partial regression of the maternal additive effect of breed m (proportion of germplasm from dam breed n; n=1,…,6); $\beta_0 Hd_o$ is the partial regression of direct heterosis expressed for the breed combinations of the six breeds (proportion of heterozygote loci with one gene from the dam breed and one gene from the sire breed; o=1,…15,); $\beta_0 Hm_p$ is the partial regression of maternal heterosis expressed for the breed combinations of the six breeds (proportion of heterozygote loci with one gene from the first dam breed and one gene from the second dam breed; p=1,…15,); and e_{ijmnop} is the random error term. Season was grouped into four categories (December, January and February=1; March, April and May=2; June, July and August=3; and September, October and November=4), with a distribution between seasons varying from 21–27% for the bulls and 14–40% for the cows. Age at slaughter was confounded with breed group. Thus, the effect of AS within the breed group was not included in the model, and the carcass weight was not corrected to a constant age/endpoint (discussed in Section 4.1). As the age at slaughter for young cows and cows is merely a measure of production persistency, this trait was analysed separately for bulls and cows. Additionally, $ADCG_b$ and $CINC/d_b$ were only analysed for bulls.

As for calving difficulties and pre-weaning weights (Section 2.3.1), restrictions were set due to singularity. Furthermore, predictions of phenotypic means for carcass traits and carcass income were obtained with equation 2.

Neither Model 1 nor Model 2 included herd effect, as herd was confounded with breed and could not be correctly estimated. However, the number of herds included were considered representative for the population of Norwegian suckler cow herds (23, 19, 52 and 64% of the herds had data for CDS, BW, WW and carcass traits, respectively).

3.0 Results

Direct and maternal breed additive effects expressed as deviations from A, and direct and maternal heterosis effects expressed as deviations from the expected mean of two purebreds are presented in Tables 1–4. Significance (p-values) of pair-wise contrasts between the direct and maternal breed additive effects for all breed combinations are not shown in the tables but commented on consecutively in this section. In Table 5 predicted phenotypic means for purebreds and selected crossbreds are presented for the most essential crossbreeding alternatives (discussed in Section 4.4).

3.1 Cow productivity traits

3.1.1 Calving difficulties

In general, analyses of calving difficulties confirmed higher direct additive effects of the Continental breeds (C, L and S) than A, HE and N (Table 1). Additionally, the pair-wise contrasts showed no differences between A, HE or N ($p>0.12$). Overall, few significant maternal breed additive effects were found for calving difficulties. The results indicated that the maternal additive effect of HE increased calving complications but were only significantly different from A. Furthermore, the pair-wise contrasts revealed that the maternal additive effect of L was smaller than C (-0.023 CDS; p<0.05).

Significant favourable direct heterosis effects were found for Limousin crossed with the other Continental breeds (C-L and L-S; Table 1). In contrast, for the Charolais combinations A-C and HE-C, and A-S combination, the direct heterosis effects were positive, which implies that more calving difficulties than the mean of purebreds are expected. However, for the same combinations the maternal heterosis was negative (A-S not significant), showing that these combinations used as dam breeds are favourable when producing offspring. Additionally, C-S dams were expected to produce offspring with less calving difficulties than mean of purebred C and S, due to the negative maternal heterosis effects (-0.042 CDS; P<0.01).

3.1.2 Birth weight

The estimated direct breed additive effects on BW, ascended in order from A, N, H, L, S to C (Table 1). The pairwise contrasts were significant for all pairs of breeds (p<0.05). Furthermore, the estimated maternal breed additive effects on BW descended from N to H and S, which were similar to A, and then to C and L, which were significantly less than A.

Negative direct and maternal heterosis effects for BW were estimated for the Limousin crossbred combinations H-L and C-L (Table 1). In contrast, positive direct heterosis effects were observed for crosses between the British breeds (A and H; 0.8 kg; P<0.001) and the British breeds and N (approximately 1.5 kg; Table 1). The NxBritish dam expressed positive maternal heterosis (0.7 and 0.6 kg, respectively; P<0.01), increasing the progeny BW, while AxH dams revealed negative maternal heterosis (-0.7 kg; P<0.05).

3.1.3 Weaning weight

The direct additive effects of breed on WW were highest for N, followed by C, S, L, H and finally A (Table 1). Overall, the pair-wise contrasts showed all breeds differed from each other ($p<0.001$), except N which had high standard errors on WW. Maternal additive effect of L and S on WW were shown to be similar, and significantly higher than the other breeds.

3.1.4 Herd life of cow

The pair-wise contrasts between direct breed additive effects revealed that herd life of H cows was significantly longer than the other breeds ($p<0.001$), while N cows had the shortest herd life ($p<0.05$; not significantly different from L). However, the maternal additive effect of H on HLC was significantly smaller than N, A, and L ($p<0.05$). The direct heterosis effects were significantly negative for the breed combinations of A-C, A-L, H-C and L-S, which implies culling at younger ages for these crossbred cows compared to the mean of the purebreds (Table 1).

3.2 Carcass traits

3.2.1 Carcass weight

The direct breed additive effects on CW were significantly greater for Continental breeds than the British breeds and N ($p<0.001$ for the pair-wise contrasts; Table 2). However, the maternal additive effect of N, H and S were similar and higher than the other breeds ($p<0.05$). The direct heterosis effects observed for the Angus combinations A-C and A-S were large and positive (7.5 and 18.0 kg, respectively; $P<0.001$), but when replacing H as a dam breed in crosses with C and S, unfavourable effects on CW were shown (-10.3 and -16.1 kg, respectively; $P<0.001$). Positive maternal heterosis effects which increase the offspring CW were significant for the dam breed combinations N-A, N-C, A-C and C-S.

3.2.2 Age at slaughter and carcass gain in bulls

Pair-wise contrasts for the direct breed additive effect between all breed groups showed that Limousin bulls were the significantly youngest at slaughter, while N bulls were eldest ($p<0.001$; Table 2). However, the maternal additive effect of N significantly reduced AS_b in bull progeny. This was also observed for C, both significantly different from A, H and L ($p<0.05$). Significant negative direct heterosis effects were found between crosses of the British breeds (A and H), and the British breeds crossed with C or S, lowering the bull AS_b compared to the mean of purebreds (Table 2). However, the direct heterosis effects were significantly unfavourable for crosses between Limousin and most other breeds. Furthermore, favourable maternal heterosis effects, which reduced the AS_b in bull progeny, were significant for the dam breed combinations N-H, N-L, N-S and H-L.

Carcass growth of N bulls was poorest, increasing with H, A, S, L and finally C, as shown by the direct breed additive effects on $ADCG_b$ (Table 2). The pair-wise contrasts confirmed that Continental breeds had significantly greater $ADCG_b$ than A, H and N ($p<0.001$). The maternal additive effect of N, S and H was large, but only N was significantly higher than the other breeds ($p<0.01$). Furthermore, several significant positive direct heterosis effects on $ADCG_b$ were observed (N-H, N-L, N-S, A-H, A-C, A-S; Table 2). All dam crosses with N and the other beef breeds expressed favourable maternal heterosis effects on the carcass growth of the bull offspring. Similar results were found for A-C, H-C and C-L dams.

3.2.3 EUROP grading

Significant differences were observed between breeds (direct additive effects) on ECS ($p<0.001$), with performance in ascending order, N, H, A, S, C and L (Table 3). However, the maternal additive effect of H on ECS was overall large and favourable ($p<0.001$), while L had the lowest maternal additive effect ($p<0.001$). The direct heterosis effects were significant for most breed combinations, but only favourable in combinations consisting of A-C, A-S, and H-N (Table 3). Significant favourable maternal heterosis was found in all dam breed combinations with Norwegian Red, except for the H-N dam breed combination, which was significantly unfavourable. Additionally, positive maternal heterosis was shown with an A-C dam but was negative with a H-C dam (0.2 and -0.1 ECS, respectively; Table 3).

Overall, the direct breed additive effects on the fat score (EFS) were significantly different between all breeds ($p<0.05$), with AA, HE, N, CH, L and S in increasing order of leanness. Except for L the maternal breed additive effects were significantly greater than for A ($p<0.05$). Several crossbred combinations showed significant direct heterosis effects that increased fatness (such as all combinations with L; Table 3). Maternal heterosis effects unfavourably influenced fatness in progeny from N-A and N-L dams, while the result was opposite for progeny from H-S dams.

3.3 Carcass income

3.3.1 Total carcass income

The best combined performance of CW, ECS and EFS gave the highest total carcass income according to the current market prices (Appendix 1). Significant differences in direct breed additive effects for total carcass income (CINC) were observed between all breeds ($p<0.05$; except A and N), where C had the highest income, decreasing with L, S, A, N and finally H (Table 4). The maternal additive effect of N, H and S on CINC were similar and contributed in general with positive economic effects, compared to A, L and C ($p<0.05$). Favourable direct heterosis effects were observed for combinations of A-C and A-S, while negative heterosis was revealed for A-L and all combinations with H and Continental breeds (Table 4). Additionally, significant positive maternal heterosis effects on total carcass income were observed from the offspring of A-C, A-N, C-S and C-N dam combinations.

3.3.2 Carcass income per kg carcass

The direct breed additive effects on carcass income per kg carcass weight were in general significantly different between all breeds ($p<0.01$). The pattern of differences in direct breed additive effects were similar to those as observed for the total carcass income, except that L was the most superior breed for CINC/kg (Table 4). However, the maternal additive effect of L and C on CINC/kg was lower than the other breeds ($p<0.05$). Overall, most direct heterosis effects were unfavourable, but the effect was positive for the A-C breed combination. Although small, positive significant maternal heterosis effects existed for dams of the breed combinations A-C, A-L, H-L, H-S and N-L.

3.3.3 Carcass income per day for bulls

The ascending order of the direct breed additive effects on CINC/d_b for bull carcasses were N, H, A, S, C and L (Table 4), where most pair-wise breed contrasts were significantly different from each other ($p<0.01$). In general, the maternal additive effect of N on CINC/d_b was the significantly most favourable ($p<0.01$). Furthermore, S and H expressed an overall larger maternal additive effect than A, C and L ($p<0.05$).

The significant negative direct heterosis effects for Limousin combinations A-L, H-L and C-L unfavourably influenced the bull carcass income per day, compared to the mean of the purebreds (Table 4). However, the direct heterosis effects were favourably positive for the A-C breed combination (1.9 NOK/day; $P<0.001$), but negative for H-C (-0.6 NOK/day; $P<0.01$). Additionally, maternal heterosis was positive for dam crosses between the British breeds and C, in addition to H-L and C-L dams, and all dam breed combinations with N.

4.0 Discussion

4.1 The data

Age at slaughter for young bulls (AS_b) was confounded with breed group, caused by the farmers' operational adaption to the industrial carcass grading system and market requirements. Tested models that included the fixed effect of age at slaughter (within classification group) adjusted breed groups with low age at slaughter to higher CW and EUROP scores, and vice versa for breed groups with high age at slaughter. To avoid favouring breed groups with low age at slaughter and compare breed groups at their relevant mean age at slaughter, this fixed effect was excluded from the models for CW, ECS and EFS. Thus, the analyses for AS_b, $ADCG_b$ and $CINC/d_b$ are essential when evaluating carcass production.

4.2 Cow productivity traits

Although the Continental breeds had more calving difficulties than N, A and H, few significant differences were found between breeds when investigating direct and maternal breed additive effects. In accordance with Gregory et al. (1991), the predicted means on CDS revealed that among beef breeds, A had the lowest score, H and L were intermediate while C and S had the highest score (Table 5). The low predicted CDS scores for N x beef breeds (Table 5) were caused by the small direct additive effect of N, as no maternal additive effect of N and no maternal heterosis effect of N x beef dam was detected (Table 1). Lower prevalence of calving difficulties in dairy (Holstein) x beef compared to beef crosses have also been found in Irish beef herds (McCabe et al., 2019).

Predicted phenotypic means for BW and WW were higher in Continental (C, L and S) than British (A and H) purebreds and crossbreds (Table 5), which is consistent with the literature (e.g. Gregory et al., 1991; Jenkins & Ferrell, 1994; Dadi et al., 2002). Furthermore, the differences in direct breed additive effects between breed groups for BW and WW (Table

1) were equal to MacNeil et al. (1982), Franke et al. (2001) and Theunissen et al. (2013). As found by Gregory et al. (1991), S had the highest WW among beef breeds, which corresponds to higher milk yield (Jenkins & Ferrell, 1992). This could be explained by both the great positive direct and maternal additive effects of Simmental in the present study (Table 1), which was also found by MacNeil et al. (1982), Williams et al. (2010) and Theunissen et al. (2013).

Schiermiester et al. (2015) and Williams et al. (2010) found significant direct and maternal heterosis effects in British x British, British x Continental and Continental x Continental breeds for BW, such as in the present study. The results in the current study were partly in conformity with Franke et al. (2001), who found significant positive direct heterosis effects between A and H for BW, but not the significant heterosis effects between C and British breeds, the latter in accordance with Theunissen et al. (2013).

As the present study did not include any purebred N with data on WW, the estimated direct and maternal breed additive effects had high standard error and were overall not significantly different from the other breeds. However, the predicted WW means of Norwegian red crossed with beef breeds were higher than the beef purebreds (Table 5). Increased WW in dairy x beef crosses were also found by Nelson et al. (1982) and McCabe et al. (2019). The high WW indicates that more milk is offered the offspring. Furthermore, Hickson et al. (2014) found positive heterosis effects between Angus and dairy (Jersey and Holstein) crosses on calf milk intake. Higher milk yield was found to increase gross margin from birth to slaughter for beef crossbreeds, although biological efficiency was unaffected (Miller et al., 1999). However, the level of milk yield in suckler cow production probably has an optimum level, balancing the calf milk requirement and the cow energy mobilisation.

4.3 Carcass traits

In conformity with other studies (Williams et al., 2010; Retallick et al., 2013), the direct additive effects of British breeds on CW were smaller than Continental breeds, where C has the greatest and H the smallest direct additive effects. Several studies have shown that crossing with Continental sires improved carcass traits more than British sires (e.g. DeRouen et al., 1992; Hyslop et al., 2006; Huuskonen & Pesonen, 2017).

In contrast to the present study, Williams et al. (2010) found a positive direct heterosis effect on CW between British x British breeds. In addition, positive heterosis effects were reported for British x Continental breeds, which were in accordance with the AxC and AxS crosses in the present study. Retallick et al. (2013) also found positive heterosis effects for CW in AxS steers. The significant positive heterosis effects between L and S on CW were conformed by Williams et al. (2010), who found direct heterosis for Continental x Continental breeds.

The direct breed additive effects of LM area and fat thickness in Williams et al. (2010) corresponded to the ascending order of breeds found for ECS and EFS in the present study. Overall, most direct heterosis effects were unfavourable for ECS in the present study, though they were positive for LM area in Williams et al. (2010). The unfavourable direct heterosis effects of EFS between British x Continental breeds in the present study was in accordance with Williams et al. (2010). Even so, the heterosis effects found for ECS and EFS were overall small in the present study.

Dairy x beef crosses improved CW and conformation compared to purebred dairy, which is confirmed by several studies (e. g. Aass & Vangen, 1998; McGee et al., 2005b; Keane & Moloney, 2010; Huuskonen et al., 2013; Huuskonen et al., 2014; Vestergaard et al., 2019). However, to the authors’ knowledge, no studies have compared dairy x beef crosses to purebred beef breeds, such as the present study does.

4.4 Evaluation of crossbreeding strategies based on phenotypic predicted means

4.4.1 Two-breed cross of Norwegian red and British breeds

The predicted performance of Norwegian red dams crossed with British sires revealed that two-breed crosses contributed to higher WW than the British purebreds, and to lower CDS than purebred H (Table 5). The positive maternal additive effect of N on CW and carcass growth for bulls resulted in higher CW, $\mathrm{ADCG_b}$, CINC and $\mathrm{CINC/d_b}$ than observed for the purebreds. NxA had slightly higher overall performance than NxH, but the standard errors for the phenotypic means overlapped for CDS, CW, $\mathrm{ADCG_b}$, ECS and EFS (Table 5). An option to produce N x British crosses is to recruit culled dairy cows from dairy farms for use as suckler cows in British beef herds (further discussed in Section 4.5). As British breeds are suitable to extensive feed regimes (Wetlesen et al., 2020), N x British crosses may be profitable when the feed intensity is low.

4.4.2 Backcross and three-breed cross of Norwegian red and British breeds

The backcross (NxA)xA was the overall best alternative, due to the positive maternal heterosis effect between N and A for CW and $\mathrm{ADCG_b}$ (+13 kg and +32 g/day; Table 2). Thus, crossing Norwegian red with A is a better alternative than H, if producing two-breed suckler cows as dams for further production of finishing calves. The results showed that recruiting NxA heifers from dairy production may be a profitable strategy. This two-breed cow should be crossed with an A sire rather than H, due to the present results indicating that (NxA)xA calves were born with less calving difficulties than (NxA)xH calves (Table 5). Additionally, carcass performance was about the same level for the two alternatives.

4.4.3 Three-breed cross of Norwegian red, British and Continental breeds

If the on-farm resource base is suitable for intensive feeding of calves after weaning, a two-breed NxA suckler cow crossed with a Continental sire may be beneficial. Due to the favourable direct heterosis effects of AxC for several carcass traits and income (Tables 2–4), the (NxA)xC cross was the best overall alternative (Table 5). This cross was predicted to have only 7 kg lower CW, 1200 NOK lower CINC and equal AS_b and CDS (overlapping standard errors) compared to purebred C. The high maternal additive effect of N on BW (1.8kg; Table 1) and positive maternal heterosis effect on BW from NxA dams (+0.7kg; Table 1), probably had an indirect influence of the relatively high CDS, as these traits are correlated (Mee, 2008).

Dairy breeds are less feed efficient expressed relative to live weight than beef breeds (Clarke et al., 2009). Additionally, McGee et al. (2005a) found that Holstein x beef cows had higher dry matter intake expressed relative to live weight than C, and concluded that a 660 kg C cow had the same feed requirement as a 600 kg Holstein x beef cow. In future studies, comparing feed efficiency of dairy x British beef crosses to British purebreds is highly relevant, in order to identify whether the higher production is efficient relative to the input of feed resources.

4.4.4 Crosses with Norwegian red and Continental breeds

Crosses between Norwegian red and Continental breeds had considerably lower carcass performance than Continental purebreds due to a relatively smaller direct additive effect of N (predicted means not shown). Thus, these crosses were less profitable in intensive commercial suckler cow production. However, crossing Continental sire to Norwegian red could be a profitable strategy for dairy farmers when producing finishing bulls suitable for intensive feed regimes.

4.4.5 Two-breed cross of British breeds

The favourable direct heterosis effect between A and H for bull $ADCG_b$ (Table 2) contributed to a higher income per kg and day than from the purebreds (Table 5). Crossing H dam to A sire was more profitable than the AxH cross, illustrated by the higher progeny CW, CINC and CINC/d (Table 5). Furthermore, the HxA cross had higher CINC/d then both purebreds. However, the HxA calves were born with more calving difficulties than purebred A, H and AxH calves. Thus, potential increased income should be considered relative to potential increased cost due to more calving difficulties for this cross. Two-breed strategies were the overall best alternative among British crosses, as the backcrosses did not have a higher performance than the purebreds (predicted mean not shown).

4.4.6 Two-breed cross of British and Continental breeds

Crossing British dams to Continental sires increased carcass production considerably, compared to purebred A and H. AxC was the overall best alternative among two breed-crosses, because of the highest $ADCG_b$, total carcass income and carcass income per kg or day (Table 5). Although the differences in overall carcass performance were small between AxC and AxS, the AxC combination had a lower CDS (0.04). Furthermore, the favourable maternal additive effect of A on calving difficulties compared to H were expressed in lower CDS (0.03; Table 5) from AxC crosses compared to HxC.

British dams crossed with Continental sires may be beneficial in production systems with extensive cow/calf feed regimes and intensive post-weaning beef production. The cow/calf production with British cows is suitable in areas with extensive pastures (i.e. pastures of natural grasslands, forest and mountain areas) (Wetlesen et al., 2020). However, considerable cultivated areas are also needed, as the British x Continental crosses need more intensive feed regimes after weaning (McGregor et al., 2012). Another alternative is co-operation between farms with different resource bases, where cow/calf herds produce crossbreed calves for non-breeding beef farms.

4.4.7 Backcross of British and Continental breeds

When comparing backcrosses and three breed crosses between British and Continental breeds, the (AxC)xC combination was the most profitable alternative due to favourable heterosis effects between A and C (CDS, CW, $ADCG_b$, ECS and carcass incomes; Tables 1–4). Although this cross gave offspring with a slightly lower CW (6 kg) than purebred C, the ADCGb was higher and the calves were born with lower CDS (0.04; Table 5). Interestingly, due to the favourable maternal heterosis between A and C (Table 1), (AxC)xC calves were born with 0.03 lower CDS than (NxA)xC calves (Table 5).

4.4.8 Crosses of Continental breeds

Predicted performance for two-breed crosses, three-breed crosses and backcrosses between the three Continental breeds showed that (CxS)xL was the overall best alternative when all traits were considered simultaneously (predicted means not shown for all crosses; Table 5). Although carcass performance was about the same level as for purebred C and two-breed cross SxC (overlapping standard errors), CDS score was clearly lower than for all Continental purebreds and SxC cross (Table 5). The predicted CDS for the (CxS)xL cross was similar to purebred N, caused by the favourable maternal heterosis effect between C-S dams (-0.042), and the corresponding reducing direct heterosis effect on CDS from C and L (-0.021), and L and S (-0.024) combinations, respectively (Table 1). The results may also be influenced by the small maternal additive effects of C on BW, and the beneficial maternal heterosis effects of C-S dams on BW (Table 1), as BW and calving difficulties are correlated (Mee, 2008). Although negative direct heterosis effects influenced ECS in crosses between L and the other Continental breeds, (CxS)xL had higher conformation scores than purebred C and S (Table 5).

When producing the (CxS)xL calves, a two-breed cow cross from C and S is needed. The SxC cross is a better alternative than a CxS cross due to higher WW, CW, $ADCG_b$ and CINC (Table 5). The SxC cross had a carcass performance at approximately the level of purebred C. Furthermore, the SxC cross is born with less calving difficulties than both purebred C and S, although the standard error slightly overlapped with C (Table 5).

4.5 Implications of the study

Reducing environmental footprints from agriculture is an important and topical political goal for several countries today, as stated in the Paris Agreement (United Nations, 2015). Utilising crossbreeding strategies with potentially favourable heterosis effects may increase carcass performance and reduce calving difficulties in beef cattle production, resulting in higher profitability and lower environmental footprints. Both higher growth rate and higher total production volume per animal could reduce the environmental footprints per kg carcass as well as in total, due to fewer cows needed for beef production (Crosson et al., 2011).

The results for this study showed that Norwegian red x British breeds had high carcass performance and income. Today, many healthy and still productive dairy cows are culled from dairy farmers, e.g. due to high somatic cell count (Ruud et al., 2013). Although these cows would be profitable in British beef herds, the demand for these cows is low in the current market. To facilitate this, both political and professional incentives are needed.

Co-operation between dairy and beef farmers are also highly relevant to produce dairy x beef suckler cows, which had fewer calving difficulties and higher weaning weights. Today, more dairy farmers utilise sexed semen to produce dairy replacement heifers (Hossein-Zadeha et al.; Hohenboken, 1999). Thus, there is potential to produce dairy x beef suckler cows from cows that do not produce replacement heifers.

Interestingly, the three-breed cross (CxS)xL excelled with lower calving difficulties and carcass performance at the same level as the purebred C. However, a crossbreeding strategy including three-bred crosses is demanding within single suckler cow herds. This requires a systematic plan for crossbreeding within herd, which probably must include a purebred nucleus herd and increased use of AI and sexed semen to avoid too many different breed combinations and offspring of both sexes. Today, the price of sexed beef semen is approximately twice that of conventional semen (Geno, 2020). Furthermore, the use of AI is challenging in beef cattle due to difficulties in the detection of estrus (Nelson et al., 2017). Co-operation between herds is probably needed. Thus, the potentially reduced costs due to lower calving difficulties should be considered relative to the costs of operating such three-breeding strategies.

5.0 Conclusion

Both two-breed and backcross strategies between dairy (Norwegian red) and British breeds had overall higher performance compared to purebred British breeds, where a dairy x Angus dam backcrossed with Angus sire excelled with highest carcass performance and fewest calving difficulties. At a similar frequency of calving difficulties as purebred Charolais, a three-breed cross between Angus, Norwegian red and Charolais had a carcass performance approaching Continental purebreds.

Crossing British and Continental breeds, an Angus x Charolais cross excelled as the best two-breed alternative. However, the backcross with Charolais was superior in overall performance for both cow productivity and carcass traits. These crosses may be highly relevant in areas with ample access to productive areas harvested for post-weaning carcass production, combined with extensive pastures for the cow/calf part of the herd.

The results from this study suggest that a systematic three-breed crossbreeding system including dairy, British and Continental breeds may have clear productive advantages in semi-intensive production systems, as dairy cows may be recruited from outside the system. However, similar three-breed crossbreeding strategies involving only beef breeds will require co-operation between farms, as well as a centralised, organisational hub. The results do not indicate that the productive advantages from such crossbreeding strategies will offset the appurtenant organisational challenges and costs. In conclusion, utilising profitable heterosis effects may have potential in commercial suckler cow production, but are dependent on the natural resource base and production systems.

6.0 Acknowledgments

This work was supported by Agriculture and Food Industry Research Funds (FFL/JA), Geno Breeding and AI Association, The Norwegian Beef Breeders Association, Animalia Meat and Poultry Research Centre, Nortura SA and The Meat and Poultry Industry Federation under grant number 233683/E50 and Nord University under grant number 244836/E50. The authors would like to thank the Animalia Meat and Poultry Research Centre for data from the Norwegian Beef Cattle Recording System. In addition, the authors would like to thank Dr. Tormod Ådnøy for contributions in the modelling work.

No conflicts of interest were associated with this publication.

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Appendix 1. Prices per kg carcass weight within EUROP conformation score (scale 1–15) and penalty within EUROP fat score (scale 1–15) for young bulls, young cows and cows. The same fat score penalties were given young cows and cows.

Prices/kg carcass weight															
EUROP score	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Young bulls															
0-140kg	36.92	38.92	39.92	40.92	42.12	43.32	44.82	46.42	47.92	49.42	50.62	51.82	52.52	53.22	53.93
140.1-175kg	37.32	39.32	40.32	41.32	42.52	43.72	45.22	46.82	48.32	49.82	51.02	52.22	52.92	53.62	54.32
175.1-200kg	37.97	39.97	40.97	41.97	43.17	44.37	45.87	47.47	48.97	50.47	51.67	52.87	53.57	54.27	54.97
200.1-225kg	38.38	40.38	41.38	42.38	43.58	44.78	46.28	47.88	49.38	50.88	52.08	53.28	53.98	54.68	55.38
225.1-250kg	39.23	41.23	42.23	43.23	44.43	45.63	47.13	48.73	50.23	51.73	52.93	54.13	54.83	55.53	56.23
250.1-375kg	40.67	42.67	43.67	44.67	45.87	47.07	48.57	50.17	51.67	53.17	54.37	55.57	56.27	56.97	57.67
375.1-400kg	40.17	42.17	43.17	44.17	45.37	46.57	48.07	50.17	51.67	53.17	54.37	55.57	56.27	56.97	57.67
>400kg	39.67	41.67	42.67	43.67	44.87	46.07	47.57	49.67	51.17	52.67	53.87	55.07	55.77	56.47	57.17
Fat score penalty	-1.30	-0.60	0	0	0	0	-1.30	-2.50	-3.70	-5.50	-7.80	-9.60	-11.80	-14.60	-16.00
Young cows															
0-150kg	36.27	38.27	39.27	40.77	41.97	43.17	44.67	46.27	47.77	49.27	50.47	51.67	52.37	53.07	53.77
150.1-175kg	36.84	38.84	39.84	41.34	42.54	43.74	45.24	46.84	48.34	49.84	51.04	52.24	52.94	53.64	54.34
175.1-200kg	37.46	39.46	40.46	41.96	43.16	44.36	45.86	47.46	48.96	50.46	51.66	52.86	53.56	54.26	54.96
200.1-225kg	37.89	39.89	40.89	42.39	43.59	44.79	46.29	47.89	49.39	50.89	52.09	53.29	53.99	54.69	55.39
225.1-250kg	38.28	40.28	41.28	42.78	43.98	45.18	46.68	48.28	49.78	51.28	52.48	53.68	54.38	55.08	55.78
>250kg	38.72	40.72	41.72	43.22	44.42	45.62	47.12	48.72	50.22	51.72	52.92	54.12	54.82	55.52	56.22
Cows															
0-150kg	36.27	38.27	39.27	40.27	41.47	42.67	44.17	45.77	47.27	48.77	49.97	51.17	51.87	52.57	53.27
150.1-175kg	36.84	38.84	39.84	40.84	42.04	43.24	44.74	46.34	47.84	49.34	50.54	51.74	52.44	53.14	53.84
175.1-200kg	37.46	39.46	40.46	41.46	42.66	43.86	45.36	46.96	48.46	49.96	51.16	52.36	53.06	53.76	54.46
200.1-225kg	37.89	39.89	40.89	41.89	43.09	44.29	45.79	47.39	48.89	50.39	51.59	52.79	53.49	54.19	54.89
225.1-250kg	38.28	40.28	41.28	42.28	43.48	44.68	46.18	47.78	49.28	50.78	51.98	53.18	53.88	54.58	55.28
>250kg	38.72	40.72	41.72	42.72	43.92	45.12	46.62	48.22	49.72	51.22	52.42	53.62	54.32	55.02	55.72
Fat score penalty	-1.30	-0.60	0	0	0	0	-0.90	-2.30	-3.30	-4.50	-6.80	-8.60	-10.80	-13.60	-15.00

Appendix 2. Number of purebreds (Norwegian red (N), Aberdeen Angus (AA), Hereford (HE), Charolais (CH), Limousin (L) and Simmental (S)) and crossbreds that had observations on calving difficulty score (CDS), birth weight (BW), weaning weight (WW) and carcass traits (CT) within young bulls (bulls) and young cows/cows (cows).

Number of observations within breed group					
	CDS	BW	WW	CT, bulls	CT cows
N	6351	222	0	71213	7236
AA	18247	10489	4069	4914	3520
HE	27319	12630	4527	7654	6703
CH	38319	24787	8734	10201	5748
L	20257	13403	3598	5117	2680
S	2538	4307	1451	1574	1042
Crossbreds	49192	17724	4335	14333	8678
Total	162223	83562	26714	115006	35607

Appendix 3. Number of breed combinations that had 100 or 50% heterozygote loci from different dam and sire breeds (Hd), and number of breed combinations that had 100% heterozygote loci from two different dam breeds (Hm), within breed combinations between Norwegian red (N), Aberdeen Angus (AA), Hereford (HE), Charolais (CH), Limousin (L) and Simmental (S) for the traits analysed. The analysed traits were birth weight (BW), weaning weight (WW), calving difficulty score (CDS) and carcass traits (CT) within young bulls (bulls) and young cows/cows (cows).

		Number of heterozygote breed combinations														
		N-AA	N-HE	N-CH	N-L	N-S	AA-HE	AA-CH	AA-L	AA-S	HE-CH	HE-L	HE-S	CH-L	CH-S	L-S
CDS	100% Hd	305	3270	1477	544	683	1902	1514	2542	853	2104	1894	832	2740	1625	2651
	50% Hd	226	2880	885	500	1093	1038	628	1104	912	1955	3996	960	1947	1730	4402
	100% Hm	164	3369	1279	234	1098	1103	865	1077	1210	1460	3662	449	2152	2499	3635
BW	100% Hd	148	1210	361	263	92	1021	605	1374	176	820	348	389	1176	260	506
	50% Hd	71	1169	314	251	289	441	236	626	264	826	1195	400	882	423	1588
	100% Hm	45	1411	463	139	279	425	348	615	424	617	1096	207	952	682	1272
WW	100% Hd	61	319	64	55	20	359	163	484	23	144	39	104	221	42	54
	50% Hd	18	295	66	51	78	135	65	199	61	189	317	99	197	89	324
	100% Hm	9	353	112	22	72	129	101	185	77	117	257	55	232	176	286
CT, bulls	100% Hd	67	838	335	146	390	454	291	795	320	562	978	194	770	612	1276
	50% Hd	19	663	160	110	379	223	122	251	237	429	1228	167	550	379	1388
	100% Hm	24	732	228	60	397	234	168	246	351	320	1117	86	601	563	1178
CT, cows	100% Hd	26	545	179	60	341	151	163	180	316	230	945	97	358	665	889
	50% Hd	18	362	92	51	211	82	64	76	164	230	700	106	249	366	762
	100% Hm	15	416	122	27	260	93	110	76	211	152	583	60	261	589	558

Table 1. Estimated intercept, direct and maternal breed and heterosis effects (and standard error) for Norwegian red (N), Aberdeen Angus (AA) Hereford (HE), Charolais (CH), Limousin (L) and Simmental (S) for calving difficulties, birth weight, weaning weight and herd life of cow. The breed effects are expressed as deviations from AA, where the intercept is equal to AA. (Stars indicate values significantly different from zero; *p<0.05, **p<0.01 and ***p<0.001).

	Calving difficulties, (scale 1-3)		Birth weight, kg		Weaning weight, kg		Herd life of cow (year)	
Intercept	1.123***		32.6***		221***		5.6***	
	Direct	Maternal	Direct	Maternal	Direct	Maternal	Direct	Maternal
Breed effects expressed as deviations from AA								
N	-0.025 (0.020)	0.012 (0.019)	0.4 (0.7)	1.8 (0.6)**	48 (23)*	11.1 (11.8)	-1.2 (0.4)**	0.1 (0.4)
HE	0.004 (0.012)	0.027 (0.012)*	2.6 (0.3)***	0.1 (0.3)	11 (3.2)***	-1.3 (3.1)	1.1 (0.4)**	-0.8 (0.3)*
CH	0.021 (0.010)*	0.017 (0.010)	8.4 (0.3)***	-1.9 (0.2)***	40 (2.9)***	-0.6 (2.9)	0.1 (0.3)	-0.6 (0.3)
L	0.040 (0.014)**	-0.007 (0.014)	5.4 (0.4)***	-1.5 (0.4)***	21 (2.8)***	11.9 (2.8)***	-0.8 (0.4)	0.1 (0.4)
S	0.039 (0.015)**	0.004 (0.014)	7.5 (0.4)***	-0.5 (0.4)	45 (4.5)***	12.2 (4.4)**	-0.1 (0.5)	-0.3 (0.5)
Heterosis effects								
N-AA	0.003 (0.013)	0.004 (0.009)	1.6 (0.5)***	0.7 (0.3)**			0.3 (0.3)	0.3 (0.2)
N-HE	-0.010 (0.011)	-0.002 (0.007)	1.4 (0.4)***	0.6 (0.2)**			-0.4 (0.2)*	0.4 (0.1)***
N-CH	0.015 (0.011)	-0.001 (0.006)	-0.2 (0.4)	0.5 (0.2)**			0.1 (0.2)	0.1 (0.1)
N-L	0.000 (0.012)	-0.002 (0.006)	0.1 (0.4)	0.2 (0.2)			0.2 (0.3)	0.0 (0.1)
N-S	-0.015 (0.014)	-0.015 (0.010)	0.8 (0.5)	0.1 (0.3)			0.0 (0.3)	-0.2 (0.2)
AA-HE	0.008 (0.009)	-0.017 (0.011)	0.8 (0.2)***	-0.7 (0.3)*			0.3 (0.2)	0.5 (0.3)
AA-CH	0.014 (0.007)*	-0.033 (0.009)***	-0.2 (0.2)	-0.3 (0.2)			-0.9 (0.2)***	-0.3 (0.3)
AA-L	-0.011 (0.009)	-0.006 (0.010)	0.0 (0.2)	0.4 (0.2)*			-1.3 (0.3)***	-0.4 (0.4)
AA-S	0.045 (0.015)**	-0.009 (0.024)	0.7 (0.4)*	0.9 (0.7)			-0.2 (0.5)	-0.9 (0.8)
HE-CH	0.013 (0.007)*	-0.011 (0.006)*	0.6 (0.2)**	0.4 (0.1)**			-0.3 (0.2)*	-0.1 (0.2)
HE-L	0.007 (0.008)	0.003 (0.007)	-0.9 (0.2)***	0.6 (0.2)***			0.0 (0.2)	-0.4 (0.2)
HE-S	0.005 (0.010)	-0.010 (0.009)	-0.4 (0.3)	0.7 (0.2)**			-0.6 (0.3)*	-0.4 (0.3)
CH-L	-0.021 (0.007)**	0.003 (0.008)	-0.8 (0.2)***	-1.1 (0.2)***			-0.2 (0.2)	-0.8 (0.3)***
CH-S	-0.007 (0.009)	-0.042 (0.015)**	0.2 (0.2)	-2.1 (0.4)***			0.2 (0.3)	0.1 (0.4)
L-S	-0.024 (0.013)*	-0.001 (0.020)	0.5 (0.3)	-1.2 (0.4)**			-1.2 (0.4)**	-1.0 (0.6)

Table 2. Estimated intercept, direct and maternal breed and heterosis effects (and standard error) for Norwegian red (N), Aberdeen Angus (AA) Hereford (HE), Charolais (CH), Limousin (L) and Simmental (S) for carcass weight (CW), age at slaughter for bulls (AS_b) and average daily carcass gain from birth to slaughter for bulls ($ADCG_b$). The breed effects are expressed as deviations from AA, where the intercept is equal to AA. (Stars indicate values significantly different from zero; *p<0.05, **p<0.01 and ***p<0.001).

	Carcass weight, kg		AS_b (month)		$ADCG_b$ (g/d)	
Intercept	267***		17.4***		486***	
	Direct	Maternal	Direct	Maternal	Direct	Maternal
Breed effects expressed as deviations from AA						
N	2.9 (4.7)	15.2 (4.6)***	1.5 (0.3)***	-0.7 (0.3)*	-22 (11)*	44 (11)***
HE	-4.8 (3.5)	12.3 (3.4)***	-0.2 (0.2)	0.2 (0.2)	-15 (8)	17 (8)*
CH	65.1 (3.1)***	-1.0 (3.0)	-0.2 (0.2)	-0.4 (0.2)*	147 (6)***	3 (6)
L	43.5 (4.1)***	2.2 (4.0)	-1.5 (0.2)***	0.0 (0.2)	137 (9)***	1 (9)
S	37.5 (4.4)***	12.1 (4.3)**	-0.1 (0.3)	-0.1 (0.3)	97 (9)***	26 (9) **
Heterosis effects						
N-AA	3.6 (2.9)	13.1 (2.2)***	0.1 (0.2)	0.0 (0.1)	10 (7)	32 (5)***
N-HE	4.9 (2.4)*	-0.8 (1.6)	-0.5 (0.2)**	-0.7 (0.1)***	22 (6)***	17 (4)***
N-CH	-1.3 (2.2)	4.5 (1.3)***	-0.2 (0.2)	-0.2 (0.1)*	9 (5)	19 (3)***
N-L	5.1 (2.7)*	0.4 (1.3)	0.3 (0.2)*	-0.6 (0.1)***	15 (6)**	23 (33)***
N-S	-2.6 (3.1)	-0.3 (2.1)	-0.3 (0.2)	-0.5 (0.1)***	15 (7)*	15 (5)**
AA-HE	-3.3 (2.6)	-2.9 (3.2)	-0.7 (0.2)***	-0.1 (0.2)	18 (6)**	8 (7)
AA-CH	7.5 (2.0)***	6.5 (2.9)*	-0.8 (0.1)***	-0.3 (0.2)	39 (4)***	31 (6)***
AA-L	-7.0 (2.6)**	1.3 (3.0)	-0.1 (0.2)	0.0 (0.2)	-2 (5)	4 (6)
AA-S	18.0 (4.8)***	7.4 (8.2)	-1.0 (0.3)***	0.0 (0.5)	47 (10)***	-5 (18)
HE-CH	-10.3 (1.7)***	-1.1 (1.6)	-0.2 (0.1)*	0.0 (0.1)	-7 (4)*	8 (4)*
HE-L	-0.6 (2.3)	-1.8 (1.9)	0.7 (0.1)***	-0.2 (0.1)*	-9 (5)	28 (9)***
HE-S	-16.1 (2.9)***	-3.1 (2.9)	-0.6 (0.2)***	0.1 (0.2)	11 (6)	-5 (6)
CH-L	-1.1 (1.9)	4.7 (2.5)	0.7 (0.1)***	0.3 (0.2)	-14 (4)**	16 (6)**
CH-S	-2.4 (2.7)	12.0 (4.4)**	0.2 (0.2)	0.4 (0.3)	-7 (6)	-2 (10)
L-S	8.0 (3.5)*	-1.3 (5.6)	0.6 (0.2)**	-0.6 (0.3)	3 (7)	20 (12)

Table 3. Estimated intercept, direct and maternal breed and heterosis effects (and standard error) for Norwegian red (N), Aberdeen Angus (AA) Hereford (HE), Charolais (CH), Limousin (L) and Simmental (S) (including young bulls and cows) for EUROP conformation score (scale 1–15), EUROP fat score (scale 1–15). The breed effects are expressed as deviations from AA, where the intercept is equal to AA. (Stars indicate values significantly different from zero; *p<0.05, **p<0.01 and ***p<0.001).

	EUROP conformation score		EUROP fat score	
Intercept	8.6***		5.7***	
	Direct	Maternal	Direct	Maternal
Breed effects expressed as deviations from AA				
N	-2.0 (0.12)***	0.3 (0.12)**	-1.7 (0.2)***	0.4 (0.2)*
HE	-0.7 (0.09)***	0.4 (0.09)***	-0.4 (0.1)**	0.4 (0.1)***
CH	1.7 (0.08)***	0.1 (0.08)	-2.3 (0.1)***	0.4 (0.1)***
L	3.3 (0.11)***	-0.3 (0.11)*	-2.4 (0.2)***	0.0 (0.1)
S	0.5 (0.12)***	0.2 (0.11)*	-2.7 (0.2)***	0.6 (0.2)***
Heterosis effects				
N-AA	0.0 (0.08)	0.2 (0.06)**	0.0 (0. 1)	0.3 (0.1)***
N-HE	0.2 (0.06)***	-0.1 (0.04)**	0.4 (0.1)***	0.0 (0.1)
N-CH	0.0 (0.06)	0.1 (0.04)**	0.2 (0.1)*	0.1 (0.0)
N-L	-0.6 (0.07)***	0.3 (0.04)***	0.6 (0.1)***	0.2 (0.0)***
N-S	-0.1 (0.08)	0.0 (0.06)	-0.2 (0.1)	0.0 (0.1)
AA-HE	-0.2 (0.07)***	-0.1 (0.08)	-0.1 (0.1)	-0.1 (0.1)
AA-CH	0.1 (0.05)**	0.2 (0.08)*	0.3 (0.1)***	-0.1 (0.1)
AA-L	-0.7 (0.07)***	0.2 (0.08)**	0.2 (0.1)**	0.2 (0.1)
AA-S	0.3 (0.13)**	0.2 (0.22)	0.7 (0.2)***	0.1 (0.3)
HE-CH	-0.3 (0.04)***	-0.1 (0.04)*	-0.2 (0.1)**	-0.1 (0.1)
HE-L	-0.6 (0.06)***	0.0 (0.05)	0.5 (0.1)***	0.0 (0.1)
HE-S	-0.3 (0.08)***	-0.1 (0.08)	-0.1 (0.1)	-0.3 (0.1)**
CH-L	-0.7 (0.05)***	-0.1 (0.07)	0.3 (0.1)***	0.1 (0.1)
CH-S	-0.2 (0.07)*	0.1 (0.12)	0.1 (0.1)	0.1 (0.2)
L-S	-0.3 (0.09)**	0.1 (0.15)	0.3 (0.1)*	0.4 (0.2)

Table 4. Estimated intercept, direct and maternal breed and heterosis effects (and standard error) for Norwegian red (N), Aberdeen Angus (AA) Hereford (HE), Charolais (CH), Limousin (L) and Simmental (S) for total carcass income, carcass income/kg carcass weight and carcass income/day for bulls. The breed effects are expressed as deviations from AA, where the intercept is equal to AA. (Stars indicate values significantly different from zero; *p<0.05, **p<0.01 and ***p<0.001).

	Total carcass income, NOK		Carcass income/kg, NOK		Carcass income/day, NOK	
Intercept	10880***		41.2***		23.9***	
	Direct	Maternal	Direct	Maternal	Direct	Maternal
Breed effects expressed as deviations from AA						
N	-1 (232)	696 (230)**	-0.6 (0.2)**	0.3 (0.2)	-1.7 (0.6)**	2.4 (0.6)***
HE	-410 (173)*	563 (171)***	-0.7 (0.2)***	0.2 (0.2)	-1.1 (0.4)**	1.0 (0.4)**
CH	4861 (153)***	-234 (150)	5.6 (0.1)***	-0.3 (0.1)*	10.9 (0.4)***	0.0 (0.3)
L	4456 (202)***	-166 (201)	7.7 (0.2)***	-0.7 (0.2)***	11.4 (0.5)***	0.0 (0.5)
S	3003 (220)***	460 (215)*	3.9 (0.2)***	-0.2 (0.2)	7.0 (0.5)***	1.3 (0.5)
Heterosis effects						
N-AA	143 (146)	592 (111)***	-0.2 (0.1)	0.0 (0.1)	0.3 (0.4)	1.7 (0.3)***
N-HE	118 (118)	-111 (80)	-0.3 (0.1)**	-0.2 (0.1)**	1.0 (0.3)*	0.8 (0.2)***
N-CH	-234 (112)*	266 (66)***	-0.4 (0.1)***	0.1 (0.1)*	0.0 (0.3)	1.0 (0.2)***
N-L	-220 (132)	104 (66)	-1.5 (0.1)***	0.3 (0.1)***	-0.1 (0.3)	1.6 (0.2)***
N-S	-122 (152)	-54 (106)	-0.1 (0.1)	-0.1 (0.1)	0.7 (0.4)	0.7 (0.3)**
AA-HE	-197 (127)	-78 (157)	-0.2 (0.1)	0.2 (0.2)	0.7 (0.3)*	0.4 (0.4)
AA-CH	341 (100)***	462 (145)***	0.3 (0.1)***	0.5 (0.1)***	1.9 (0.2)***	2.0 (0.3)***
AA-L	-726 (127)***	128 (147)	-1.0 (0.1)***	0.3 (0.1)*	-0.7 (0.3)*	0.3 (0.3)
AA-S	788 (240)***	280 (406)	0.1 (0.2)	-0.1 (0.4)	2.4 (0.6)***	-0.4 (1.0)
HE-CH	-595 (83)***	-7 (79)	-0.2 (0.1)**	0.0 (0.1)	-0.6 (0.2)**	0.4 (0.2)*
HE-L	-424 (115)***	-5 (93)	-1.1 (0.1)***	0.3 (0.1)***	-1.3 (0.3)***	0.7 (0.2)**
HE-S	-701 (144)***	-52 (142)	0.1 (0.1)	0.3 (0.1)*	0.5 (0.4)	-0.1 (0.3)
CH-L	-378 (95)***	210 (126)	-1.1 (0.1)***	-0.1 (0.1)	-1.3 (0.2)***	0.7 (0.3)*
CH-S	-159 (136)	561 (219)*	-0.2 (0.1)	0.1 (0.2)	-0.5 (0.3)	-0.2 (0.5)
L-S	226 (174)	-177 (278)	-0.5 (0.2)***	-0.1 (0.3)	0.0 (0.4)	1.0 (0.6)

Table 5. Predicted phenotypic means for Norwegian red (N), Aberdeen Angus (AA) Hereford (HE), Charolais (CH), Limousin (L), Simmental (S) and selected crosses[1] for calving difficulties (CDS), birth weight (BW), weaning weight (WW), herd life of cow (HLC), carcass weight (CW), EUROP conformation score (ECS), EUROP fat score (EFS), age at slaughter for bulls (ASb), average daily carcass gain for bulls (ADCGb; g/d), total carcass income in NOK (CINC), carcass income/kg carcass (CINC/kg) and carcass income per day for bulls (CINC/d).

Breed group	CDS, 1-3	BW, kg	WW, kg	HCL, yr	CW, kg	AS_b, mo	$ADCG_b$	ECS, 1-15	EFS, 1-15	CINC	CINC/kg	$CINC/d_b$
N	1.109 (0.006)	34.8 (0.3)	280 (12)	4.5 (0.1)	285 (1)	18.2 (0.02)	505 (1)	4.0 (0.01)	7.2 (0.02)	11575 (21)	40.9 (0.02)	24.6 (0.1)
AA	1.123 (0.003)	32.6 (0.1)	221 (1)	5.6 (0.1)	267 (1)	17.4 (0.04)	484 (1)	5.7 (0.02)	8.6 (0.02)	10880 (32)	41.2 (0.03)	23.9 (0.1)
HE	1.153 (0.003)	35.2 (0.1)	230 (1)	5.9 (0.1)	274 (1)	17.4 (0.04)	486 (1)	5.4 (0.01)	8.7 (0.02)	11033 (27)	40.8 (0.02)	23.8 (0.1)
CH	1.160 (0.003)	39.1 (0.1)	260 (1)	5.2 (0.1)	331 (1)	16.9 (0.03)	634 (1)	7.6 (0.01)	6.6 (0.02)	15506 (27)	46.5 (0.02)	34.7 (0.1)
L	1.156 (0.003)	36.5 (0.1)	254 (1)	4.9 (0.1)	312 (1)	16.0 (0.04)	622 (1)	8.7 (0.02)	6.2 (0.02)	15170 (34)	48.2 (0.03)	35.3 (0.1)
S	1.166 (0.004)	39.5 (0.1)	278 (1)	5.2 (0.1)	316 (1)	17.3 (0.07)	607 (2)	6.4 (0.03)	6.5 (0.04)	14343 (52)	45.0 (0.05)	32.2 (0.1)
NxAA	1.125 (0.010)	36.2 (0.3)	256 (2)	5.4 (0.2)	287 (2)	17.5 (0.14)	526 (5)	5.0 (0.05)	8.1 (0.07)	11718 (98)	41.1 (0.09)	25.8 (0.3)
NxHE	1.114 (0.007)	37.3 (0.3)	261 (3)	5.2 (0.1)	286 (1)	16.9 (0.10)	531 (4)	4.9 (0.04)	8.3 (0.05)	11488 (71)	40.6 (0.07)	25.9 (0.2)
(NxAA)xHE	1.134 (0.013)	36.8 (0.4)	244 (2)	6.4 (0.3)	286 (3)	17.0 (0.21)	538 (7)	5.0 (0.09)	8.4 (0.12)	11587 (163)	40.7 (0.15)	26.3 (0.4)
(NxAA)xAA	1.128 (0.009)	35.1 (0.3)	238 (1)	5.7 (0.2)	290 (2)	17.5 (0.14)	537 (5)	5.5 (0.06)	8.6 (0.08)	11890 (109)	41.2 (0.10)	26.5 (0.3)
(NxAA)xCH	1.152 (0.011)	38.3 (0.3)	258 (2)	5.3 (0.2)	324 (3)	16.9 (0.16)	629 (6)	6.5 (0.07)	7.7 (0.09)	14303 (125)	44.0 (0.12)	32.8 (0.2)
HExAA	1.159 (0.008)	34.8 (0.2)	225 (2)	5.6 (0.2)	273 (2)	16.8 (0.15)	494 (8)	5.5 (0.06)	8.7 (0.09)	11041 (115)	40.9 (0.11)	25.1 (0.3)
AAxHE	1.132 (0.013)	34.7 (0.4)	226 (2)	6.4 (0.4)	261 (4)	16.6 (0.24)	511 (5)	5.1 (0.10)	8.3 (0.14)	10477 (183)	40.7 (0.17)	24.1 (0.5)
HExCH	1.175 (0.006)	38.7 (0.1)	245 (2)	5.0 (0.1)	299 (1)	17.2 (0.09)	559 (3)	6.3 (0.04)	7.5 (0.05)	13074 (69)	43.7 (0.06)	29.3 (0.2)
AAxCH	1.147 (0.009)	36.5 (0.2)	241 (2)	4.8 (0.3)	307 (2)	16.6 (0.15)	597 (5)	6.7 (0.06)	7.7 (0.09)	13651 (119)	44.3 (0.11)	31.3 (0.3)
AAxL	1.132 (0.006)	35.3 (0.1)	231 (2)	3.9 (0.2)	281 (2)	16.5 (0.09)	550 (3)	6.7 (0.04)	7.6 (0.06)	12381 (81)	44.1 (0.08)	28.9 (0.2)
AAxS	1.187 (0.016)	37.0 (0.4)	243 (2)	5.3 (0.5)	303 (5)	16.4 (0.31)	580 (11)	6.3 (0.13)	7.9 (0.19)	13169 (250)	43.3 (0.23)	29.8 (0.6)
(AAxCH)xCH	1.121 (0.009)	37.5 (0.2)	250 (1)	4.7 (0.3)	325 (3)	16.4 (0.17)	646 (6)	7.3 (0.08)	7.1 (0.11)	15041 (141)	45.8 (0.13)	35.0 (0.3)
CHxS	1.162 (0.011)	38.8 (0.3)	262 (2)	5.2 (0.3)	314 (3)	17.1 (0.19)	602 (7)	6.8 (0.08)	6.6 (0.12)	14418 (156)	45.4 (0.14)	32.3 (0.4)
SxCH	1.149 (0.012)	40.2 (0.3)	275 (2)	5.5 (0.3)	328 (3)	17.4 (0.19)	625 (8)	6.9 (0.09)	6.7 (0.13)	15113 (172)	45.5 (0.16)	33.6 (0.4)

(CHxS)xCH	1.108 (0.014)	35.5 (0.4)	258 (2)	5.4 (0.4)	325 (4)	17.6 (0.28)	591 (10)	6.9 (0.11)	7.3 (0.16)	14655 (213)	44.8 (0.20)	31.3 (0.5)
(CHxS)xL	1.104 (0.016)	35.8 (0.4)	258 (1)	4.2 (0.5)	335 (5)	17.5 (0.31)	620 (11)	7.7 (0.13)	6.9 (0.18)	15672 (237)	46.5 (0.22)	33.9 (0.6)
(CHxS)xS	1.112 (0.014)	35.2 (0.3)	259 (2)	5.3 (0.4)	318 (4)	17.7 (0.28)	578 (10)	6.6 (0.11)	7.2 (0.16)	14191 (213)	44.3 (0.20)	30.3 (0.5)

[1] First breed given is the dam breed(s) and the last breed is the sire breed.