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Review

Heritability estimates for carcass traits of cattle: a review

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ABSTRACT. We present estimates of heritability for carcass traits of cattle published in the scientific literature. Seventy-two papers published from 1962 to 2004, which reported estimates of heritability for carcass traits, were reviewed. The unweighted means of estimates of heritability for 14 carcass traits by slaughter end point (age, weight, and fat depth) were calculated. Among the three end points, carcass weight, backfat thickness, longissimus muscle area, and marbling score were the carcass traits with the most estimates of heritability ($56 \leq n \leq 66$). The averages for these traits indicate that they are similarly and moderately heritable (0.40, 0.36, 0.40, and 0.37, respectively). However, heritability estimates for most traits varied greatly, which could be due to differences in breed groups, methods of estimation, effects in the model, number of records, measurement errors, sex, and management. Few studies have compared heritability estimates for carcass traits adjusted to different end points. Results from such studies have been inconsistent, although some studies revealed that heritability estimates for several carcass traits are sensitive to the covariate included in the model for the end point, implying that direct response to selection would be different for some traits depending on slaughter end point. The effect of different end points on estimates of heritability for many carcass traits has not been studied.

Key words: Cattle, Carcass traits, Heritability, Slaughter end points

INTRODUCTION

An exhaustive review of estimates of heritability for a broad spectrum of beef production traits published in the scientific literature 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 heritability 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 heritability for some additional carcass traits, but only for cattle reared under U.S. conditions and, basically, estimates presented were on an age-constant or time-in-feedlot-constant basis. In addition, because of the limited number of estimates for the additional traits at that time, averages of estimates of heritability for several carcass traits were based on only one to three observations. Neither of these two reviews focused on the effect of end point on estimates of heritability.

During the last ten years, as a consequence of the increased interest of many beef producers in carcass yield and quality to satisfy consumer demand, numerous studies of carcass traits have published estimates of heritability, doubling, at least, the number of estimates for many carcass traits. We reviewed estimates of heritability for carcass traits published in the scientific literature. Because animals are slaughtered at, or carcass traits are adjusted to, different end points, the effects of age, weight, and finish end points on such estimates were also examined.

MATERIAL AND METHODS

Seventy-two papers published in the scientific literature from 1962 to 2004 that reported estimates of heritability for carcass traits of cattle were reviewed. The number and the unweighted means of estimates of heritability for each carcass trait by slaughter end point (slaughter age, slaughter weight, backfat thickness) were calculated. The number, the unweighted means, and the ranges of estimates of heritability over the three different end points were also calculated. Standard errors were not reported for many heritability estimates and several different methods of estimation were used (e.g., animal model, son on sire regression, paternal half-sib covariance). Therefore, weighted means of heritability were not calculated. Papers that did not specify at which end point animals were slaughtered or to which end point carcass traits were adjusted were not included in this review. Traits included in this review were carcass weight, dressing percentage, backfat thickness, longissimus muscle area, kidney, pelvic, and heart fat percentage, marbling score, yield grade, predicted percentage of retail product, retail product weight, fat weight, bone weight, actual retail product percentage, fat percentage, and bone percentage.

RESULTS

Estimates of heritability, number of estimates and unweighted mean estimates of heritability for 14 carcass traits measured at, or adjusted to, constant age, weight or backfat thickness end points reported in the scientific literature from 1962 to 2004 were recorded (Table 1). References repeated in two or three categories compared estimates of heritability adjusted to two or three different end points; otherwise, only one kind of adjustment was performed. The

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.

Author	Carcass trait[a]													
	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)[c]			94	2		-15			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)[d]	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						
Morris et al. (1999)	48	31		42					48	30	51	33	39	31
Fouilloux et al. (1999)[e]		50												
Lee et al. (2000)		12		17		8								
Oikawa et al. (2000)[f]	15		15	2		49								
Reverter et al. (2000)[g]	31													
Reverter et al. (2000)	54													
Wheeler et al. (2001)	33		84	69	28	57	85							

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Table 1. Continued

Author	Carcass trait[a]													
	CW	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
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)[h]	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[c]	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 Busch (1973)		15	57	25		31		66						
Wilson et al. (1976)			41	42	0			44						
Benyshek (1981)		35	51	41		46		48						
Renand (1985)[i]		27		33										
Renand (1985)		69												
Benyshek et al. (1988)	19		44	44		38								
Morris et al. (1990)[d]			11	28										
Morris et al. (1990)			42	28										
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)[h,j]		37	18											
Robinson et al. (1998)		15	29											
Fouilloux et al. (1999)		43												
Reverter et al. (2000)[g]			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 Jr. and Kemp (2001)[k]	38		46	54		55		42						
Newman et al. (2002)[h,l]	35		28									53		
Newman et al. (2002)	40		24									44		

Continued on next page

Table 1. Continued

Author	Carcass trait[a]													
	CW	DP	FT	LA	KF	MS	YG	ER	RW	FW	BW	RP	FP	BP
Reverter et al. (2003)[m]	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)	52													
Brackelsberg et al. (1971)[n]			43	40	72	73				50				
Morris et al. (1990)[d]	17													
Morris et al. (1990)	51													
Johnston et al. (1992)	9			38		26								
Gilbert et al. (1993)	26		14	48		28		55						
Wulf et al. (1996)	10	21		52		16	76							
O'Connor et al. (1997)						52								
Elzo et al. (1998)[o]	46		14	42	3	14								
Elzo et al. (1998)	39		24	53	14	16								
Lee et al. (2000)		9		18		10								
Shanks et al. (2001)	33			29		13		17						
Devitt and Wilton (2001)	57			52		30								
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[c]	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

[a]CW = 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 percentage; FP = fat percentage; BP = bone percentage.
[b]First row of estimates for Dunn et al. (1970) is for purebreds; second row is for crossbreds.
[c]The single negative estimate for MS was not used to calculate the number of estimates, range and unweighted means.
[d]First 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.
[e]Age-constant estimate for Fouilloux et al. (1999) is for Limousin; weight-constant estimate is for Charolais.
[f]LA and MS without covariate (nonsignificant), and DP and FT heritabilities are age-constant estimates.
[g]First row of estimates for Reverter et al. (2000) is for Angus; second row is for Hereford.
[h]FT is fat depth over the rump at the P8 site.
[i]First and second rows of estimates for Renand (1985) are for two different stations.
[j]First row of estimates for Robinson et al. (1998) is for tropical breeds; second row is for temperate breeds.
[k]Animals slaughtered when live weight and fat depth reached minimums of 500 kg and 7 mm, respectively.
[l]First row of estimates for Newman et al. (2002) is for purebreds; second row is for crossbreds.
[m]First row of estimates for Reverter et al. (2003) is for tropical breeds; second row is for temperate breeds.
[n]Animals slaughtered at a constant quality-grade end point.
[o]First row of estimates for Elzo et al. (1998) is for Angus; second row is for Brahman.

exception is Fouilloux et al. (1999), who reported estimates of heritability for dressing percentage at constant age and at constant weight, but estimates were for different breeds (Limousin and Charolais, respectively). The age-constant category includes estimates of heritability on an age-constant or time-on-feed-constant basis. Those in the weight-constant category are estimates of heritability that were adjusted for weight at slaughter or for carcass weight.

Carcass weight

Carcass weight had many estimates of heritability (N = 56). Estimates were adjusted for age, weight, or backfat thickness, with averages of 0.42 (N = 36), 0.37 (N = 8) and 0.35 (N = 12), respectively. Age-constant estimates of heritability were greater than weight- and backfat thickness-constant estimates; although fewer estimates were on a weight- and backfat thickness-constant basis. Mean estimate across end points was 0.40, which indicates that carcass weight would respond well to selection if selection were practiced. Large variation existed in estimates of heritability. Range of estimates was from 0.09, obtained by REML, for a backfat thickness adjustment (Johnston et al., 1992) to 0.92, obtained by Henderson's Method 2, for 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 Benyshek et al. (1988) for Hereford cattle reported low heritability 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, respectively.

Only three studies that compared estimates of heritability for carcass weight adjusted for age or for backfat thickness were found. The differences in estimates of heritability obtained with these two adjustments were variable across studies. For crossbred steers representing 11 cattle breeds that were slaughtered at 20 months of age, Morris et al. (1990) found that hot carcass weight adjusted to a constant age had a larger estimate of heritability than hot carcass weight adjusted to a constant backfat thickness (0.28 *vs* 0.17). In a recent study, Devitt and Wilton (2001), using crossbred steers, also obtained differences between age- and backfat thickness-constant estimates of heritability for carcass weight, but the estimate adjusted for backfat thickness 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 backfat thickness (522 *vs* 1,051 kg^2) could mainly explain this difference, because phenotypic variances were not much different with these two adjustments. In contrast, Shanks et al. (2001) found no significant difference between age- and backfat thickness-constant heritabilities (0.32 *vs* 0.33) for carcass weight of Simmental and percentage Simmental steers.

Dressing percentage

The number (32) of heritability estimates for dressing percentage found in the literature was about half of that found for carcass weight. Most estimates of heritability were adjusted for age (N = 18), which had a mean of 0.28. Fewer estimates adjusted for backfat thickness (N = 3) had a mean of 0.36. Eleven weight-constant heritability estimates had a mean of 0.38. Average estimate of heritability was 0.32 across end points, indicating that dressing percentage is lowly to moderately heritable, which suggests that response to selection would be possible. Estimates of heritability for dressing percentage 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 (1985), respectively, revealing significant variability among estimates, which may reflect the relatively limited number of records in most studies.

Few studies compared estimates of heritability for dressing percentage adjusted for different end points. Veseth et al. (1993), with paternal half-sib analyses, obtained similar estimates of heritability with age (0.25) or weight (0.26) as covariates in the model. Also, Koots et al. (1994), in their review of heritability estimates, found that weighted average of heritability estimates for dressing percentage were about the same on a weight- or age-constant basis (0.38 and 0.39, respectively). Similarly, in a recent study (Lee et al., 2000), estimates of heritability to age- and weight-constants were similar (0.12 and 0.16, respectively), but somewhat larger than estimates of heritability to backfat thickness-constant (0.09).

Adjusted backfat thickness

Adjusted backfat thickness also had many estimates of heritability (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 heritability were to a backfat thickness-constant (N = 6). Averages of estimates of heritability 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 heritability ranged from 0.03 (Morris et al., 1990; REML analysis) 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 heritability were small (0.07, 0.14 and 0.15) by Hoque et al. (2002), Gilbert et al. (1993) and Oikawa et al. (2000), respectively, 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 heritability (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., 1996; Shanks et al., 2001; Devitt and Wilton, 2001) compared estimates of heritability for backfat thickness adjusted for age or weight. All agreed that estimates were similar regardless of the type of covariate included in the model.

Longissimus muscle area

Longissimus muscle area was the carcass trait with the most heritability estimates (N = 66) reported, reflecting its relative importance and easy measurement. Averages of heritability estimates were 0.41 (N = 36), 0.37 (N = 19) and 0.41 (N = 11) with age, weight or backfat thickness constants, respectively. Average estimates of heritability (0.40) over all end points indicate that longissimus muscle area is moderately heritable and genetic gain might be achieved through selection. However, estimates of heritability varied significantly among studies. Estimates ranged from almost the minimum (0.01; Reynolds et al., 1991, Hereford bulls, son-sire regression analysis) to almost the maximum for heritability (0.97; Pariacote et al., 1998, American Shorthorn steers, REML analysis).

Estimates of heritability for longissimus muscle area adjusted for age or weight reported by Benyshek (1981) for Hereford steers and heifers, by Morris et al. (1990) for crossbred steers, and by 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 heritability estimate for longissimus muscle area increased from 0.26 to 0.46 when an adjustment was made for slaughter weight instead of age. In a study using Hanwoo (Korean native) cattle, Lee et al. (2000) reported that the age- (0.17) and backfat thickness-constant (0.18) estimates of heritability were slightly smaller than the weight-constant estimate (0.24). Similar differences between weight- and backfat thickness-adjusted heritability 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 backfat thickness-constant heritabilities were estimated to be slightly larger than the weight-constant heritability (0.26 and 0.29 *vs* 0.22, respectively). Larger estimates of heritability when adjusted to a weight-constant (0.45) or a backfat thickness-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 larger reduction in the heritability estimate for longissimus muscle area (0.45 *vs* 0.36).

Kidney, pelvic, and heart fat percentage

Comparatively few estimates of heritability (N = 14) were found in the literature for kidney, pelvic, and heart fat percentage relative to carcass traits previously discussed. 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 backfat thickness with an average of 0.34. Average over the 14 studies was 0.40. Estimates of heritability ranged from 0.00 (Wilson et al., 1976) on a weight-constant basis to 0.83 (Koch et al., 1982) on an age-constant basis. Low, moderate and high estimates of heritability were found in the literature. Elzo et al. (1998) and Wheeler et al. (2001) reported heritability 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 one genetic study (Veseth et al., 1993) contrasted estimates of heritability for kidney, pelvic, and heart fat percentage adjusted for different covariates with quite similar estimates when age (0.37) or weight (0.38) were included as covariates in a model based on paternal half-sibs.

Marbling score

Marbling score is one of the most genetically evaluated carcass traits. Age-, weight- and backfat thickness-constant estimates had averages of 0.45 (N = 29), 0.29 (N = 15) and 0.30

(N = 12), respectively. Average of estimates across end points was 0.37. Only one out-of-range estimate (-0.15; Dunn et al., 1970, crossbred steers) was found, and it was not included in summary calculations. Similar to estimates of heritability for carcass traits discussed previously, estimates of heritability for marbling score were highly variable across studies, with a large range, from 0.01 (Lee et al., 2000, REML analysis) using weight as a covariate to 0.88 (Pariacote et al., 1998, REML analysis) 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 moderate estimates of heritability 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 (three) studies in the literature have reported estimates of heritability for marbling score obtained by adjusting data for age-, weight- or backfat thickness. Using field records of the American Simmental Association, Shanks et al. (2001) reported similar estimates of heritability for marbling score adjusted for age (0.12), weight (0.12) or backfat thickness (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 heritability estimates for marbling score. In contrast, Devitt and Wilton (2001), using Canadian data from crossbred steers, reported that weight-constant heritability (0.43) was significantly larger than backfat thickness-constant heritability (0.30), and was slightly larger than age-constant heritability (0.35).

Yield grade

Only six estimates of heritability for yield grade were reported in the literature, four were adjusted for age and two for backfat thickness, with averages of 0.60 and 0.74, respectively. Average of estimates of heritability was 0.64 across the two end points, indicating that this carcass trait is highly heritable and genetic merit might be improved through selection. In studies conducted to a constant age, low (0.24, Hereford bulls) and moderate (0.54, American Shorthorn steers) estimates of heritability were obtained by Lamb et al. (1990) and Pariacote et al. (1998), respectively. On the contrary, on a backfat thickness-constant basis, Wulf et al. (1996) for crossbred steers and heifers, and Riley et al. (2002) for Brahman steers, and on an age-constant basis, Wheeler et al. (1996) and Wheeler et al. (2001) for crossbred steers obtained larger estimates of heritability of 0.76, 0.71, 0.76, and 0.85, respectively.

No reports that compared estimates of heritability for yield grade adjusted to constant age, weight or backfat thickness were found.

Predicted percentage of retail product

The column labeled as ER in Table 1 lists estimates of heritability for various cutability-type traits, which are cited as predicted percentage of retail product in this review.

Few (N = 17) estimates of heritability for predicted percentage of retail product have been published relative to estimates for actual carcass traits. More estimates found were on an age- (N = 8) than on a weight- (N = 6) or backfat thickness-constant basis (N = 3), with averages of 0.28, 0.41 and 0.48, respectively. Across end points, average of estimates of heritability was 0.36. Heritability estimates for predicted percentage of retail product were in a low-to-high range, from 0.07 (age-constant) obtained with REML analysis by Hassen et al. (1999) for crossbred steers and bulls, to 0.71 (backfat thickness-constant) estimated with REML analysis by Riley et al. (2002) for Brahman steers. Examples of moderate estimates of heritability 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 backfat thickness, 0.55 by Gilbert et al. (1993) for Canadian Angus and Hereford bulls.

Estimates of heritability for predicted percentage of retail product adjusted to different end points were found in only two reports. In an early genetic study (Cundiff et al., 1971), the heritability estimate for predicted percentage of retail product increased somewhat in the moderate range when data were adjusted to a constant weight relative to a constant age (0.28 *vs* 0.35). Similarly, Shanks et al. (2001) obtained larger estimates of heritability for predicted percentage of retail product adjusted for backfat thickness or for weight than when adjusted for age (0.17 and 0.12 *vs* 0.09).

Retail product weight

Of the 13 estimates of heritability for retail product weight most (N = 11) were adjusted for age, less with one each for backfat thickness and weight. Age-constant estimates of heritability ranged from low to moderate (0.28) for purebred and composite steers (Gregory et al., 1995) to high (0.66) for purebred, composite and F_1 crossbred steers (Shackelford et al., 1995). Heritability estimates on an age-constant basis averaged 0.51. Estimates at constant weight or backfat thickness were estimated to be 0.42 and 0.50 by Cundiff et al. (1969) and Riley et al. (2002), respectively. The average age-constant estimates and weight- and backfat thickness-constant estimates of heritability imply that significant genetic variation exists to improve retail product weight by selection.

Estimates of heritability for retail product weight based on different covariates were published in only one report (Cundiff et al., 1969), which found that the estimate of heritability using age as covariate in the model was larger than the estimate using weight as the covariate (0.64 *vs* 0.42).

Fat weight

Only nine estimates of heritability for fat weight were found. Seven estimates were with adjustment to constant age, one to constant weight and one to constant backfat thickness. Estimates of heritability 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) to high (0.94) for Hereford heifers (Koch, 1978). Almost all estimates, however, were moderate, except those obtained by Koch (1978) and Shackelford et al. (1995). The estimates of heritability at constant weight or backfat thickness were from Cundiff et al. (1969) and Brackelsberg et al. (1971), who reported estimates of 0.37 and 0.50, respectively. Average estimates of heritability across end points was 0.50, suggesting that selection against fat weight or to an intermediate level, for example, would respond well to selection.

Only one report (Cundiff et al., 1969) compared estimates of heritability for fat weight obtained with different covariates in the model; the age-constant estimate of heritability was larger than the weight-constant estimate (0.46 *vs* 0.37).

Bone weight

Seven estimates of heritability for bone weight were found, six adjusted to constant age, and one to constant weight, with none for constant backfat thickness. For a constant age, the average of estimates of heritability was 0.51. All age-constant estimates of heritability for bone weight 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). Regardless of end point, estimates of heritability averaged 0.49. The heritability estimate of 0.39 for bone weight adjusted to a weight-constant basis was reported by Cundiff et al. (1969). This report was the only one found evaluating heritability estimates for bone weight adjusted for different covariates, but no significant effect of covariate was observed, as the estimates of heritability were 0.38 and 0.39 with common age and common weight, respectively.

Actual retail product percentage

The number of estimates of heritability for actual retail product percentage was 17, with 9 on an age-constant basis and 8 on a weight-constant basis. No estimates of heritability for retail product percentage on a backfat thickness-constant basis were found. Estimates of heritability on an age-constant basis averaged 0.54, and ranged from moderate (0.33; Morris et al., 1999, REML analysis) to high (0.67; Shackelford et al., 1995, REML analysis), but most estimates were moderate. On a weight-constant basis, average of estimates of heritability (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).

Comparisons of estimates of heritability for actual retail product percentage obtained using different covariates in the model in the same study were not found.

Fat percentage

Seven estimates of heritability for fat percentage found in the literature were age-constant estimates. Estimates of heritability 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 F_1 crossbred steers (Shackelford et al., 1995). This range also includes estimates of heritability 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. 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 information about estimates of heritability for fat percentage evaluated at different end points in the same study was found.

Bone percentage

All estimates of heritability (N = 8) for bone percentage 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 heritability indicate that bone percentage 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 of heritability included in this range were moderate and were reported to be 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 heritability for bone percentage adjusted for different covariates in the same study were found.

CONCLUSIONS

The review of estimates of heritability published in the scientific literature during the last 42 years revealed that most estimates of heritability were on an age-constant or time-on-feed-constant basis. Carcass weight, backfat thickness, longissimus muscle area, and marbling score were the carcass traits with the most estimates of heritability. The average estimates indicate that they are similarly and moderately heritable. In contrast, the number of estimates of heritability for dressing percentage was about half or less than half of those for the carcass traits listed above. The average estimate also indicates that dressing percentage is moderately heritable. Carcass traits with the fewest estimates of heritability were for traits that require the most effort to measure: kidney, pelvic, and heart fat percentage, yield grade, predicted percentage of retail product, retail product weight, fat weight, bone weight, actual retail product percentage, fat percentage, and bone percentage. However, the estimates indicate they are more heritable, except for kidney, pelvic, and heart fat percentage and predicted percentage of retail product, than the more frequently studied carcass traits. Yield grade had the smallest number of heritability estimates, but the largest estimates of heritability. Heritability estimates 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. Few studies have compared heritability estimates for carcass traits adjusted to different end points. Results from such studies were inconsistent, although some studies revealed that heritability estimates for several carcass traits were sensitive to the covariate (end point) included in the model implying that direct response to selection would be different for some traits depending on slaughter end point. The effect of different end points on estimates of heritability has not been studied for several carcass traits.

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