Genetic Evaluation of Carcass Traits: Looking at the Effects of Slaughter End Points

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Introduction

An exhaustive review of estimates of heritability (\mathbf{h}^2) for a broad spectrum of beef production traits published in the scientific literature from 1945 to 1991 was conducted by Koots et al. (1994), but their review did not include other important carcass traits (e.g., kidney, pelvic, and heart fat percentage, yield grade, fat weight) and due to the purpose of their study, individual estimates of h² for the traits reviewed were not reported, but only the weighted and unweighted averages. On the other hand, the review by Marshall (1994) reported estimates of h^2 for some additional carcass traits, but only for cattle reared under U.S. conditions and, basically, estimates presented were on an age-constant basis. In addition, due to few estimates for the additional traits at that time, averages of estimates of h^2 for several carcass traits were based on only one to three observations. Neither of the two reviews focused on the effect of end point on estimates of h². In the last ten years, as a consequence of the increased interest of many beef producers on carcass yield and quality to satisfy consumer demand, numerous studies of carcass traits have published estimates of h^2 and genetic correlations (\mathbf{r}_{σ}), doubling, at least, the number of estimates for many carcass traits. This review was conducted to present estimates of h^2 and r_{σ} for carcass traits published in the scientific literature from 1962 to 2004. Because animals are slaughtered at, or carcass traits are adjusted to, different end points, the effects of adjusting for age, weight or fat depth on such estimates are also discussed.

Review of Literature

Estimates of Heritability

Table 1 provides estimates of h^2 , numbers of estimates and unweighted means of estimates of h^2 for 14 carcass traits measured at, or adjusted to, constant age, weight or backfat thickness **(BT)** end points. References repeated in two or three categories compared estimates adjusted to two or three different end points; otherwise, only one kind of adjustment was performed. The exception is Fouilloux et al. (1999), who reported estimates of h^2 for dressing percentage at constant age and at constant weight, but estimates were for different breeds. The age-constant category includes estimates on an age-constant or time -on-feed-constant basis. Those in the weight-constant category are estimates that were adjusted for weight at slaughter or for carcass weight.

Carcass Weight (CW). CW had many estimates of h^2 (n=56) in the literature. Estimates were adjusted for age, weight, or BT, with averages of 0.42 (n=36), 0.37 (n=8) and 0.35 (n=12), respectively. Age-constant estimates of h² were greater than weight- and BT-constant estimates; although, fewer estimates were on a weight- and BT-constant basis. Mean estimate across end points was 0.40, which indicates that CW would respond well to selection. Large variation existed in estimates of h. Range of estimates was from 0.09, obtained by paternal half-sib analysis with REML with a BT adjustment (Johnston et al., 1992) to 0.92, obtained by paternal half-sibs analysis with Henderson's Method 2 with an age adjustment (Blackwell et al., 1962), but most estimates were moderate. Wulf et al. (1996) for crossbred steers and heifers, Wheeler et al. (1996) for crossbred steers, Oikawa et al. (2000) for Japanese Black (Wagyu) steers, Morris et al. (1990) for crossbred steers, and Benvshek et al. (1988) for Hereford cattle reported low h^2 estimates (0.10, 0.15, 0.15, 0.17 and 0.19, respectively). Koch et al. (1982) for crossbred steers, MacNeil et al. (1984) for purebred and crossbred steers, Elzo et al. (1998) for Angus steers, and Benyshek (1981) for Hereford steers and heifers reported moderate estimates (0.43, 0.44, 0.46 and 0.48, respectively). Large estimates (0.59, 0.60 and 0.68) were obtained by Moser et al. (1998) for Brangus steers and heifers, Pariacote et al. (1998) for American Shorthorn steers, and Koch (1978) for Hereford heifers.

Only three studies compared estimates of h^2 for CW adjusted for age or for BT. Differences in estimates of h^2 with these two adjustments were variable. For crossbred steers representing 11 cattle breeds that were slaughtered at 20 months of age, Morris et al. (1990) found that CW adjusted to a constant age had a larger estimate of h^2 than CW adjusted to a constant BT (0.28 vs 0.17). In a recent study, Devitt and Wilton (2001), using crossbred steers, also obtained differences between age- and BT-constant estimates of h^2 for CW, but the estimate adjusted for BT was larger than the estimate adjusted for age (0.57 vs 0.47). The reduction in the estimate of genetic variance caused by age adjustment relative to that for BT (522 vs 1,051 kg²) could explain most of this difference, because phenotypic

variances were not much different with the two adjustments. In contrast, Shanks et al. (2001) found no significant difference between age- and BT-constant estimates of h^2 (0.32 vs 0.33) for CW of Simmental and percentage Simmental steers.

Dressing Percentage (**DP**). The number (32) of h^2 estimates for DP found in the literature was about half of that found for CW. Most estimates of h^2 were adjusted for age (n=18), which had a mean of 0.28. Fewer estimates adjusted for BT (n=3) had a mean of 0.36. Eleven weightconstant h² estimates had a mean of 0.38. Average estimate of h^2 was 0.32 across end points, indicating that DP is lowly to moderately heritable, which suggests that response to selection would be possible. Estimates of h² for DP ranged from very low (0.01) estimated as twice the son on sire regression coefficient on an age-constant basis (Reynolds et al., 1991), to very high (0.97) obtained with a paternal half-sib analysis on a weight-constant basis (Hinks and Bech Andersen, 1969). This range includes estimates of 0.06, 0.12, 0.37, 0.39, 0.50 and 0.69 reported by Wheeler et al. (1996), Lee et al. (2000), Robinson et al. (1998), Kim et al. (1998), Fouilloux et al. (1999) and Renand et al. (1985), revealing significant variability among estimates, which may reflect the relatively limited number of records in most studies. Few studies in the scientific literature compared estimates of h^2 for DP adjusted for different end points. Veseth et al. (1993), by a paternal half-sib model with Henderson's Method 3, obtained similar estimates of h^2 with age (0.25) or weight (0.26) as covariates in the model. Also, Koots et al. (1994), in their review of h^2 estimates, found that weighted average of h² estimates for DP were about the same on a weight- or age-constant basis (0.38 and 0.39, respectively). In a recent study (Lee et al., 2000), estimates of h² to age- and weight-constants were similar (0.12 and 0.16, respectively), but somewhat larger than estimates of h^2 to BT-constant (0.09).

Backfat Thickness. BT also had many estimates of h (n=63) in the literature. Most of the estimates were to an age-constant (n=34), followed by many to a weight-constant (n=23). Few estimates of h^2 were to a BT-constant (n=6). Averages of estimates of h^2 were 0.39, 0.33 and 0.29, respectively. The average across end points was 0.36, which suggests that genetic progress to single trait selection would be possible if records were available. Across end points, estimates of h^2 ranged from 0.03 (Morris et al., 1990, REML analysis with a sire model) to 0.94 (Dunn et al., 1970, paternal half-sib analysis). These two extreme estimates were for carcasses of crossbred steers adjusted for age. Estimates of h were small (0.07, 0.14 and 0.15) by Hoque et al. (2002), Gilbert et al. (1993) and Oikawa et al. (2000), and large (0.63, 0.68 and 0.84) by Riley et al. (2002), Koch (1978) and Wheeler et al. (2001), respectively. Moderate estimates of h^2 (0.43, 0.44, and 0.46) were reported by Brackelsberg et al. (1971), Yoon et al. (2002) and Pariacote et al. (1998). Five studies (Shelby et al., 1963; Cundiff et al., 1969; Hirooka et al., 1998; Shanks et al.,

2001; Devitt and Wilton, 2001) compared estimates of h^2 for BT adjusted for age or weight. All agreed that estimates were similar regardless of the type of covariate used.

Longissimus Muscle Area (LMA). LMA was the carcass trait with the most \mathbf{h} estimates (n=66) reported, reflecting its relative importance and easy measurement. Averages of h^2 estimates were 0.41 (n=36), 0.37 (n=19) and 0.41 (n=11) with age, weight or BT constants, respectively. The average of estimates of h^2 (0.40) over all end points indicates that LMA is moderately heritable and genetic gain might be achieved through selection. However, estimates of h^2 vary significantly among studies. Estimates ranged from almost the minimum (0.01, Reynolds et al., 1991, Hereford bulls, son on sire regression analysis) to almost the maximum for h^2 (0.97, Pariacote et al., 1998, American Shorthorn steers, REML analysis with a sire model). Estimates of h² for LMA adjusted for age or weight reported by Benyshek (1981) for Hereford steers and heifers, Morris et al. (1990) for crossbred steers, and Hirooka et al. (1996) for Japanese Brown steers, indicate no significant effect of end point on estimates. In contrast, Shelby et al. (1963) reported that the h^2 estimate for LMA increased from 0.26 to 0.46 when the adjustment was made for slaughter weight instead of age. In a study using Hanwoo (Korean Native) cattle, Lee et al. (2000) reported that age- (0.17) and BT-constant (0.18) estimates of h^2 were slightly smaller than the weight-constant estimate (0.24). Similar differences between weight- and BT-adjusted h^2 estimates were obtained by other authors; although, the differences had opposite sign. In a more recent study (Shanks et al., 2001) that included Simmental and percentage Simmental cattle, the age- and BT-constant h² were estimated to be slightly larger than the weight-constant h² (0.26 and 0.29 vs 0.22, respectively). Larger estimates of h^2 with a weight-constant (0.45) or a BT-constant (0.52) basis were reported by Devitt and Wilton (2001), but the difference (0.07) between estimates was of the same magnitude. More recently, Kemp et al. (2002), after adding weight to a model that included age as a covariate, obtained a much smaller h^2 estimate for LMA (0.45 vs 0.36).

Kidney, Pelvic, and Heart Fat Percentage (KPH). Comparatively few estimates of h^2 (n=14) were found in the literature for KPH. Eight estimates were adjusted for age with an average of 0.48, two were adjusted for weight with an average of 0.19, and four were adjusted for BT with an average of 0.34. The overall average was 0.40. Estimates of h² ranged from 0.00 (Wilson et al., 1976, paternal half-sib analysis) on a weight-constant basis to 0.83 (Koch et al., 1982, paternal half-sibs analysis with Henderson's Method 3) on an age-constant basis. Elzo et al. (1998) and Wheeler et al. (2001) reported h^2 estimates of 0.03 and 0.28, Wheeler et al. (1996) and Riley et al. (2002) obtained moderate estimates (0.32 and 0.46) and Brackelsberg et al. (1971) and Nephawe et al. (2004) reported high estimates of 0.72 and 0.65, respectively. Only Veseth et al. (1993) contrasted estimates of h² for KPH adjusted for different covariates but estimates where similar when age (0.37) or weight (0.38) were used as covariates in a model based on paternal half-sibs.

Marbling Score (MS). MS is one of the most genetically evaluated carcass traits. Age-, weight- and BT-constant estimates averaged 0.45 (n=29), 0.29 (n=15) and 0.30 (n=12), respectively. The average across end points was 0.37. Similar to estimates of h^2 for carcass traits discussed previously, estimates of h² for MS were highly variable across studies with a large range, from 0.01 (Lee et al., 2000, DFREML analysis with an animal model) using weight as a covariate to 0.88 (Pariacote et al., 1998, REML analysis with a sire model) using age. Most estimates, however, were moderate within a range of 0.30 to 0.57. For example, Devitt and Wilton (2001), Lamb et al. (1990), Splan et al. (2002), Fernandes et al. (2002), Benyshek et al. (1988), Barkhouse et al. (1996), Kemp et al. (2002), Van Vleck et al. (1992), Gregory et al. (1995), O'Connor et al. (1997) and Yoon et al. (2002) reported estimates of 0.30, 0.33, 0.35, 0.37, 0.38, 0.40, 0.42, 0.43, 0.48, 0.52 and 0.57, respectively. Few (3) studies in the literature have compared estimates of h^2 for MS obtained by adjusting for age, weight or BT. Using field records of the American Simmental Association, Shanks et al. (2001) reported similar estimates of h^2 for MS adjusted for age (0.12), weight (0.12) or BT (0.13) for bulls, steers and heifers. Similarly, Hirooka et al. (1996) concluded that choice of covariate in the model (slaughter age vs slaughter weight) had little effect on h estimates for MS. In contrast, Devitt and Wilton (2001), for crossbred steers, reported that weight-constant h^2 (0.43) was significantly larger than BT-constant h^2 (0.30), and was slightly larger than age-constant h^2 (0.35).

Yield Grade (*YG*). Only six estimates of h^2 for YG were reported in the literature, four with data adjusted for age and two for BT, with averages of 0.60 and 0.74, respectively. Average of estimates of h^2 was 0.64 across the two end points, indicating that this trait is highly heritable and genetic merit might be improved by selection. In studies conducted to a constant age, low (0.24, Hereford bulls) and moderate (0.54, American Shorthorn steers) estimates of h² were obtained by Lamb et al. (1990) and Pariacote et al. (1998), respectively. However, on a BT-constant basis, Wulf et al. (1996) for crossbred steers and heifers and Riley et al. (2002) for Brahman steers and heifers reported estimates of 0.76 and 0.71, and on an age-constant basis, Wheeler et al. (1996) and Wheeler et al. (2001) for crossbred steers obtained larger estimates of 0.76 and 0.85, respectively. No reports were found that compared estimates of h^2 for YG adjusted to constant age, weight or BT.

Predicted Percentage of Retail Product (**ER**). The column labeled as ER in Table 1 lists estimates of l^2 for various cut-out-type traits, which are cited as predicted percentage of retail product in this review. Few (n=17) estimates of h^2 for ER have been published in the literature relative to estimates for actual carcass traits. More estimates found were on an age- (n=8) than on a weight- (n=6) or

BT-constant basis (n=3), with averages of 0.28, 0.41 and 0.48, respectively. Across end points, average of estimates was 0.36. Estimates of h^2 for ER were in a low-to-high range, from 0.07 (age-constant) obtained with DFREML analysis with an animal model by Hassen et al. (1999) for Angus- and Simmental-sired steers and bulls, to 0.71 (BT-constant) estimated with animal model with DFREML analysis by Riley et al. (2002) for Brahman steers and heifers. Examples of moderate estimates of h^2 included: at constant age, 0.53 by Mukai et al. (1995) for Japanese Black steers and heifers; at constant weight, 0.44 by Wilson et al. (1976) for crossbred steers and heifers; and at constant BT, 0.55 by Gilbert et al. (1993) for Canadian Angus and Hereford bulls. Estimates of h^2 for ER adjusted to different end points were found in only two reports. In an early genetic study (Cundiff et al., 1971), the h^2 estimate for ER increased somewhat in the moderate range when data were adjusted to a constant weight relative to adjustment to a constant age (0.28 vs 0.35). Similarly, Shanks et al. (2001) obtained somewhat larger estimates of h² for ER adjusted for BT or for weight than when adjusted for age (0.17 and 0.12 vs 0.09).

Retail Product Weight (**RW**). Of the 13 estimates of h^2 for RW found in the literature most (n=11) were adjusted for age: and one each for BT and weight. Age-constant estimates of h^2 ranged from low to moderate (0.28) for purebred and composite steers (Gregory et al., 1995, Henderson's Method 3 with a sire model) to high (0.66) for purebred, composite and F1 crossbred steers (Shackelford et al., 1995, DFREML with an animal model). Estimates of h² on an age-constant basis averaged 0.51. Estimates at constant weight or BT were 0.42 and 0.50 by Cundiff et al. (1969) and Riley et al. (2002), respectively. The average of age-constant estimates and weight- and BT-constant estimates of h² imply that significant genetic variation exists to improve RW by selection. Estimates of h^2 for RW based on different covariates were published in only one report (Cundiff et al., 1969), which found that the estimate of h^2 using age as the covariate in the model was larger than the estimate using weight as the covariate (0.64 vs 0.42).

Fat Weight (FW). Only nine estimates of h^2 for FW were found in the literature. Seven estimates were with adjustment to constant age, one to constant weight and one to constant BT. Estimates of h² adjusted for age averaged 0.52 and ranged from low to moderate (0.30) for purebred and crossbred steers and heifers (Morris et al., 1999, animal model and REML) to high (0.94) for Hereford heifers (Koch, 1978, sire model and Henderson's Method 2). Almost all estimates, however, were moderate, except those obtained by Koch (1978) and Shackelford et al. (1995). The estimates of h^2 at constant weight or BT found in the literature were by Cundiff et al. (1969) and Brackelsberg et al. (1971), who reported estimates of 0.37 and 0.50, respectively. The average of estimates of h² across end points was 0.50, suggesting that selection against FW or to an intermediate level, for example, would respond well to

selection. Only one report (Cundiff et al., 1969) compared estimates of h^2 for FW obtained with different covariates; the age-constant estimate of h^2 was larger than the weigh-constant estimate (0.46 vs 0.37).

Bone Weight (**BW**). Seven estimates of h^2 for BW were found in the literature; six adjusted to constant age, and one to constant weight, with none for constant BT. For a constant age, the average was 0.51; all estimates were moderate to large (0.38, Cundiff et al., 1969; 0.39, Gregory et al., 1995; 0.51, Morris et al., 1999; 0.56, Koch, 1978; 0.57, Koch et al., 1982; 0.62, Shackelford et al., 1995). The h^2 estimate of 0.39 for BW adjusted to a weight-constant basis was reported by Cundiff et al. (1969), who also reported an estimate of 0.38 adjusted to a common age.

Actual Retail Product Percent (RP). The numbers of estimates of h^2 for RP in the scientific literature were 9 on an age-constant basis and 8 on a weight-constant basis. Estimates of h^2 on an age-constant basis averaged 0.54, and ranged from moderate (0.33, Morris et al., 1999, REML analysis with an animal model) to high (0.67, Shackelford et al., 1995, DFREML analysis with an animal model), but most estimates were moderate. On a weight-constant basis, the average of estimates (0.50) was similar to that on an age-constant basis, but estimates ranged from low (0.18) for Danish Red males (Hinks and Bech Andersen, 1969, paternal half-sib analysis) to high (0.71) for bulls of Holstein Friesian and Brown Swiss sires (Jensen et al., 1991, REML analysis with a sire model). No comparisons of estimates of h² for RP obtained using different covariates in the same study were found.

Fat Percent (*FP*). Seven estimates of h^2 for FP in the literature were age-constant estimates. Estimates averaged 0.51 and ranged from moderate (0.35) for purebred and composite steers (Gregory et al., 1995) to high (0.65) for purebred, composite and F₁ crossbred steers (Shackelford et al., 1995). This range also includes estimates of h^2 of 0.39, 0.49, 0.53, 0.57 and 0.59 reported by Morris et al. (1999), Splan et al. (2002), Nephawe et al. (2004), Koch et al. (1982) and Wheeler et al. (1997), respectively. The two estimates on a weight-constant basis were very different: 0.12 by Hinks and Bech Andersen (1969) for Danish Red males and 0.89 by Jensen et al. (1991) for Holstein Friesian and Brown Swiss bulls, respectively. No comparisons of estimates of h^2 for FP evaluated at different end points in the same study were found.

Bone Percent (**BP**). All estimates of h^2 (n=8) for BP were adjusted for age, except the weight-constant estimate of 0.35 reported by Hinks and Bech Andersen (1969) for Danish Red males. In general, the estimates of h^2 indicate that BP is moderately heritable, averaging 0.44. The range was from 0.21 (Gregory et al., 1995) to 0.69 (Shackelford et al., 1995). Most estimates in this range were moderate: 0.31, 0.44, 0.48, 0.52, and 0.53 by Morris et al. (1999), Wheeler et al. (1997), Splan et al. (2002), Nephawe et al. (2004) and Koch et al. (1982), respectively. No reports of estimates of

 h^2 for BP adjusted for different covariates in the same study were found.

Estimates of Genetic Correlations

Estimates, unweighted means, minima, and maxima of rg among carcass traits are displayed in Tables 2 (constant age or constant time-on-feed), 3 (constant slaughter weight or constant CW) and 4 (constant BT). Papers repeated in two or three Tables compared the effect of two or three different end points on estimates of rg among carcass traits. Estimates of rg on an age-constant or time -on-feed-constant basis will be referred as age-constant estimates and those on a slaughter weight-constant or CW-constant basis as weight-constant estimates. Table 5 contains minima, maxima and unweighted averages of estimates of r, among carcass traits over the three end points. The column labeled as ER in the Tables refers to various cutability-type traits, which are cited as predicted percentage of retail product in this review. Extensive information is given in the Tables, but due to space restrictions discussion is limited to most important trait combinations and with the most number of observations.

Almost all (n=7) the estimates of r_g between CW and DP were on an age-constant basis and averaged 0.38, indicating that these two traits are moderately associated. Estimates were in a low-to-high range from 0.04 (Reynolds et al., 1991, son-sire regression analysis) for Hereford bulls to 0.65 (Pariacote et al., 1998, REML analysis with a sire model) for American Shorthorn steers. The other estimates within this range were 0.19, 0.32, 0.35, 0.52 and 0.62 by Yoon et al. (2002), Veseth et al. (1993), Shelby et al. (1963), Morris et al. (1999) and Hoque et al. (2002), showing significant variability among estimates. The only estimate of r_g for CW and DP of 0.47 obtained at constant BT (median=10 mm) was published by Riley et al. (2002) for 504 Brahman steers and heifers in central Florida.

Most (n=21) estimates of r_g for CW and BT were adjusted for age, followed by weight- and BT-constant estimates with four reports. Means of estimates were 0.13, -0.10 and 0.21, respectively. The overall average was 0.11, suggesting that the two traits are lowly associated. Estimates were highly variable within each end point. At constant age, for example, estimates ranged from -0.85, obtained by REML with a sire model (Morris et al., 1990, 1908 crossbred steers), to 0.95, obtained by Henderson's Method 2 with a sire model (Koch, 1978, 377 Hereford heifers). Estimates of -0.37, -0.22 and -0.10 by Shanks et al. (2001), Pariacote et al. (1998) and Moser et al. (1998), respectively, are other negative estimates. Other positive estimates by Wheeler et al. (1996), Cundiff et al. (1971) and Hoque et al. (2002) were 0.24, 0.34 and 0.42, respectively.

Of the 34 estimates of the r_g between CW and LMA 23 were for common age, 4 for common weight, and 7 for common BT. Estimates adjusted for age, weight and BT were, respectively, 0.44, 0.05 and 0.53. The mean of the 34 estimates was 0.41, revealing a moderate genetic

association. Estimates with equal age or equal weight end points were more variable than those with equal BT, but at equal weight the range included not only positive, but negative estimates. The positive estimates on an age constant basis ranged from very low (0.02) for 377 Hereford heifers (Koch, 1978) to very high (0.82) for 161 Hanwoo steers (Hoque et al., 2002), including variable estimates of 0.11, 0.23, 0.44, 0.58 and 0.76 by Wheeler et al. (2001), Mukai et al. (1995), Koch et al. (1982), Kemp et al. (2002) and Hassen et al. (1999), respectively. With constant BT, estimates were in a positive moderate-to-high range from 0.40 (Elzo et al., 1998) for Brahman steers to 0.69 (Devitt and Wilton, 2001) for Canadian crossbred steers. The estimates at constant weight by Reverter et al. (2003) for Belmont Red, Santa Gertrudis and Brahman, Benyshek et al. (1988) for Hereford cattle, Arnold et al. (1990) for Hereford steers and Reverter et al. (2003) for Murray Grey, Shorthorn, Angus and Hereford were -0.28, -0.07, 0.09 and 0.45, respectively. Only two studies evaluated the effects of age and BT end points on estimates of rg between CW and LMA. Using Simmental field records, Shanks et al. (2001) reported that the estimate of the rg was slightly reduced from 0.57 to 0.49 using age as a covariate in the model instead of BT. For Canadian crossbred steers, a larger difference was obtained by Devitt and Wilton (2001), who reported that the estimate adjusted for age (0.42) was significantly less than the estimate adjusted for BT (0.69).

Age- (n=16), weight- (n=4) and BT-constant estimates (n=9) of rg for CW and MS were found. Mean estimates by end point were 0.16, 0.08 and 0.15, respectively. The 29 estimates had a mean of 0.14, indicating a weak genetic association between the two traits. Estimates were highly variable with positive and negative signs within each end point. With fixed age, estimates ranged from -0.33 for Hereford heifers (Koch, 1978) to 0.64 for Hereford bulls (Lamb et al., 1990); with fixed weight, the range was from -0.20 for Murray Grey, Shorthorn, Angus and Hereford (Reverter et al., 2003) to 0.35 (Benyshek et a., 1988) for Hereford cattle; and with fixed BT, was from -0.31 for Charolais steers and heifers (Johnston et al., 1992) to 0.67 for Charolais - and Limousin-sired steers and heifers (Wulf et al., 1996). Two studies compared estimates of rg for CW and MS for different end points. Devitt and Wilton (2001), using Canadian carcass data, reported that the genetic correlation was much stronger at constant age than at constant BT (-0.30 vs -0.03). Similarly, Shanks et al. (2001) found that estimate of rg was slightly greater with constant age than with constant BT (0.30 vs 0.20), but the estimates had different (positive) sign than those by Devitt and Wilton (2001).

Mean estimate of r_g between CW and ER on an age-constant (-0.10) or a BT-constant basis (0.25) indicate a low genetic correlation, but the sign of the estimated correlation did change with different end points. Shanks et al. (2001) reported negative estimates for the r_g between CW and ER, but the estimate adjusted for age was

significantly larger than the estimate adjusted for bakcfat thickness (-0.21 vs -0.05).

On average, CW was highly positively correlated genetically with RW, FW and BW (0.84, 0.64 and 0.75 respectively) as expected on an age-constant basis. Estimates of r_g for these three pairs of traits were much less variable than estimates of r_g discussed previously. No estimates of r_g with constant weight or constant BT were in the literature. In contrast, averages of estimates of r_g of CW with RP (-0.06), FP (0.02) and BP (-0.04) at common age indicate little genetic association with these traits.

Few estimates of r_g for DP and BT were in the literature; most were adjusted for age (n=6) with one estimate each adjusted for weight and BT. Mean of age-constant estimates was 0.28. Reported estimates were - 0.16, 0.02, 0.31, 0.36, 0.52, 0.61 by Pariacote et al. (1998), Oikawa et al. (2000), Yoon et al. (2002), Kuchida et al. (1990), Hoque et al. (2002) and Shelby et al. (1963), showing significant variation. The weight- (0.25) and BT-constant (0.42) estimates were reported by Dinkel and Busch (1973) and Riley et al. (2002). The mean (0.29) over all end points indicates a small genetic association.

Averages of estimates of r_{g} between DP and LMA suggest changes in magnitude and sign with different end points. Means were: 0.36 (n=9) at constant age, 0.62 (n=3) at constant weight and -0.05 (n=2) at constant BT. Estimates for age end point were variable, ranging from lowly negative (-0.11) for 411 Hereford bulls (Veseth et al., 1993, Henderson's Method 3 with patemal half-sibs) to highly positive (0.92) for 535 Japanese Black (Wagyu) steers (Oikawa et al., 2000, REML fitting an animal model). Only one study (Lee et al., 2000) assessed the effects of end point on estimates of r_{g} for DP and LMA. Changes in magnitude and sign were reported with different end points. The estimate of r_{g} was nearly zero (0.01) at constant age, nearly one (0.91) at constant weight and lowly negative (-0.11) at constant BT.

Averages of estimates of r_g between DP and MS were -0.32, 0.24 and 0.01 with constant age, weight and BT, suggesting possible changes in sign and magnitude with different end points, although these averages are based on few studies and observations (n=7, 2 and 3, respectively). Lee et al. (2000), for Korean Native (Hanwoo) cattle, found significant effects on magnitude of estimates of r_g for DP and MS reporting much larger estimates when adjusted for age and BT than when adjusted for weight (-0.88 and -0.99 vs -0.03).

Most of the estimates of r_g for BT and LMA were with common age (n=24) with fewer with common weight (n=8) and common BT (n=5). Means of estimates of r_g were -0.16, -0.28 and -0.06, respectively. Regardless of end point, the overall mean (-0.17) suggests that the two traits are lowly and negatively correlated genetically. Estimates obtained on an age-constant basis were more variable than estimates on a weight- or BT-constant basis. Estimates with constant age ranged from -1.00 for Japanese Black (Oikawa et al., 2000, n=535 steers) to 0.38 for Hanwoo (Hoque et al., 2002, n=161 steers). Two recent studies (Shanks et al., 2001; Devitt and Wilton, 2001) concluded that age and weight end points had no significant effect on estimates of r_g for BT and LMA.

About half (n=19) of the 33 estimates of rg for BT and MS were at constant age. Fewer estimates were at constant weight (n=8) and constant BT (n=6). Averages of estimates indicate the g at equal age (0.24), weight (0.23) or BT (0.21) are similar to each other. The average of estimates (0.20) across the three end points indicates BT and MS are lowly and positively genetically correlated. Shanks et al. (2001) reported similar estimates of r for BT and MS at constant age (0.17) and constant weight (0.18). Devitt and Wilton (2001) reported the weight-constant estimate was somewhat larger than the age-constant estimate (0.41 vs)0.30). All estimates with constant weight were positive, whereas four and two estimates were negative with constant age and constant BT, respectively. The near-to-zero estimate (0.01) by Wheeler et al. (1996) suggests that selection for increased MS would not affect BT. Average of BT-constant estimates does not include the estimate (-0.83) by Gilbert et al. (1993). This estimate should be interpreted with care because the scale of measurement for MS increased with decreased levels of marbling, i.e., higher levels of marbling were associated with increased BT. More variability was observed among estimates at constant age or constant BT than at constant weight. Range of estimates was from -0.42 (Kuchida et al., 1990) to 1.00 (Dunn et al., 1970) with fixed age and from -0.19 (Fernandes et al., 2002) to 0.62 (Brackelsberg et al., 1971) with fixed BT.

Few estimates of r_g between BT and ER for each end point (n=4) were in the literature. Overall mean (0.76) indicates BT and ER are highly and negatively correlated genetically. Estimates within each end point were less variable compared to estimates of r_g for combinations of traits discussed previously. The only study (Shanks et al., 2001) that contrasted estimates of r_g for BT and ER reported a larger estimate using weight as a covariate in the model than using age (-0.53 vs -0.29).

The r_g of LMA with MS had the most estimates (n=40) reported in the literature. Twenty were on an age-, 9 on a weight- and 11 on a BT-constant basis, which averaged 0.06, -0.07 and 0.05. Over the 40 estimates the mean was 0.03, indicating little genetic association with the implication that selection for increased LMA would not decrease marbling. At any slaughter end point, estimates had important variability. With common age, the range of estimates was from -0.61 for Canadian crossbred steers (Devitt and Wilton, 2001) to 0.83 for Wagyu steers (Oikawa et al., 2000), including estimates of -0.40, -0.36, -0.17, -0.10, 0.02, 0.12, and 0.49 by Van Vleck et al. (1992), Wheeler et al. (2001), Pariacote et al. (1998), Kemp et al. (2002), Mukai et al. (1995), Hirooka et al. (1996) and Kim et al. (1998), respectively. With common weight, estimates ranged from -0.38 for steers and heifers of Hereford sires

and Angus-Holstein cows (Wilson et al., 1976) to 0.39 for Korean Native cattle (Lee et al., 2000). Other estimates reported by Reverter et al. (2003), Din kel and Busch (1973), Benyshek et al. (1988) and Shanks et al. (2001) were -0.23, -0.17, 0.04 and 0.26, respectively. End point had a significant effect on the estimates of r_g of LMA with MS in each of three recent studies. Lee et al. (2000) found that estimates were different depending on the covariate used as the end point: 0.20 with BT, and 0.39 and 0.47 with slaughter weight and slaughter age covariates. Shanks et al. (2001) concluded that the estimates of r_g were moderate at age (0.46) and BT (0.48) end points but smaller on a weight-constant basis (0.26). Estimates reported by Devitt and Wilton (2001) were -0.61, -0.37 and -0.35 when using age, BT or weight end points, respectively.

The first insight into the effects of slaughter end points on estimates of r_g among carcass traits was by Cundiff et al. (1969). They reported a change in magnitude and direction of the r_g between RW and FW with constant age (0.55) or with constant weight (-0.90) end points. Two years later, Cundiff et al. (1971) reported that age end point caused a significant reduction in estimates of r_g of MS with RW, FW and BW relative to weight end point. Estimates were -0.13, 0.82 and -0.27 with constant age and -0.89, 0.98 and -0.78 with constant weight, respectively.

Conclusions and Implications

The review of estimates of h^2 and r_g published in the scientific literature during the last 42 years revealed that most estimates were on an age-constant basis. The traits with the most estimates of h^2 were CW, BT, LMA and MS. The average estimates for these traits indicate that they are similarly and moderately heritable. In contrast, the number of estimates of h² for DP was about half or less than half of those for carcass traits listed above. The average estimate also indicates that DP is moderately heritable. Fewest estimates of h² reported in the literature were for traits that require the most effort to measure: KPH, YG, ER, RW, FW, BW, RP, FP, and BP. The estimates, however, indicate they are more heritable, except for KPH and ER, than the more frequently studied carcass traits. The smallest number of estimates was for YG, which also had the largest estimates of h^2 . Estimates of h^2 and r_g for most carcass traits varied greatly, which could be due to differences in breed groups, methods of estimation, effects in the model, number of observations, measurement errors, sex, and management differences. Few studies have compared h^2 and r_g estimates for carcass traits adjusted to different end points. Results from those few studies were inconsistent although some studies revealed that h^2 and r_{g} estimates for several traits were sensitive to the covariate (end point) included in the model implying that direct and correlated responses to selection would be different for some traits depending on slaughter end point. The effect of different end points on estimates of h^2 and r_{g} has not been studied for several

carcass traits. Estimates averaged over slaughter end points suggests that BT is highly correlated genetically with YG and ER, indicating that selection for reduced BT would be most efficient for improving YG and increasing ER. Carcass quality, however, would be affected negatively because of the positive estimate of rg between MS and BT across end points. These relationships could discourage beef producers who desire to improve quality grade without increasing BT. Other researchers (Bertrand et al., 1993; Vieselmeyer et al., 1996), however, have demonstrated that marbling can be increased without increasing BT through selection based on estimated progeny differences. Based on age-constant estimates, an alternative would be to select for increased LMA, which could improve YG and increase ER without altering marbling.

Bibliography

- Arnold, J. W., J. K. Bertrand, L. L. Benyshek, and C. Ludwig. 1991. Estimates of genetic parameters for live animal ultrasound, actual carcass data, and growth traits in beef cattle. J. Anim. Sci. 69:985-992.
- Barkhouse, K. L., L. D. Van Vleck, L. V. Cundiff, M. Koohmaraie, D. D. Lunstra, and J. D. Crouse. 1996. Prediction of breeding values for tenderness of market animals from measurements on bulls. J. Anim. Sci. 74:2612-2621.
- Benyshek, L. L. 1981. Heritabilities for growth and carcass traits estimated from data on Hereford under commercial conditions. J. Anim. Sci. 53:49-56.
- Benyshek, L. L., J. W. Comerford, D. E. Little, and C. Ludwig. 1988. Estimates of carcass trait genetic parameters from Hereford field data. J. Anim. Sci. 66 (Suppl. 1):10 (Abstr.).
- Bertrand, J. K., W. O. Herring, S. E. Williams, and L. L. Benyshek. 1993. Selection for increased marbling and decreased backfat in Angus cattle using expected progeny differences. J. Anim. Sci. 71(Suppl. 1):93 (Abstr.).
- Blackwell, R. L., J. H. Knox, C. E. Shelby, and R. T. Clark. 1962. Genetic analysis of economic characteristics of young Hereford cattle. J. Anim. Sci. 21:101-107.
- Brackelsberg, P. O., E. A. Kline, R. L. Willham, and L. N. Hazel. 1971. Genetic parameters for selected beefcarcass traits. J. Anim. Sci. 33:13-17.
- Crews, D. H., Jr., and R. A. Kemp. 2001. Genetic parameters for ultrasound and carcass measures of yield and quality among replacement and slaughter beef cattle. J. Anim. Sci. 79:3008-3020.
- Crews, D. H., Jr., E. J. Pollak, R. L. Weaber, R. L. Quaas, and R. J. Lipsey. 2003. Genetic parameters for carcass traits and their live animal indicators in Simmental cattle. J. Anim. Sci. 81:1427-1433.
- Cundiff, L. V., D. Chambers, D. F. Stephens, and R. L. Willham. 1964. Genetic analysis of some growth and carcass traits in beef cattle. J. Anim. Sci. 23:1133-1138.

- Cundiff, L. V., K. E. Gregory, R. M. Koch, and G. E. Dickerson. 1969. Genetic variation in total and differential growth of carcass components in beef cattle. J. Anim. Sci. 29:233-244.
- Cundiff, L. V., K. E. Gregory, R. M. Koch, and G. E. Dickerson. 1971. Genetic relationships among growth and carcass traits of beef cattle. J. Anim. Sci. 33:550-555.
- Cunningham, E. P., and T. Broderick. 1969. Genetic and environmental parameters of growth and carcass traits in dual-purpose cattle. Ir. J. Agric. Res. 8:397-416.
- Devitt, C. J. B., and J. W. Wilton. 2001. Genetic correlation estimates between ultrasound measurements on yearling bulls and carcass measurements on finished steers. J. Anim. Sci. 79:2790-2797.
- Dinkel, C. A., and D. A. Busch. 1973. Genetic parameters among production, carcass composition and carcass quality traits of beef cattle. J. Anim. Sci. 36:832-846.
- DuBose, L. E., and T, C. Cartwright. 1967. Relationships among production and carcass traits in cattle. J. Anim. Sci. 26:203 (Abstract).
- Dunn, R. J., W. T. Magee, K. E. Gregory, L. V. Cundiff, and R. M. Koch. 1970. Genetic parameters in straightbred and crossbred beef cattle. J. Anim. Sci. 31:656-663.
- Elzo, M. A., R. L. West, D. D. Johnson, and D. L. Wakeman. 1998. Genetic variation and prediction of additive and nonadditive genetic effects for six carcass traits in an Angus-Brahman multibreed herd. J. Anim. Sci. 76:1810-1823.
- Fernandes, T. L., J. W. Wilton, I. B. Mandel, and C. J. B. Devitt. 2002. Genetic parameter estimates for meat quality traits in beef cattle managed under a constant finishing program. In: Proc. 7th World Congr. Genet. Appl. Livest. Prod., Montpellier, France. Session 02. Breeding ruminants for meat production. Communication No. 02-93.
- Fouilloux, M. N., G. Renand, J. Gaillard, and F. Ménissier. 1999. Genetic parameters of beef traits of Limousin and Charolais progeny-tested AI sires. Genet. Sel. Evol. 31:465-489.
- Fouilloux, M. N., G. Renand, and D. Laloë. 2002. Genetic evaluation using commercial carcass data in French beef cattle. h: Proc. 7^h World Congr. Genet. Appl. Livest. Prod., Montpellier, France. Session 02. Breeding ruminants for meat production. Communication No. 02-20.
- Gilbert, R. P., D. R. C. Bailey, and N. H. Shannon. 1993. Body dimensions and carcass measurements of cattle selected for postweaning gain fed two different diets. J. Anim. Sci. 71:1688-1698.
- Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1995. Genetic and phenotypic (co)variances for growth and carcass traits of purebred and composite populations of beef cattle. J. Anim. Sci. 73:1920-1926.

- Gregory, K. E., L. V. Cundiff, R. M. Koch, M. E. Dikeman, and M. Koohmaraie. 1994. Breed effects, retained heterosis, and estimates of genetic and phenotypic parameters for carcass and meat traits of beef cattle. J. Anim. Sci. 72:1174-1183.
- Hanset, R., R. Michaux, and A. Stasse. 1987. Relationships between growth rate, carcass composition, feed intake, feed conversion ratio and income in four biological types of cattle. Genet. Sel. Evol. 19:225-248.
- Hassen, A., D. E. Wilson, and G. H. Rouse. 1999. Evaluation of carcass, live, and real-time ultrasound measures in feedlot cattle: I. Assessment of sex and breed effects. J. Anim. Sci. 77:273-282.
- Hinks, C. J. M., and B. Bech Andersen. 1969. Genetic aspects of growth and carcass quality in veal calves. Anim. Prod. 11:43-45.
- Hirooka, H., A. F. Groen, and M. Matsumoto. 1996. Genetic parameters for growth and carcass traits in Japanese Brown cattle estimated from field records. J. Anim. Sci. 74:2112-2116.
- Hoque, M. A., D. H. Baik, and C. S. Na. 2002. Parameter estimates for genetic and environmental effects on meat potential of Korean native (Hanwoo) cattle. In: Proc. 7th World Congr. Genet. Appl. Livest. Prod., Montpellier, France. Session 02. Breeding ruminants for meat production. Communication No. 02-92.
- Jensen, J., I. L. Mao, B. Bech Andersen, and P. Madsen. 1991. Genetic parameters of growth, feed intake, feed conversion and carcass composition of dual-purpose bulls in performance testing. J. Anim. Sci. 69:931-939.
- Johnston, D. J., L. L. Benyshek, J. K. Bertrand, M. H. Johnson, and G. M. Weiss. 1992. Estimates of genetic parameters for growth and carcass traits in Charolais cattle. Can. J. Anim. Sci. 72:493-499.
- Kemp, D. J., W. O. Herring, and C. J. Kaiser. 2002. Genetic and environmental parameters for steer ultrasound and carcass traits. J. Anim. Sci. 80:1489-1496.
- Kim, J. J., S. K. Davis, J. O. Sanders, J. W. Turner, R. K. Miller, J. W. Savell, S. B. Smith, and J. F. Taylor. 1998. Estimation of genetic parameters for carcass and palatability traits in *Bos indicus/Bos taurus* cattle. In: Proc. 6th World Congr. Genet. Appl. Livest. Prod., Armidale, NSW, Australia. 25:173-176.
- Koch, R. M. 1978. Selection in beef cattle. III. Correlated response of carcass traits to selection for weaning weight, yearling weight and muscling score in cattle. J. Anim. Sci. 47:142-150.
- Koch, R. M., L. V. Cundiff, and K. E. Gregory. 1982. Heritabilities and genetic, environmental and phenotypic correlations of carcass traits in a population of diverse biological types and their implications in selection programs. J. Anim. Sci. 55:1319-1329.
- Koots, K. R., J. P. Gibson, C. Smith, and J. W. Wilton. 1994. Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. Anim. Breed. Abstr. 62:309-338.

- Kuchida, K., T. Yamagishi, K. Yamaki, and Y. Mizuma. 1990. The estimation of genetic parameters for growth and carcass traits of Japanese Shorthorn. Jpn. J. Zootech. Sci. 61:401-405.
- Lamb, M. A., O. W. Robison, and M. W. Tess. 1990. Genetic parameters for carcass traits in Hereford bulls. J. Anim. Sci. 68:64-69.
- Lee, J. W., S. B. Choi, J. S. Kim, J. F. Keown, and L. D. Van Vleck. 2000. Parameter estimates for genetic effects on carcass traits of Korean native cattle. J. Anim. Sci. 78:1181-1190.
- MacNeil, M. D., D. R. C. Bailey, J. J. Urick, R. P. Gilbert, and W. L. Reynolds. 1991. Heritabilities and genetic correlations for postweaning growth and feed intake of beef bulls and steers. J. Anim. Sci. 69:3183-3189.
- MacNeil, M. D., L. V. Cundiff, C. A. Dinkel, and R. M. Koch. 1984. Genetic correlations among sex-limited traits in beef cattle. J. Anim. Sci. 58:1171-1180.
- Marshall, D.M. 1994. Breed differences and genetic parameters for body composition traits in beef cattle. J. Anim. Sci. 72:2745-2755.
- More O'Ferrall, G. J., R. L. Joseph, P. V. Tarrant, and P. McGloughlin. 1989. Phenotypic and genetic parameters of carcass and meat-quality traits in cattle. Lives. Prod. Sci. 21:35-47.
- Morris, C. A., R. L. Baker, A. H. Carter, the late, and S. M. Hickey. 1990. Evaluation of eleven cattle breeds for crossbred beef production: carcass data from males slaughtered at two ages. Anim. Prod. 50:79-92.
- Morris, C. A., N. G. Cullen, and D. G. McCall. 1999. Genetic and phenotypic relationships among carcass measurements in beef cattle. N. Z. J. of Agric. Res. 42:415-421.
- Moser, D. W., J. K. Bertrand, I. Miztal, L. A. Kriese, and L. L. Benyshek. 1998. Genetic parameter estimates for carcass and yearling ultrasound measurements in Brangus cattle. J. Anim. Sci. 76:2542-2548.
- Mukai, F., K. Oyama, and S. Kohno. 1995. Genetic relationships between performance test traits and field carcass traits in Japanese Black cattle. Livest. Prod. Sci. 44:199-205.
- Nephawe, K. A., L. V. Cundiff, M. E. Dikeman, J. D. Crouse, and L. D. Van Vleck. 2004. Genetic relationships between sex-specific traits in beef cattle: Mature weight, weight adjusted for body condition score, height and body condition score of cows, and carcass traits of their steer relatives. J. Anim Sci. 82:647-653.
- Newman, S., A. Reverter, and D. J. Johnston. 2002. Purebred-crossbred performance and genetic evaluation of postweaning growth and carcass traits in *Bos indicus* x *Bos taurus* crosses in Australia. J. Anim. Sci. 80:1801-1808.

- O'Connor, S. F., J. D. Tatum, D. M. Wulf, R. D. Green, and G. C. Smith. 1997. Genetic effects on beef tenderness in *Bos indicus* composite and *Bos taurus* cattle. J. Anim. Sci. 75:1822-1830.
- Oikawa, T., T. Sanehira, K. Sato, Y. Mizoguchi, H. Yamamoto, and M. Baba. 2000. Genetic parameters for growth and carcass traits of Japanese Black (Wagyu) cattle. Anim. Sci. 71:59-64.
- Pariacote, F., L. D. Van Vleck, and R. E. Hunsley. 1998. Genetic and phenotypic parameters for carcass traits of American Shorthorn beef cattle. J. Anim. Sci. 76:2584-2588.
- Pitchford, W. S., M. P. B. Deland, B. D. Siebert, A. E. O. Malau-Aduli, and C. D. K. Bottema. 2002. Genetic variation in fatness and fatty acid composition of crossbred cattle. J. Anim. Sci. 80:2825-2832.
- Renand, G. 1985. Genetic parameters of French beef breeds used in crossbreeding for young bull production. II. Slaughter performance. Genet. Sel. Evol. 17:265-282.
- Reverter, A., D. J. Johnston, H. U. Graser, M. L. Wolcott, and W. H. Upton. 2000. Genetic analyses of live-animal ultrasound and abattoir carcass traits in Australian Angus and Hereford cattle. J. Anim. Sci. 78:1786-1795.
- Reverter, A., D. J. Johnston, D. Perry, M. E. Goddard, and H. M. Burrow. 2003. Genetic and phenotypic characterization of animal, carcass, and meat quality traits from temperate and tropically adapted beef breeds. 2. Abattoir carcass traits. Aust. J. Agric. Res. 54:119-134.
- Reynolds, W. L., J. J. Urick, D. A. Veseth, D. D. Kress, T. C. Nelsen, and R. E. Short. 1991. Genetic parameters by son-sire covariances for growth and carcass traits of Hereford bulls in a nonselected herd. J. Anim. Sci. 69:1000-1007.
- Riley, D. G., C. C. Chase, Jr., A. C. Hammond, R. L. West, D. D. Johnson, T. A. Olson, and S. W. Coleman. 2002. Estimated genetic parameters for carcass traits of Brahman cattle. J. Anim. Sci. 80:955-962.
- Robinson, D. L., D. M. Ferguson, and J. W. Skerritt. 1998.
 Genetic parameters for beef tenderness, marbling and yield. In: Proc. 6th World Congr. Genet. Appl. Livest.
 Prod., Armidale, NSW, Australia. 25:169-172.
- Shackelford, S. D., L. V. Cundiff, K. E. Gregory, and M. Koomaraie. 1995. Predicting beef carcass cutability. J. Anim. Sci. 73:406-413.
- Shackelford, S. D., M. Koomaraie, L. V. Cundiff, K. E. Gregory, G. A. Rohrer, and J. W. Savell. 1994. Heritabilities and phenotypic and genetic correlations for bovine postrigor calpastatin activity, intramuscular fat content, Warner-Bratzler shear force, retail product yield, and growth rate. J. Anim. Sci. 72:857-863.
- Shanks, B. C., M. W. Tess, D. D. Kress, and B. E. Cunningham. 2001. Genetic evaluation of carcass traits in Simmental-sired cattle at different slaughter end points. J. Anim. Sci. 79:595-604.

- Shelby, C. E., W. R. Harvey, R. T. Clark, J. R. Quesenberry, and R. R. Woodward. 1963. Estimates of phenotypic and genetic parameters in ten years of Miles City R.O.P steer data. J. Anim. Sci. 22:346-353.
- Splan, R. K., L. V. Cundiff, M. E. Dikeman, and L. D. Van Vleck. 2002. Estimates of parameters between direct and maternal genetic effects for weaning weight and direct genetic effects for carcass traits in crossbred cattle. J. Anim. Sci. 80:3107-3111.
- Van Vleck, L. D., A. F. Hakim, L. V. Cundiff, R. M. Koch, J. D. Crouse, and K. G. Boldman. 1992. Estimated breeding values for meat characteristics of crossbred cattle with an animal model. J. Anim. Sci. 70:363-371.
- Veseth, D. A., W. L. Reynolds, J. J. Urick, T. C. Nelsen, R. E. Short, and D. D. Kress. 1993. Paternal half-sib heritabilities and genetic, environmental, and phenotypic correlation estimates from randomly selected Hereford cattle. J. Anim. Sci. 71:1730-1736.
- Vieselmeyer, B. A., R. J. Rasby, B. L. Gwartney, C. R. Calkins, R. A. Stock, and J. A. Gosey. 1996. Use of expected progeny differences for marbling in beef. I. Production traits. J. Anim. Sci. 74:1009-1013.
- Wheeler, T. L., L. V. Cundiff, R. M. Koch, and J. D. Crouse. 1996. Characterization of biological types of cattle (Cycle IV): Carcass traits and longissimus palatability. J. Anim. Sci. 74:1023-1035.
- Wheeler, T. L., L. V. Cundiff, R. M. Koch, M. E. Dikeman, and J. D. Crouse. 1997. Characterization of different biological types of steers (Cycle IV): Wholesale, subprimal, and retail product yields. J. Anim. Sci. 75:2389-2403.
- Wheeler, T. L., L. V. Cundiff, S. D. Shackelford, and M. Koohmaraie. 2001. Characterization of biological types of cattle (Cycle V): Carcass traits and longissimus palatability. J. Anim. Sci. 79:1209-1222.
- Wilson, D. E., R. L. Willham, S. L. Northcutt, and G. H. Rouse. 1993. Genetic parameters for carcass traits estimated from Angus field records. J. Anim. Sci. 71:2365-2370.
- Wilson, L. L., J. R. McCurley, J. H. Ziegler, and J. L. Watkins. 1976. Genetic parameters of live and carcass characters from progeny of polled Hereford sires and Angus-Holstein cows. J. Anim. Sci. 43:569-576.
- Wilson, L. L., J. M. Stout, J. H. Ziegler, M. J. Simpson, H. Varela-Alvarez, M. C. Rugh, and J. L. Watkins. 1971. Heritability of live and carcass characters in a crossbred beef herd. J. Hered. 62:123-125.
- Woodward, B. W., E. J. Pollak, and R. L. Quaas. 1992. Parameter estimation for carcass traits including growth information of Simmental beef cattle using restricted maximum likelihood with a multiple-trait model. J. Anim. Sci. 70:1098-1109.

- Wulf, D. M., J. D. Tatum, R. D. Green, J. B. Morgan, B. L. Golden, and G. C. Smith. 1996. Genetic influences on beef longissimus palatability in Charolais - and Limousin-sired steers and heifers. J. Anim. Sci. 74:2394-2405.
- Yoon, H. B., K. S. Seo, S. D. Kim, Y. M. Cho, S. H. Na, C. J. Park, and G. J. Jeon. 2002. Estimation of genetic parameters for direct genetic effect for carcass traits of Hanwoo (Korean Brown cattle) steers. In: Proc. 7th World Congr. Genet. Appl. Livest. Prod., Montpellier, France. Session 02. Breeding ruminants for meat production. Communication No. 02-89.

							Carcas	s trait ^a						
Author	CW	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
Constant age														
Blackwell et al. (1962)	92	25												
Shelby et al. (1963)	57	57	24	26										
Cundiff et al. (1964)			43	73				40						
Cundiff et al. (1969)									64	46	38			
Dunn et al. (1970) ^b			39	60		42			59					
Dunn et al. (1970)			94	2					65					
Cundiff et al. (1971)	56		50	41		31		28						
Koch (1978)	68		68	28		34			38	94	56			
Benyshek (1981)	48	31	52	40		47		49	45					
Koch et al. (1982)	43		41	56	83	40			58	47	57	63	57	53
MacNeil et al. (1984)	44								45	50				
Hanset et al. (1987)		53												
More O'Ferrall et al. (1989)	32													
Lamb et al. (1990)	31		24	28		33	24	23						
Morris et al. (1990) ^c	28	14	3	30										
Morris et al. (1990)	44	39	37	29										
Kuchida et al. (1990)		15	62	65		86								
MacNeil et al. (1991)			52											
Reynolds et al. (1991)	33	1		1										
Van Vleck et al. (1992)				62		43								
Woodward et al. (1992)						23		18						
Wilson et al. (1993)	31		26	32		26								
Veseth et al. (1993)	38	25		51	37	31								
Gregory et al. (1994)			30			52						50		
Shackelford et al. (1994)												45		
Shackelford et al. (1995)									66	65	62	67	65	69
Gregory et al. (1995)	23	19	25	22		48			28	32	39	47	35	21
Mukai et al. (1995)	39		55	47		52		53						
Barkhouse et al. (1996)						40								
Wheeler et al. (1996)	15	6	56	65	32	73	76							
Hirooka et al. (1996)	37		35	38		40								
Wheeler et al. (1997)									50			62	59	44
Pariacote et al. (1998)	60	49	46	97	45	88	54							
Moser et al. (1998)	59		27	39										
Kim et al. (1998)		39	34	49	30	78								
Hassen et al. (1999)	33		14	15				7						

Table 1. Estimates of heritability (%) for carcass traits measured at, or adjusted to, different end points reported in the scientific literature from 1962 to 2004.

							Carcas	s trait	L					
Author	CW	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
Morris et al. (1999)	48	31		42					48	30	51	33	39	31
Fouilloux et al. (1999) ^d		50												
Lee et al. (2000)		12		17		8								
Oikawa et al. (2000) ^e	15		15	2		49								
Reverter et al. (2000) ^f	31													
Reverter et al. (2000)	54													
Wheeler et al. (2001)	33		84	69	28	57	85							
Shanks et al. (2001)	32		10	26		12		9						
Devitt and Wilton (2001)	47		41	45		35								
Splan et al. (2002)	49		46	58	60	35						58	49	48
Pitchford et al. (2002) ^g	36		26											
Kemp et al. (2002)	48		35	45		42								
Fouilloux et al. (2002)	35													
Yoon et al. (2002)	29	17	44	39		57								
Hoque et al. (2002)	37	19	7	18										
Crews et al. (2003)	48		35	46		54								
Nephawe et al. (2004)	52		46	57	65	46						59	53	52
n	36	18	34	36	8	29	4	8	11	7	6	9	7	7
Unweighted mean	42	28	39	41	48	45	60	28	51	52	51	54	51	45
Constant weight														
Shelby et al. (1963)			22	46										
DuBose and Cartwright (1967)	65													
Cundiff et al. (1969)									42	37	39			
Hinks and Bech Andersen (1969)		97										18	12	35
Cundiff et al. (1971)			53	32		33		35						
Wilson et al. (1971)			18	47		9								
Dinkel and Bush (1973)		15	57	25		31		66						
Wilson et al. (1976)			41	42	0			44						
Benyshek (1981)		35	51	41		46		48						
Renand et al. (1985) ^h		27		33										
Renand et al. (1985)		69												
Benyshek et al. (1988)	19		44	44		38								
Morris et al. (1990) ^c			11	28										
Morris et al. (1990)			42	28										

 Table 1 (continued). Estimates of heritability (%) for carcass traits measured at, or adjusted to, different end points reported in the scientific literature from 1962 to 2004.

							Carcas	ss trait'	1					
Author	CW	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
Arnold et al. (1991)	24		49	46		35								
Jensen et al. (1991)		33										71	89	
Johnston et al. (1992)			24	44		22								
Veseth et al. (1993)		26			38	28								
Hirooka et al. (1996)			33	42		42								
Robinson et al. (1998) ^{g,i}		37	18											
Robinson et al. (1998)		15	29											
Fouilloux et al. (1999)		43												
Reverter et al. $(2000)^{f}$			28									68		
Reverter et al. (2000)			27									36		
Lee et al. (2000)		16		24		1								
Shanks et al. (2001)			14	22		12		12						
Devitt and Wilton (2001)			38	45		43								
Crews and Kemp (2001) ^j	38		46	54		55		42						
Newman et al. (2002) ^{g,k}	35		28									53		
Newman et al. (2002)	40		24									44		
Reverter et al. (2003) ¹	36		41	32		25						50		
Reverter et al. (2003)	39		27	30		17						57		
n	8	11	23	19	2	15	0	6	1	1	1	8	2	1
Unweighted mean	37	38	33	37	19	29	-	41	42	37	39	50	51	35
Constant fat thickness														
Cunningham and Broderick (1969)	50													
Brackalshare at al. (1071) ^m	32		12	40	72	72				50				
Maximized at $(1000)^{\circ}$	17		43	40	12	15				50				
Morris et al. (1990)	1/ 51													
Morris et al. (1990)	51			20		26								
Cilbert et al. (1992)	9		14	20 19		20		55						
Wulf et al. (1995)	20 10	21	14	48 52		20 16	76	55						
$O'_{Component of (1007)}$	10	21		32		10	/0							
O Connor et al. (1997)	10		14	10	2	52								
EIZO et al. (1998)	40		14	42 52	5 14	14								
E120 et al. (1998)	39	0	24	33 19	14	10								
Lee et al. (2000)	22	9		18		10		17						
Denits et al. (2001)	33 57			29 50		13		1/						
Devitt and wilton (2001)	57			52		30								

 Table 1 (continued). Estimates of heritability (%) for carcass traits measured at, or adjusted to, different end points reported in the scientific literature from 1962 to 2004.

							Carcas	ss trait'	1					
Author	CW	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
Fernandes et al. (2002)	30		17	40		37								
Riley et al. (2002)	55	77	63	44	46	44	71	71	50					
n	12	3	6	11	4	12	2	3	1	1	0	0	0	0
Unweighted mean	35	36	29	41	34	30	74	48	50	50	-	-	-	-
Total n	56	32	63	66	14	56	6	17	13	9	7	17	9	8
Minimum	9	1	3	1	0	1	24	7	28	30	38	18	12	21
Maximum	92	97	94	97	83	88	85	71	66	94	62	71	89	69
Total mean	40	32	36	40	40	37	64	36	51	50	49	52	51	44

Table 1 (continued). Estimates of heritability (%) for carcass traits measured at, or adjusted to, different end points reported in the scientific literature from 1962 to 2004.

^aCW=carcass weight, DP=dressing percentage, FT=backfat thickness, LA=longissimus muscle area,

KF=kidney, pelvic, and heart fat percentage, MS=marbling score, YG=yield grade, ER=predicted percentage of retail product, RW=retail product weight, FW=fat weight, BW=bone weight, RP=actual retail product percent, FP=fat percent, BP=bone percent.

^bFirst row of estimates for Dunn et al. (1970) is for purebreds; second row is for crossbreds.

^cFirst row of estimates for Morris et al. (1990) is for animals slaughtered at 20 mo of age; second row is for animals slaughtered at 31 mo of age.

^dAge-constant estimate for Fouilloux et al. (1999) is for Limousin; weight-constant estimate is for Charolais.

^eLA and MS without covariate (nonsignificant), and DP and FT heritabilities are age-constant estimates.

^fFirst row of estimates for Reverter et al. (2000) is for Angus; second row is for Hereford.

^gFT is fat depth over the rump at the P8 site.

^hFirst and second rows of estimates for Renand et al. (1985) are for two different stations.

¹First row of estimates for Robinson et al. (1998) is for tropical breeds; second row is for temperate breeds.

^jAnimals slaughtered when live weight and fat depth reached minimums of 500 kg and 7mm, respectively.

^kFirst row of estimates for Newman et al. (2002) is for purebreds; second row is for crossbreds.

¹First row of estimates for Reverter et al. (2003) is for tropical breeds; second row is for temperate breeds.

^mAnimals slaughtered at a constant quality-grade end point.

ⁿFirst row of estimates for Elzo et al. (1998) is for Angus; second row is for Brahman.

						Ca	rcass tra	ait ^b					
-	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
CW													
Shelby et al. (1963)	.35	.47	.15										
Cundiff et al. (1971)		.34	.66		.23		33	.94	.80	.86			
Koch (1978)		.95	.02		33			.80	.90	.57			
Koch et al. (1982)		.08	.44	.22	.25			.81	.45	.71	11	.13	20
Morris et al. (1990) ^c		85	.09										
Morris et al. (1990)		30	.09										
Lamb et al. (1990)		.14	.68		.64								
Reynolds et al. (1991)	.04												
Veseth et al. (1993)	.32		.80	.21	.38								
Wilson et al. (1993)		.38	.47		06								
Mukai et al. (1995)		.39	.23		.36		08						
Gregory et al. (1995)		.13	.66		.31			.76	.51	.75	12	.08	.18
Hirooka et al. (1996)		.39	.23		05								
Wheeler et al. (1996)		.24	.25		03	.18							
Wheeler et al. (1997)								.73			.19	19	.08
Moser et al. (1998)		10	.12										
Pariacote et al. (1998)	.65	22	.70	30	10	39							
Morris et al. (1999)	.52		.75					.98	.54	.85	20	.06	21
Hassen et al. (1999)		.25	.76				.24						
Shanks et al. (2001)		37	.49		.30		21						
Devitt and Wilton (2001)		.15	.42		32								
Wheeler et al. (2001)		.06	.11		.44	.23							
Kemp et al. (2002)		.17	.58		.27								
Hoque et al. (2002)	.62	.42	.82										
Yoon et al. (2002)	.19	02	.65		.20								
Minimum	.04	85	.02	30	33	39	33	.73	.45	.57	20	19	21
Maximum	.65	.95	.82	.22	.64	.23	.24	.98	.90	.86	.19	.13	.18
Unweighted mean	.38	.13	.44	.04	.16	.01	10	.84	.64	.75	06	.02	04
DP													
Shelby et al. (1963)		61	40										
Kuchida et al. (1903)		.01	.40		- 18								
Veseth et al. (1990)		.50	- 11	- 06	18								
Pariacote et al (1993)		- 16	11	00	.00	- 56							
Kim et al (1998)		.10	.17	.10	- 20	.50							
Morris et al. (1999)			40		.20			57	35	18	24	09	- 58
Lee et al. (2000)			.+0		- 88			.51		.10	.27	.07	.50
Oikawa et al. (2000)		.02	.92		-1.0								

Table 2. Estimates of genetic correlations among carcass traits measured at, or adjusted to, constant age or constant time-on-feed reported in the scientific literature^a.

						Ca	rcass tra	ait ^b					
	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
Hoque et al. (2002)		.52	.68										
Yoon et al. (2002)		.31	07		05								
Minimum		16	11	10	-1.0	56	-	.57	.35	.18	.24	.09	58
Maximum		.61	.92	06	.08	56	-	.57	.35	.18	.24	.09	58
Unweighted mean		.28	.36	08	32	56	-	.57	.35	.18	.24	.09	58
FT													
Shelby et al. (1963)			.30										
Cundiff et al. (1964)			.08				95						
Dunn et al. (1970)			27		1.0			24					
Koch (1978)			.03		.73			.65	.95	.30			
Koch et al. (1982)			44	.10	.16			34	.74	30	74	.78	52
Morris et al. (1990) ^c			07										
Morris et al. (1990)			07										
Lamb et al. (1990)			04		.73								
Kuchida et al. (1990)			11		42								
Wilson et al. (1993)			06		13								
Gregory et al. (1994)					.32						76		
Mukai et al. (1995)			33		04		76						
Gregory et al. (1995)			06		.44			48	.80	05	76	.82	27
Hirooka et al. (1996)			12		12								
Wheeler et al. (1996)			43		.01	.86							
Wheeler et al. (1997)								29			62	.66	53
Moser et al. (1998)			05										
Pariacote et al. (1998)			31	21	.26	.67							
Kim et al. (1998)					.12								
Hassen et al. (1999)			30				74						
Oikawa et al. (2000)			-1.0		.15								
Shanks et al. (2001)			06		.17		29						
Devitt and Wilton (2001)			.02		.30								
Wheeler et al. (2001)			42		.42	.89							
Kemp et al. (2002)			20		.38								
Hoque et al. (2002)			.38										
Yoon et al. (2002)			28		.17								
Minimum			-1.0	21	13	.67	95	48	.74	30	76	.66	53
Maximum			.38	.10	1.0	.89	29	.65	.95	.30	62	.82	27
Unweighted mean			16	06	.24	.81	69	14	.83	02	72	.75	44

Table 2 (continued). Estimates of genetic correlations among carcass traits measured at, or adjusted to, constant age or constant time-on-feed reported in the scientific literature^a.

						Ca	rcass tra	ait ^b					
	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
LA													
Cundiff et al. (1964)							.28						
Dunn et al. (1970)					38			.95					
Koch (1978)								02	.10	36			
Koch et al. (1982)				.01	14			.72	28	.35	.53	48	04
Lamb et al. (1990)					.57								
Kuchida et al. (1990)					.43								
Van Vleck et al. (1992)					40								
Veseth et al. (1993)				.36	.51								
Wilson et al. (1993)					04								
Mukai et al. (1995)					.02		.75						
Gregory et al. (1995)					02			.86	.07	.31	.32	26	25
Hirooka et al. (1996)					.12								
Wheeler et al. (1996)					37	79							
Wheeler et al. (1997)								.67			.76	75	.37
Pariacote et al. (1998)				31	17	85							
Kim et al. (1998)					.49								
Morris et al. (1999)								.74	.02	.59	08	51	39
Hassen et al. (1999)							.57						
Lee et al. (2000)					.47								
Oikawa et al. (2000)					.83								
Shanks et al. (2001)					.46		.75						
Devitt and Wilton (2001)					61								
Wheeler et al. (2001)					36	72							
Kemp et al. (2002)					10								
Yoon et al. (2002)					10								
Minimum				31	61	85	.28	02	28	36	08	75	39
Maximum				.36	.83	72	.75	.95	.10	.59	.76	26	.37
Unweighted mean				.02	.06	79	.59	.65	02	.22	.38	50	08
KF													
Koch et al. (1982)					.29			04	.48	05	43	.46	33
Veseth et al. (1993)					.59								
Pariacote et al. (1998)					.10	.22							
Kim et al. (1998)					.22								
Minimum					.10	.22	-	04	.48	05	43	.46	33
Maximum					.59	.22	-	-04	.48	05	43	.46	33
Unweighted mean					.30	.22	-	04	.48	05	43	.46	33

Table 2 (continued). Estimates of genetic correlations among carcass traits measured at, or adjusted to, constant age or constant time-on-feed reported in the scientific literature^a.

						Car	rcass tra	lit ^b					
	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
MS													
Dunn et al. (1970)								48					
Cundiff et al. (1971)								13	.82	27			
Koch (1978)									.33				
Koch et al. (1982)								02	.42	.15	37	.34	04
Lamb et al. (1990)						.32	36						
Woodward et al. (1992)							12						
Gregory et al. (1994)											56		
Mukai et al. (1995)							.09						
Gregory et al. (1995)								12	.65	.08	60	.66	28
Wheeler et al. (1996)						.19							
Wheeler et al. (1997)								24			36	.32	01
Pariacote et al. (1998)						.26							
Shanks et al. (2001)							.01						
Wheeler et al. (2001)						.60							
Minimum						.19	36	48	.33	27	60	.32	28
Maximum						.60	.09	02	.82	.15	36	.66	01
Unweighted mean						.34	10	20	.56	01	47	.44	11
YG													
Wheeler et al. (1997)							-	41	-	-	76	.78	53
ER													
Cundiff et al. (1971)								08	85	.17	-	-	-
RW													
Cundiff et al. (1969)									55	98			
Koch (1978)									46	.90			
Koch et al. (1982)									- 12	72	46	- 44	03
Gregory et al. (1995)									16	.54	.56	59	.19
Wheeler et al. (1997)											.80	77	.30
Morris et al. (1999)									28	79	17	- 22	- 29
Minimum									16	.54	.17	77	29
Maximum									.55	.98	.80	22	.30
Unweighted mean									.20	.76	.50	51	.06
FW													
Cundiff et al. (1969)										.38			
Koch (1978)										.22			

Table 2 (continued). Estimates of genetic correlations among carcass traits measured at, or adjusted to, constant age or constant time-on-feed reported in the scientific literature^a.

						Ca	rcass tra	ait ^b					
	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
Koch et al. (1982)										.03	91	.94	51
Gregory et al. (1995)										.35	88	.90	07
Morris et al. (1999)										.39	85	.94	28
Minimum										.03	91	.90	51
Maximum										.39	85	.94	07
Unweighted mean										.27	88	.93	29
BW													
Koch et al. (1982)											.14	25	.54
Gregory et al. (1995)											20	.03	.79
Morris et al. (1999)											34	02	.48
Minimum											34	25	.48
Maximum											.14	.03	.79
Unweighted mean											13	08	.60
RP													
Koch et al. (1982)												98	.35
Gregory et al. (1995)												98	.08
Wheeler et al. (1997)												98	.47
Morris et al. (1999)												94	21
Minimum												98	21
Maximum												94	.47
Unweighted mean												97	.17
FP													
Koch et al. (1982)													51
Gregory et al. (1995)													14
Wheeler et al. (1997)													63
Morris et al. (1999)													19
Minimum													63
Maximum													14
Unweighted mean													37

Table 2 (continued). Estimates of genetic correlations among carcass traits measured at, or adjusted to, constant age or constant time-on-feed reported in the scientific literature^a.

^a"-" indicates no estimates found.

^bCW=carcass weight, DP=dressing percentage, FT=backfat thickness, LA=longissimus muscle area, KF=kidney, pelvic, and heart fat percentage, MS=marb ling score, YG=yield grade, ER=predicted percentage of retail product, RW=retail product weight, FW=fat weight, BW=bone weight, RP=actual retail product percent, FP=fat percent, BP=bone percent. ^cFirst row of estimates for Morris et al. (1990) is for animals slaughtered at 20 months of age; second row is for animals slaughtered at 31 months of age.

						Car	cass tra	ait ^b					
	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
CW													
Benyshek et al. (1988)		.04	07		.35								
Arnold et al. (1991)		.36	.09		.33								
Reverter et al. (2003) ^c		39	.45		15						.06		
Reverter et al. (2003) <i>Minimum</i>		42 - 42	28	_	20 - 20	_	_	_	_	_	.16	_	_
Maximum	_	.36	20 .45	-	.35	_	-	_	-	_	.00	-	_
Unweighted mean	-	10	.05	-	.08	-	-	-	-	-	.11	-	-
0													
DP													
Dinkel and Busch (1973)		.25	.47		.50		23						
Renand et al. (1985)			.47										
Jensen et al. (1991)											.04	.01	
Lee et al. (2000)			.91		03								
Minimum		.25	.47	-	03	-	23	-	-	-	.04	.01	-
Maximum		.25	.91	-	.50	-	23	-	-	-	.04	.01	-
Unweighted mean		.25	.62	-	.24	-	23	-	-	-	.04	.01	-
FT													
Dinkel and Busch (1973)			59		.38		75						
Wilson et al. (1976)			47		.37		95						
Benyshek et al. (1988)			52		.08								
Arnold et al. (1991)			37		.19								
Reverter et al. $(2000)^d$											74		
Reverter et al. (2000)											50		
Shanks et al. (2001)			03		.18		53						
Devitt and Wilton (2001)			03		.41								
Reverter et al. (2003) ^c			13		.12						65		
Reverter et al. (2003)			10		.13						29		
Minimum			59	-	.08	-	95	-	-	-	74	-	-
Maximum			03	-	.41	-	53	-	-	-	29	-	-
Unweigniea mean			28	-	.23	-	74	-	-	-	55	-	-
LA													
Dinkel and Busch (1973)					17		.72						
Wilson et al. (1976)					38		.87						
Benyshek et al. (1988)					.04								
Arnold et al. (1991)					01								
Lee et al. (2000)					.39								
Shanks et al. (2001)					.26		.75						
Devitt and Wilton (2001)					35								

Table 3. Estimates of genetic correlations among carcass traits measured at, or adjusted to, constant weight reported in the scientific literature^a.

						Ca	rcass tra	ait ^b					
	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
Reverter et al. (2003) ^c					14						.44		
Reverter et al. (2003)					23						.25		
Minimum				-	38	-	.72	-	-	-	.25	-	-
Maximum Unweighted mean				_	.39	_	.87 78	_	_	_	.44	_	_
Onweignieu meun				-	07	-	.70	-	-	-	.33	-	-
KF					-	-	-	-	-	-	-	-	-
MS													
Cundiff et al. (1971)								89	.98	78			
Dinkel and Busch (1973)							.26						
Wilson et al. (1976)							20						
Shanks et al. (2001)							.05						
Reverter et al. $(2003)^{c}$											39		
Reverter et al. (2003)											56		
Minimum						-	20	89	.98	78	56	-	-
Maximum						-	.26	89	.98	78	39	-	-
Unweighted mean						-	.04	89	.98	78	48	-	-
YG							-	-	-	-	-	-	-
ER													
Cundiff et al. (1971)								.80	-	.89	-	-	-
RW													
Cundiff et al. (1969)									90	.96	-	-	-
FW										00			
Cundiff et al. (1969)										99	-	-	-
BW											-	-	-
RP												00	
Jensen et al. (1991)												92	-
FP													-

Table 3 (continued). Estimates of genetic correlations among carcass traits measured at, or adjusted to, constant weight reported in the scientific literature^a.

^a"-" indicates no estimates found.

^bCW=hot carcass weight, DP=dressing percentage, FT=backfat thickness, LA=longissimus muscle area, KF=kidney, pelvic, and heart fat percentage, MS=marbling score, YG=yield grade, ER=predicted percentage of retail product, RW=retail product weight, FW=fat weight, BW=bone weight, RP=actual retail product percent, FP=fat percent, BP=bone percent. ^cFirst row of estimates for Reverter et al. (2003) is for temperate breeds; second row is for tropical breeds. ^dFirst row of estimates for Reverter et al. (2000) is for Angus; second row is for Hereford.

						Car	rcass tra	uit ^b					
	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
CW													
Johnston et al. (1992)			.45		31								
Gilbert et al. (1993)					.55								
Wulf et al. (1996)					.67								
Elzo et al. (1998) ^c		.06	.45	03	15								
Elzo et al. (1998)		01	.40	.05	.11								
Shanks et al. (2001)			.57		.20		05						
Devitt and Wilton (2001)			.69		03								
Riley et al. (2002)	.47	.60	.52	.27	.39	.56	.55						
Fernandes et al. (2002)		.17	.62		10								
Minimum	.47	01	.40	03	31	.56	05	-	-	-	-	-	-
Maximum	.47	.60	.69	.27	.67	.56	.55						
Unweighted mean	.47	.21	.53	.10	.15	.56	.25	-	-	-	-	-	-
DP													
Wulf et al. (1996)					.68								
Lee et al. (2000)			11		99								
Riley et al. (2002)		.42	.02	.24	.35	.48	48						
Minimum		.42	11	.24	99	.48	48	-	-	-	-	-	-
Maximum		.42	.02	.24	.68	.48	48	-	-	-	-	-	-
Unweighted mean		.42	05	.24	.01	.48	48	-	-	-	-	-	-
FT													
Brackelsberg et al. (1971)			09	.87	.62				.97				
Gilbert et al. (1993)					83		98						
Elzo et al. (1998) ^c			.02	02	.05								
Elzo et al. (1998)			03	.03	.03								
Riley et al. (2002)			.02	.63	.56	.93	93						
Fernandes et al. (2002)			22		19								
Minimum			22	02	19	.93	98	-	.97	-	-	-	-
Maximum			.02	.87	.62	.93	93	-	.97	-	-	-	-
Unweighted mean			06	.38	.04	.93	96	-	.97	-	-	-	-
LA													
Brackelsberg et al. (1971)				35	12				53				
Johnston et al. (1992)					24								
Gilbert et al. (1993)					.63								
Wulf et al. (1996)					.13								
Elzo et al. (1998) ^c				02	11								
Elzo et al. (1998)				.03	01								

Table 4. Estimates of genetic correlations among carcass traits measured at, or adjusted to, constant backfat thickness reported in the scientific literature^a.

	Carcass trait ^b												
	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
Lee et al. (2000)					.20								
Shanks et al. (2001)					.48		.81						
Devitt and Wilton (2001)					37								
Riley et al. (2002)				.18	.44	.26	.23						
Fernandes et al. (2002)					48								
Minimum				35	48	.26	.23	-	53	-	-	-	-
Maximum U				.18	.63	.26	.81	-	53	-	-	-	-
Unweightea mean				04	.05	.26	.52	-	53	-	-	-	-
KF													
Brackelsberg et al. (1971)					.63				.81				
Elzo et al. (1998) ^c					.07								
Elzo et al. (1998)					.03								
Riley et al. (2002)					.27	.60	67						
Minimum					.03	.60	67	-	.81	-	-	-	-
Maximum					.63	.60	67	-	.81	-	-	-	-
Unweighted mean					.25	.60	67	-	.81	-	-	-	-
MS													
Brackelsberg et al. (1971)									.54				
Gilbert et al. (1993)							.63						
Wulf et al. (1996)						.04	0.5						
Shanks et al. (2001) Bilow et al. (2002)						15	.06						
Minimum						.43 04	45 - 43	-	54	-	-	-	-
Maximum						.45	.63	-	.54	-	-	-	-
Unweighted mean						.25	.09	-	.54	-	-	-	-
YG													
Riley et al. (2002)							99	-	-	-	-	-	-
ER								-	-	-	-	-	-
RW									-	-	-	-	-
FW										-	-	-	-
BW											_	_	_
рр													
ĸr												-	-
FP													-

Table 4 (continued). Estimates of genetic correlations among carcass traits measured at, or adjusted to, constant backfat thickness reported in the scientific literature^a.

^a"-" indicates no estimates found.

^bCW=carcass weight, DP=dressing percentage, FT=backfat thickness, LA=longissimus muscle area, KF=kidney, pelvic, and heart fat percentage, MS=marbling score, YG=yield grade, ER=predicted percentage of retail product, RW=retail product weight, FW=fat weight, BW=bone weight, RP=actual retail product percent, FP=fat percent, BP=bone percent. ^cFirst row of estimates for Elzo et al. (1998) is for Angus; second row is for Brahman.

		Carcass trait ^b											
-	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
CW													
Minimum	.04	85	28	30	33	39	33	.73	.45	.57	20	19	21
Maximum	.65	.95	.82	.27	.67	.56	.55	.98	.90	.86	.19	.13	.18
Mean	.40	.11	.41	.07	.14	.15	.02	.84	.64	.75	003	.02	04
DP													
Minimum		16	11	10	-1.0	56	48	.57	.35	.18	.04	.01	58
Maximum		.61	.92	.24	.68	.48	23	.57	.35	.18	.24	.09	58
Mean		.29	.36	.03	14	04	36	.57	.35	.18	.14	.05	58
FT													
Minimum			-1.0	21	19	.67	98	48	.74	30	76	.66	53
Maximum			.38	.87	1.0	.93	29	.65	.97	.30	29	.82	27
Mean			17	.23	.24	.84	76	14	.87	02	63	.75	44
LA										_			
Minimum				35	61	85	.23	02	53	36	08	75	39
Maximum				.36	.83	.26	.87	.95	.10	.59	.76	26	.37
Mean				01	.03	53	.64	.65	12	.22	.37	50	08
KE													
Kr					02	22	67	04	10	05	12	16	22
Minimum					.05	.22	07	04	.48	05	45	.40	33
Maximum					.05	.00	07	04	.81	05	45	.40	33
Mean					.28	.41	07	04	.03	05	43	.40	55
MS													
Minimum						04	- 43	- 89	33	- 78	- 60	32	- 28
Maximum						60	63	- 02	98	15	- 36	66	- 01
Mean						31	- 001	- 31	.20 62	- 21	- 47	.00	- 11
						101	1001	101					
YG													
Minimum							99	41	-	-	76	.78	53
Maximum							99	41	-	-	76	.78	53
Mean							99	41	-	-	76	.78	53
ER													
Minimum								08	85	.17	-	-	-
Maximum								.80	85	.89	-	-	-
Mean								.36	85	.53	-	-	-

Table 5. Minimum, maximum and unweighted average of estimates of genetic correlations among carcass traits for all end points published in the scientific literature from 1963 to 2003^a.

	Carcass trait ^b												
	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
RW													
Minimum									90	.54	.17	77	29
Maximum									.55	.98	.80	22	.30
Mean									.02	.80	.50	51	.06
FW													
Minimum										99	91	.90	51
Maximum										.39	85	.94	07
Mean										.06	88	.93	29
BW													
Minimum											34	25	.48
Maximum											.14	.03	.79
Mean											13	08	.60
RP													
Minimum												98	21
Maximum												94	.47
Mean												97	.17
FP													
Minimum													63
Maximum													14
Mean													37

Table 5 (continued). Minimum, maximum and unweighted average of estimates of genetic correlations among carcass traits for all end points published in the scientific literature from 1963 to 2003^a.

^a"-" indicates no estimates found.

^bCW=carcass weight, DP=dressing percentage, FT=backfat thickness, LA=longissimus muscle area, KF=kidney, pelvic, and heart fat percentage, MS=marbling score, YG=yield grade, ER=predicted percentage of retail product, RW=retail product weight, FW=fat weight, BW=bone weight, RP=actual retail product percent, FP=fat percent, BP=bone percent.