1-2012

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Index selection in terminal sires improves early lamb growth[1]

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ABSTRACT: The use of terminal sires (TS) for crossbreeding is integral to the UK sheep industry where approximately 71% of market lambs are sired by TS rams. Early growth of these crossbred lambs affects profitability. The objectives of this study were i) to evaluate the effectiveness of index selection among TS on BW and ADG of their crossbred offspring; and ii) to compare the efficacy of that selection within TS breeds. The most widely used TS breeds in the United Kingdom are Charollais, Suffolk, and Texel. These participated in sire referencing schemes in which they were evaluated on a lean growth index designed to increase carcass lean weight at a given age. From 1999 to 2002, approximately 15 high and 15 low lean growth index rams per breed (93 in total, differing in index on average by 4.6 SD) were selected from within their sire referencing schemes and mated to Welsh and Scottish Mule ewes. Their crossbred offspring were reared commercially on 3 experimental farms in England, Scotland, and Wales. A total of 6,515 lambs were born between 2000 and 2003. Lambs were weighed at birth (BWT), 5 wk (5WT), and 10 wk (10WT), and their ADG from birth to 10 wk was calculated. Lambs sired by high index rams were on average, across breeds, heavier at all ages ($P < 0.01$) with 0.07 ± 0.03, 0.3 ± 0.1, and 0.4 ± 0.1 kg greater BWT, 5WT, and 10WT, respectively. Their ADG was 5.1 ± 1.9 g/d greater than low-index-sired lambs ($P < 0.01$). Suffolk-sired lambs were on average heavier at all ages, with greater ADG, whereas Charollais-sired lambs were lightest with smallest ADG. Overall, there was no significant interaction between sire index and sire breed ($P > 0.10$). Within Suffolk-sired lambs, there was little difference between high and low index sires for the traits studied ($P > 0.3$). High and low index Charollais-sired lambs differed in BWT (0.09 ± 0.04 kg) and 5WT (0.3 ± 0.1 kg), and Texel-sired lambs differed in 5WT (0.5 ± 0.1 kg), 10WT (0.9 ± 0.2 kg), and ADG (10.2 ± 3.3 g/d; $P < 0.01$). Lambs from Scottish Mule dams were heavier, with greater ADG, than lambs born to Welsh Mules ($P < 0.01$). Lambs reared in Scotland were heavier at all ages ($P < 0.01$). The results suggest that using index selection in TS can improve the growth of their commercial offspring reared on grass.

Key words: index selection, lamb growth, sheep, terminal sire

J. Anim. Sci. 2012. 90:142–151
doi:10.2527/jas.2011-4294

INTRODUCTION

The use of terminal sire (**TS**) breeds in crossbreeding programs is an integral part of sheep production in the United Kingdom. The UK enjoys a stratified crossbreeding structure, with sheep raised in 3 main environments: hills, uplands, and lowlands. The hill sector is a source of ewes for the upland, where they are mated to Longwool (primarily Bluefaced Leicester) crossing rams. Crossbred ewes resulting from these matings are moved to the lowlands and bred to TS rams. The main TS breeds used in the United Kingdom are Charollais, Suffolk, and Texel, and their TS cross progeny and together account for approximately 71% of lambs slaugh-

[1]We acknowledge the Meat and Livestock Commission [now EBLEX (Kenilworth, UK), Quality Meat Scotland (QMS; West Mains, Ingliston, Newbridge, UK), and Hybu Cig Cymru–Meat Promotion Wales (HCC; Ty Rheidol, Pave Merlin, Aberystwyth, UK)]; the Department of Environment, Food and Rural Affairs (London, UK); The British Charollais Sheep Society (Norfolk, UK); the Suffolk Sheep Society (Ballymena, UK); and the British Texel Sheep Society (Kenilworth, UK) for funding of this study. We also thank the technical staff for their support of the experimental program and E. Stephens for technical editing.

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Received May 24, 2011.
Accepted August 16, 2011.

tered (Pollott and Stone, 2004). These lambs typically grow quickly to yield high-quality carcasses.

In the early 1990s, Charollais, Suffolk, and Texel breeders established sire referencing schemes (**SRS**), which are cooperative breeding programs with genetic links created among flocks by the mutual use of reference sires (Simm et al., 2001). Their goal was to improve carcass quality, basing selection on an index to improve lean growth rate (Simm and Dingwall, 1989). The enormous influence of TS breeds on slaughter lamb production in the United Kingdom allowed selection to be targeted to these breeds with great effect on the market (Cameron and Bracken, 1992).

Several studies have compared sire breeds for growth characteristics (e.g., Cameron and Drury, 1985; Yaqoob et al., 2005b). However, evaluation of the effects of index selection on TS breeds has not been thoroughly undertaken. The TS are often reared under pedigree conditions with supplementary concentrates, whereas their crossbred offspring are reared commercially at grass. This environmental difference means that it is important to directly evaluate the performance of their lambs in a commercial system. The research had 2 purposes: i) to evaluate the effectiveness of TS index selection on growth and ADG of crossbred lambs reared commercially, and ii) to compare the efficacy of that selection within 3 TS breeds.

MATERIALS AND METHODS

The Animal Experiment Committees at the Institute of Biological, Environmental and Rural Sciences (**IBERS**), the Scottish Agricultural College (**SAC**), and ADAS UK Ltd. (**ADAS**) approved all procedures and protocols used in the experiment.

Animal Resources

The Charollais, Suffolk, and Texel TS rams used came from SRS within their breeds and were selected based on their values for the lean growth index of Simm and Dingwall (1989). The index was designed to increase carcass lean weight, while keeping carcass fat weight constant at a fixed age end point. The selection criteria were BW at finishing, ultrasound fat depth, and ultrasound muscle depth, adjusted to 150 d. Relative economic values of +3 and −1 were used for lean and fat weight, respectively. These relative economic values were chosen to achieve the desired gains in the traits of the breeding goal rather than being based on market returns and costs of production. Thus this index is equivalent to a restricted selection index, with changes in fat restricted to zero, or alternatively a desired gains index (Simm and Dingwall, 1989). It was derived in this manner because of the weak relationship between carcass price and fatness in Britain at the time of its development (Simm et al., 2002). Annual response to the index has ranged from approximately 6 to 14 index points (Simm et al., 2001).

A resource of "Mule" (crossbred) ewes was developed by mating Scottish Blackface and (Welsh) Hardy Speckled Face hill ewes to Bluefaced Leicester rams. These matings produced flocks of Scottish and Welsh Mules, respectively, described previously (van Heelsum et al., 2003, 2006; Mekkawy et al., 2009). A description of genetic evaluation system, and genetic progress in UK sheep, can be found in Amer et al. (2007).

In the first year of the experiment (2000), all ewes were primiparous 2 yr olds. In 2001 and 2002, new 2-yr-old ewes were added to the ewe flock, and the older ewes remained. In 2003, no new ewes were added. Thus the average age of the flock increased over time. These Mule ewes were distributed among 3 experimental farms in the United Kingdom: Rosemaund, England (ADAS; 52°04′ N, 02°43′ W); Edinburgh, Scotland (SAC; 55°57′ N, 3°12′ W); and Aberystwyth, Wales (IBERS; 52°25 N, 4°4′ W).

TS Ram Selection

From 1999 to 2002, the Mule ewes were mated to TS rams from the Charollais, Suffolk, and Texel breeds. The rams were selected to fall into either the high or low lean growth index category. They were purchased from the SRS of their respective breed. In the first 2 yr of the study, breeders brought rams to the Ram Selection days for each SRS. In 2001, there was an outbreak of foot and mouth disease in the United Kingdom, which resulted in a ban on animal movement. In 2001 and 2002, rams were no longer selected at Ram Selection days, but instead purchased directly off farms. Selected rams were extreme in index score within their breed. The rams were inspected and confirmed as physically sound by a veterinarian and approved to be of suitable breed type by scheme judges. Between 15 and 17 high and low index rams were used from each breed over the length of the study.

In the first year of selection (1999), all rams chosen as high index had index scores above 250 points (top 5% of available rams), whereas those chosen as low index all had index scores below 100 points. Given the foot and mouth disease outbreak in 2001 and difficulties in obtaining low index rams, the eligible index scores increased over time. In the final year of selection (2002), a score of 300 points was considered high and 150 low; thus, the differential between high and low index rams was maintained within a year.

Mating Design

Matings between TS and Mule ewes were designed to balance number of rams between high and low index, and between the 3 TS breeds in each mating year (Table 1). The matings were also designed so genetic links were achieved among farms and years. No AI was used because assessment of the natural reproductive capacity of the Mule ewes was a priority for a previous study (van Heelsum et al., 2003, 2006). To create

Table 1. Number of sires used for mating by index and breed category, and number of dams used

		Birth year of lambs							
		2000		2001		2002		2003	
Category	Breed	High[1]	Low	High	Low	High	Low	High	Low
Sire	Charollais	3	3	6	6	8	7	9	9
	Suffolk	2	3	6	6	7	7	10	7
	Texel	3	3	6	7	7	7	9	8
Dam	Scottish Mule	242		455		593		565	
	Welsh Mule	249		486		645		644	

[1]Lean growth selection index category, where high and low index categories differed by, on average, 150 index points or 4.6 SD.

genetic links between farms without AI, sires were used in successive breeding seasons, being moved between farms. Sires were typically used as ram lambs (8 mo of age) at the first mating, and as shearlings (20 mo of age) at the second mating.

After the first mating, approximately 1/3 of sires stayed at the same farm, and the remaining 2/3 were moved to other farms. Thus rams had progeny in 2 locations and genetic connections existed between all farms. The design allowed for performance information on the crossbred offspring to be combined and analyzed across the 3 locations where the Mule ewes were distributed.

On all 3 farms, similar numbers of ewes (from 26 to 39) were mated on pasture to a single sire. Rams remained with ewes for 4 to 6 wk. In some cases ram fertility was deemed low (based on raddle marks). In those instances, approximately 1 wk after the ram was removed another ram was placed in their pasture. Thus all ewes were mated and parentage identification was possible based on lamb birth dates. The number of ewes from each breed used each year is shown in Table 1. Approximately 35 ewes, one-half from each Mule genotype, were mated to a ram each year.

Farms

The number and percentage of lambs born, and the number of sires used in each farm and year, are in Table 2. Management was standardized among farms. However, the mating period in England and Wales began in mid-October, whereas, because of the later onset of spring weather, it began 2 wk later in Scotland.

Lambs were reared in 3 lowland farms that differed in climate and topography. The Rosemaund farm in England is at an altitude range of 75 to 105 m above sea level, with mean annual rainfall of 660 mm and average temperatures ranging from 3 to 22°C. In Scotland, the SAC farm ranges in altitude from 150 to 200 m above sea level, with 1,000 mm of rainfall per year and average temperature ranging from 7 to 26°C. The Welsh farm has annual rainfall of 1,170 mm, and average temperatures ranging from 3 to 20°C. It ranges from 10 to 70 m above sea level.

Production and Finishing of Crossbred Lambs

Lamb pedigree, sex, and BW were recorded at birth. Male lambs were castrated, and all tails were docked. The ewes were condition scored, weighed, and any lambing difficulties noted. Within 48 h of lambing, Mule ewes were turned out to pasture with no more than 2 lambs. Ewes with twin lambs were grazed separately from those with singletons and offered supplementary feed where needed. The lambs were reweighed at approximately 5 and 10 wk of age.

Statistical Analysis

All lambs evaluated had sire and dam identification available. Birth dates were checked against mating period to confirm parentage, and lambs with uncertain

Table 2. Number of lambs born in each location each birth year and number of rams used in that location each birth year

	Birth year of lambs							
	2000		2001		2002		2003	
Location	Lambs,[1] No. (%)	Rams	Lambs, No. (%)	Rams	Lambs, No. (%)	Rams	Lambs, No. (%)	Rams
Wales	262 (34)	6	500 (33)	12	525 (25)	14	677 (32)	17
Scotland	264 (34)	5	603 (40)	13	804 (38)	14	703 (33)	18
England	254 (32)	6	419 (27)	12	776 (37)	15	728 (35)	17

[1]No. of lambs in each farm and percentage (in parentheses) by location within a year.

parentage were removed. Lambs with poor BW gain indicative of illness were excluded from the data. Data were further edited so that lambs were at least 14 d old and at most 56 d old at their 5-wk BW. A total of 6,515 lambs had birth weight (**BWT**) and 5-wk weight (**5WT**) records, and 6,508 lambs had 10-wk weight (**10WT**) records. Further, the ADG of each lamb from birth to its 10WT was calculated in grams per day. A 2-generation pedigree was assembled on the paternal side, and a 1-generation pedigree on the maternal side, using all available ancestors.

The BW and ADG data were analyzed with SAS software (SAS Inst. Inc., Cary, NC) fitting a linear mixed model. Fixed effects were sire index (high or low) and breed (Charollais, Suffolk, or Texel), and their interaction, sex (wether or ewe lamb), dam breed (Scottish or Welsh Mule), age of dam (**AOD**; 2-yr, 3-yr, or 4- and 5-yr), and farm and birth year, and their interaction. For BWT, birth rank (single, twin, triplet) was fitted as an additional fixed effect. For 5WT, 10WT, and ADG, a combined birth-rearing rank fixed effect instead was fitted. The 4 categories were single born/single reared, twin or more born/single reared, single or twin born/twin reared, and triplet or quadruplet born/twin reared. The sire of the lamb, nested within index and breed, and the rearing dam were included as random effects in addition to the residual.

For BWT the birth date of the lamb each breeding season in each farm was fitted as a covariate. Day 1 was considered the first day a lamb was born on a farm in a particular year. Day of birth therefore was adjusted for each year-farm combination and centered to its mean birth date. For 5WT and 10WT, the age of the lamb at recording was fitted as a covariate. These were centered to their expected age (e.g., 35 d for 5WT) to adjust BW to their target age. No covariate was fitted for ADG.

Adjusted means were obtained, and differences among means were tested for significance using a Tukey-Kramer adjustment for multiple comparisons (Westfall et al., 1999). An ANOVA was carried out to investigate the statistical significance of fixed effects. For interactions of sire index and breed, simple effects were tested, which assess the effects of sire index on each of the sire breeds separately. Additionally, orthogonal contrasts were performed to test the nature of any present interaction.

To disentangle the confounding of ewe age and birth year, the data were divided into 3 subsets based on AOD, which were analyzed separately. The 3 age categories used were 2-yr-old, 3-yr-old, and 4- to 5-yr-old dams. The BW and ADG of lambs from these subsets were analyzed with the linear mixed model described earlier, except the AOD fixed effect was omitted. The same analysis was conducted for 3 subsets of data but instead separated by birth year (2001, 2002, and 2003).

Some evidence of nonnormality and heteroscedasticity of the variables analyzed was observed with Anderson-Darling (Anderson and Darling, 1952) and Levene's (Levene, 1960) test. The residuals from the BW and ADG models were then tested for skewness, kurtosis, and normality. The SE of skewness and kurtosis were calculated as $\sqrt{6/n}$ and $\sqrt{24/n}$, respectively, where n was the number of records (Kutner et al., 2005). Given the large n (6,515 or 6,508), the SE were inherently small and most residuals exhibited skewness and kurtosis to an extent judged to be formally significant at $P < 0.05$. However, in all cases the mean and median were similar, and further inspection of the distributions indicated that skewness and kurtosis were not severe. The distributions of the residuals were inspected through plots of predicted values vs. residuals, and quantile-quantile plots, and appeared normal.

There was concern that any heterogeneity in variance among sire breed and index categories could bias evaluation of these effects, including their interaction. To deal with this possibility, the BW data were tested for heteroscedasticity. Standard normal scores were calculated for each BW on animal by subtracting the mean BW of a sire breed-index category and then dividing it by its SD. Body weights were then standardized as

$$WTz_i = \hat{\mu}_{BI_j} + z_i \times \hat{\sigma}_{SuffH},$$

where WTz_i is the ith transformed weight of an animal, $\hat{\mu}_{BI_j}$ is the mean of each combined sire breed-index category, z_i is the standard normal deviate, and $\hat{\sigma}_{SuffH}$ is the SD of the BW of high-index Suffolk-sired lambs. The WTz_i scores were fitted to the linear mixed model described above. The transformation ensured that WTz_i scores and the sire index category-breed variances were homoscedastic. Differences among means of index-breed categories were tested to determine whether any heteroscedasticity in the data was substantial enough to affect those comparisons.

RESULTS

Animal Resources

The number of sires used and lambs born in each location are in Table 2. Lambs were relatively evenly distributed across locations, although the number of lambs born each year increased as more Mule ewes were mated. There was also, as shown in Table 1, a relative balance between ewes of each breed mated each year.

A 2-generation pedigree was assembled to summarize paternal ancestry, and a 1-generation pedigree was assembled for maternal ancestry. No sires in the project were full sibs, although some were half sibs. Almost all paternal grand sires (67 of 75) had only 1 ram offspring included in the study, but 2 paternal grand sires had 2 half-sib offspring, and 6 paternal grand sires had 3 half-sib offspring. No high and low index sires in the project were related at the level of the pedigree assembled.

Table 3. Differences (high − low) in index scores and mean EBV for scanning traits by breed for rams used in the project[1]

Sire breed	Birth year of lambs	Difference in Index ± SED, points	Difference in EBV[2] BW ± SED, kg	UMD ± SED, mm	UFD ± SED, mm
Charollais	2000	185 ± 6	7.05 ± 0.84	0.67 ± 0.74	−1.51 ± 0.55
	2001	236 ± 15	7.42 ± 0.96	2.56 ± 0.38	−1.12 ± 0.50
	2002	205 ± 16	3.91 ± 1.31	2.53 ± 0.59	−1.12 ± 0.31
	2003	232 ± 18	6.47 ± 1.53	2.77 ± 0.47	−0.89 ± 0.38
	Avg.[3]	213 ± 13	5.97 ± 0.78	2.15 ± 0.35	−1.14 ± 0.21
Suffolk	2000	217 ± 9	8.14 ± 1.01	5.29 ± 0.58	−0.45 ± 0.46
	2001	243 ± 27	4.72 ± 1.28	2.48 ± 0.91	−0.99 ± 0.30
	2002	165 ± 5	6.23 ± 1.18	1.23 ± 0.56	0.03 ± 0.36
	2003	205 ± 20	7.12 ± 1.14	2.03 ± 0.42	0.15 ± 0.22
	Avg.[3]	211 ± 14	6.51 ± 0.75	2.53 ± 0.40	−0.27 ± 0.18
Texel	2000	146 ± 10	4.96 ± 0.95	3.36 ± 0.44	0.01 ± 0.17
	2001	186 ± 10	8.66 ± 1.62	1.96 ± 0.40	0.05 ± 0.58
	2002	184 ± 18	6.35 ± 1.13	1.76 ± 0.84	−0.58 ± 0.22
	2003	174 ± 17	9.13 ± 0.88	1.69 ± 0.93	0.06 ± 0.22
	Avg.[3]	172 ± 10	7.37 ± 0.74	2.10 ± 0.37	−0.11 ± 0.16
Overall across breeds	Avg.[4]	198 ± 8	6.60 ± 0.5	2.30 ± 0.2	−0.49 ± 0.12

[1]EBV were obtained from across-flock animal model BLUP conducted within each sire referencing scheme.
[2]At 150 d of age: UMD = ultrasonic muscle depth; UFD = ultrasonic fat depth.
[3]Differences averaged over years.
[4]Differences averaged over years and breeds.

Table 3 shows the differences between high and low index rams of each breed for index score and EBV for scanning and BW at 150 d in each birth year of the lambs. The EBV were obtained from the across-flock animal model BLUP evaluation conducted within breed in each year. High-index rams were on average 198 ± 8 points greater in index score than low-index rams. In all breeds, high-index rams had more positive EBV for BW (6.6 ± 0.5 kg) and ultrasonic muscle depth (**UMD**; 2.3 ± 0.2 mm) than low index rams. Overall, high-index rams had more negative EBV for ultrasonic fat depth (**UFD**; −0.49 ± 0.12 mm), although the differences were small and significant ($P < 0.01$) only for the Charollais.

Effects of Sire Index, and Sire and Dam Breed

The mean ages at weighing for 5WT and 10WT were 37 d (SD 6) and 71 d (SD 7), respectively. For all traits studied, the effects of the index and breed of the sire were significant ($P < 0.01$), although their overall interaction was not ($P > 0.10$). Least squares means for sire index and breed are presented in Table 4. Lambs sired by high index rams were 0.07 ± 0.03, 0.3 ± 0.1, and 0.4 ± 0.1 kg heavier at BWT, 5WT, and 10WT, respectively, with 4.9 ± 1.9 g/d greater ADG ($P < 0.01$).

On average, Suffolk-sired lambs were heavier for all BW traits and had greatest ADG ($P < 0.01$). This is

Table 4. Adjusted least squares means of growth traits in lambs by sire breeds and index categories and dam breeds[1]

Item	No.[2]	BWT ± SE, kg	5WT ± SE, kg	No.[3]	10WT ± SE, kg	ADG ± SE, g/d
Sire index						
High	3,265	4.62 ± 0.05[a]	16.6 ± 0.1[a]	3,262	27.4 ± 0.1[a]	321.8 ± 1.7[a]
Low	3,250	4.54 ± 0.05[a]	16.3 ± 0.1[b]	3,246	26.9 ± 0.1[b]	316.8 ± 1.7[b]
Sire breed						
Charollais	2,323	4.53 ± 0.05[b]	16.2 ± 0.1[b]	2,321	26.9 ± 0.2[b]	315.7 ± 2.0[b]
Suffolk	2,038	4.64 ± 0.05[a]	16.6 ± 0.1[a]	2,035	27.6 ± 0.2[a]	324.4 ± 2.0[a]
Texel	2,154	4.56 ± 0.05[ab]	16.5 ± 0.1[a]	2,152	27.1 ± 0.2[b]	317.9 ± 2.0[b]
Dam breed						
Scottish Mule	3,090	4.73 ± 0.05[a]	16.8 ± 0.1[a]	3,086	27.8 ± 0.13[a]	325.5 ± 1.6[a]
Welsh Mule	3,425	4.43 ± 0.05[b]	16.1 ± 0.1[b]	3,422	26.6 ± 0.13[b]	313.1 ± 1.6[b]

[a,b]Means within a category in a column with different subscripts are significantly different ($P < 0.05$).
[1]BWT = birth weight; 5WT = 5 wk BW; 10WT = 10 wk BW; ADG = ADG from birth to 10 wk.
[2]No. of lambs weighed at birth and 5 wk.
[3]No. of lambs weighed at 10 wk.

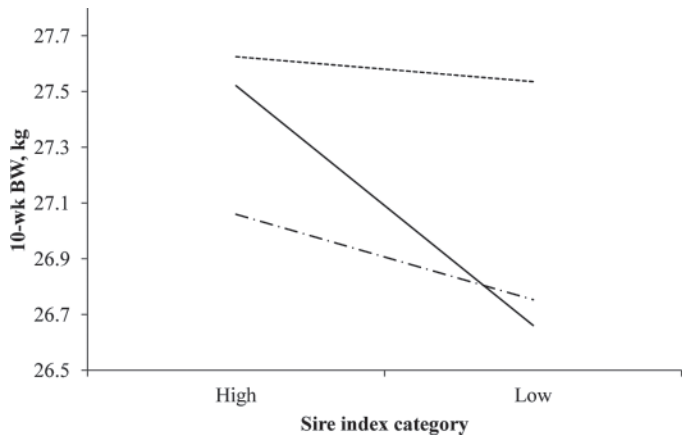

Figure 1. Adjusted means for 10-wk BW of lambs sired by high or low index sires of the Charollais (dotted and dashed line), Suffolk (dotted line), and Texel (solid line) breeds.

shown for 10WT in Figure 1. Charollais-sired lambs were the lightest and had the least ADG, although they did not differ in BW from Texel-sired lambs at birth, 10 wk or for ADG ($P > 0.10$). Suffolk-sired lambs were not different from Texel-sired lambs in BWT and 5WT ($P > 0.10$).

Analysis of the simple effect of index category within a breed revealed that high-index Charollais-sired lambs were heavier than low-index-sired lambs for BWT (0.09 ± 0.04 kg) and 5WT (0.3 ± 0.1 kg; $P < 0.01$), but not for 10WT ($P = 0.2$) or ADG ($P = 0.4$). Within Suffolk-sired lambs, there were no differences between high and low index sires in the BW of their offspring for BWT ($P = 0.3$), 5WT ($P = 0.6$), 10WT ($P = 0.2$), or ADG ($P = 0.7$). For Texel-sired lambs, there was no difference between high and low index categories for BWT ($P = 0.06$). However, the high index Texel-sired lambs had greater values for 5WT (0.5 ± 0.1 kg), 10WT (0.9 ± 0.2 kg), and ADG (10.7 ± 3.3 g/d; $P < 0.01$). In all instances, high-index-sired lambs were numerically heavier than low-index-sired lambs within a breed, as shown for BWT in Figure 2.

Although no overall interaction between index and sire breed was detected, the difference between index categories varied among breeds. Body weights and ADG were most distinct between index categories in the Texel-sired lambs. Orthogonal contrasts were therefore constructed to test the interaction between Texel vs. combined Suffolk and Charollais sire breeds with index category. For 10WT and ADG, an interaction was detected ($P < 0.05$), substantiating the larger difference between index categories in Texel-sired lambs for these 2 traits.

Dam breed was a significant source of variation for all traits studied ($P < 0.01$). Adjusted means are shown in Table 4. Lambs born to Scottish Mule dams were heavier ($P < 0.01$) than lambs born to Welsh Mules for BWT (0.29 ± 0.03 kg), 5WT (0.8 ± 0.1 kg), and 10WT (1.2 ± 0.1 kg) and had greater ADG (12.5 ± 1.2 g/d; $P < 0.01$).

Analysis of normalized BW scores (WTz) revealed no interaction between sire index and sire breed (BWT, $P = 0.8$; 5WT, $P = 0.2$; 10WT, $P = 0.1$; ADG, $P = 0.1$), whereas the individual effects of sire index and sire breed did affect performance ($P < 0.01$). This indicated that the lack of significant interaction between sire index and sire breed in the nonnormalized data was not due to heterogeneity of variance within sire index and breed categories.

Effects of Location and Year

The main effects of farm, year, and their interaction, were significant ($P < 0.01$). Even though the interaction was present, in all cases the ranking of farms did not change over the years; lambs in Scotland were always heavier, followed by those in England and Wales. Body weights fluctuated with year, but not in a systematic way.

Adjusted means for the 3 farm locations are in Table 5. On average, lambs born in Scotland were heavier at all ages and had greater ADG than lambs born in other farms ($P < 0.01$). These lambs were born later in the year because mating was 2 wk later. Lambs differed in BWT between farms across all years ($P < 0.01$). Lambs in Wales and England did not differ in 5WT or 10WT ($P > 0.1$).

The analysis of the 3 subsets of data formed by AOD (i.e., 2-yr-old, 3-yr-old, and 4- and 5-yr-old), showed that 5WT, 10WT, and ADG of lambs increased with dam age. This pattern was less consistent for BWT. When the data were split into birth year rather than AOD subsets, similar results were obtained. In 2001 and 2002, lambs born to older ewes were heavier and grew more quickly than lambs born to younger ewes ($P < 0.001$). In 2003, 4- and 5-yr-old ewes did not differ among themselves, but lambs from 3-yr-old ewes weighed less and grew more slowly ($P < 0.001$).

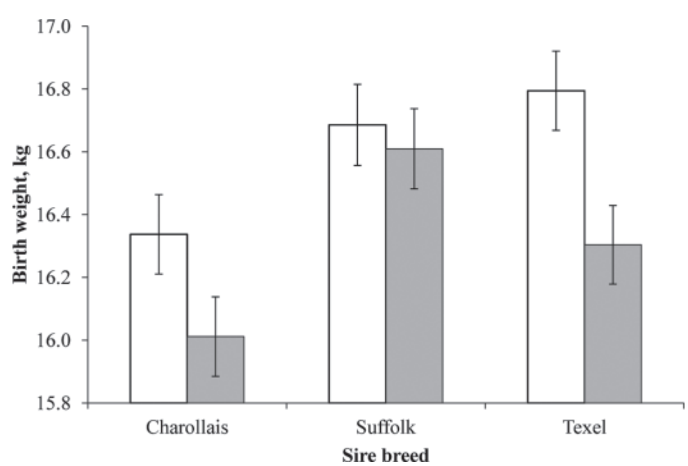

Figure 2. Adjusted means with SE bars for birth weight of lambs sired by high (white) or low (gray) index sires from the Charollais, Suffolk, or Texel breeds.

Table 5. Adjusted least squares means of growth traits in lambs by location[1]

Location	No.[2]	BWT ± SE, kg	5WT ± SE, kg	No.[3]	10WT ± SE, kg	ADG ± SE, g/d
England	2,177	4.37 ± 0.05[c]	15.8 ± 0.1[b]	2,177	25.8 ± 0.1[b]	304.4 ± 1.9[b]
Scotland	2,374	4.80 ± 0.05[a]	17.8 ± 0.1[a]	2,373	29.7 ± 0.2[a]	349.8 ± 2.0[a]
Wales	1,964	4.57 ± 0.05[b]	15.7 ± 0.1[b]	1,958	26.1 ± 0.1[b]	303.8 ± 1.9[b]

[a–c]Means within a column with different subscripts are significantly different ($P < 0.05$).

[1]BWT = birth weight; 5WT = 5 wk BW; 10WT = 10 wk BW; ADG = weight ADG from birth to 10 wk.

[2]No. of lambs weighed at birth and 5 wk.

[3]No. of lambs weighed at 10 wk.

DISCUSSION

Comparison of Index Categories

Mule ewes were mated to TS rams to test the efficacy of the index selection that had been used in the 3 sire breeds since the early 1990s. Using sires of different lean growth index categories allowed quantification of the progress achieved by the different SRS in improving lamb performance. The design of this experiment allowed valid comparisons among lambs reared in different environments and sired by rams of different breeds.

Differences between index categories of rams for BW and scanning traits were expected given the selection on index scores. Because of the way the index was devised, high-index sheep typically had positive EBV for LW and UMD and, in general, slightly negative EBV for UFD (Simm et al., 2002). The differences between UFD EBV of Texel and Suffolk rams were for the most part not different from 0. This may be due to preference of the breeders for rams that are fatter at the same index score; they may see this as a way to achieve sufficient fatness at the target finish weight in commercial lambs. The difference in index points between high and low index sires in each breed was substantial. Therefore we anticipated differences in lean growth rate between sire categories would be expressed in the performance of their crossbred progeny. Such an effect has been observed previously (Lewis et al., 1996, 2004; Simm and Murphy, 1996; Jones et al., 1999), and here.

Sire Index and Breed Influences

Index selection has been found to be an efficient way to improve economically relevant traits in sheep. In TS SRS where the lean growth index used in this study was applied, annual response to selection ranged from approximately 6 to 14 index points (Simm et al., 2001). The results from other experiments have also shown that the use of the lean growth index has increased lean weight in the carcass while reducing fat weight (Lewis and Emmans, 2007). Lewis et al. (1996) found that commercial lambs sired by high lean growth index sires produced leaner and more valuable carcasses. Corroborating these results, van Heelsum et al. (2003), studying the Scottish and Welsh Mules used as dams in the current study, found that their Bluefaced Leicester sires with greater index scores produced wethers with more lean and less fat content in all carcass joints (e.g., shoulder, leg, and loin).

In the current study, sire breed affected 5WT, 10WT, and ADG ($P < 0.01$), indicating that breed differences can be exploited for the economic benefit of producers. The lack of difference in BWT was favorable given possible problems of dystocia associated with greater BWT. Some studies on the effects of sire breed have found no influence on BWT (More O'Ferrall and Timon, 1977; Leymaster and Jenkins, 1993; Fogarty et al., 2000), whereas other studies, using more diverse sire breeds, have found differences (Cameron and Drury, 1985; Fogarty et al., 2000; Freking et al., 2000). Yaqoob et al. (2005b) found that weaning weights of Texel-sired lambs were greater than those of Charollais-sired lambs, but Suffolk-sired lambs did not differ from either of these breeds. Cameron and Drury (1985) did not detect such a difference between Texel- and Charollais-sired lambs; their ADG did not differ either. Conversely, Yaqoob et al. (2005a) found that the ADG of Texel-, Suffolk-, and Charollais-sired lambs did not differ from birth to 30 d, but that ADG of Suffolk was greater than that for Texel-sired lambs from birth to weaning and from birth to slaughter. Charollais-sired lambs did not differ from the other breeds at these ages.

Possibly conflicting results between experiments may be due to different strains of the sire breeds used. For example, in the United States, Kuehn et al. (2009) reported that Suffolks were being selected for 2 biological types: one for traditional TS characteristics like large mature size, and another with emphasis on moderate mature size and muscling. Two main strains of Texel are used in the United Kingdom: Dutch Texel and French Texel, which may differ in several respects. French Texel was the strain primarily used in the present study.

Suffolk-sired lambs were heavier at all ages than those sired by the other 2 breeds. The lack of difference in performance between high- and low-index Suffolk-sired lambs was unexpected. We hypothesize that the progeny of the high-index Suffolk rams performed less well than anticipated and that this may be due to one or more factors. First, this may be an environmental (nutritional) constraint, which is first seen as growth and metabolic demands become greater. It has been found that superior genotypes can express their superiority only to an extent that is set by the quality of the environment (Lewis et al., 2002; Macfarlane et al., 2004). The genetic difference in growth rate was found to decrease steadily as the environment worsened, both between selection lines (Lewis et al., 2002) and between breeds (Macfarlane et al., 2004).

Similarly, differences in husbandry between purebred and commercial farms may play a role. On commercial farms where conditions were limiting, with little or no supplementary concentrates and a reliance on grass, the genetic potential of Suffolk rams may not have been achieved. This is in agreement with Eikje et al. (2008), who observed that genetic change was greater than phenotypic change in Norwegian sheep. In that case, the environment was not sufficiently beneficial for lambs to realize their genetic potential.

Unlike the current results, index selection has been effective for Suffolk sheep in the past. A long-term selection experiment tested the efficacy of index selection in Suffolks, and differential responses in growth between the selection and control line were observed (Simm and Murphy, 1996; Simm et al., 2002; Lewis et al., 2004; Lewis and Emmans, 2007). Lewis and Emmans (2007) reported that the growth rate in the selection line of Suffolk was 1.17 times greater than the control line at 40 kg.

High-index Charollais- and Texel-sired lambs performed better than low-index-sired lambs in this study. Lean growth index category affected some traits but not others in these breeds, but the lack of differences was not persistent across all traits as it was in Suffolk-sired lambs. It must be noted that, even though not significant, high-index-sired lambs within a breed were always numerically heavier, with greater ADG. The goal of the index was to improve the carcass of animals, and several studies have shown its effectiveness in doing so (e.g., Simm et al., 2001, 2002). Selection programs designed to improve lean growth rate will improve carcass merit, and their uptake should be encouraged.

Fixed Effects Relating to Dams

The influence of ewes on lamb growth and development is substantial (e.g., Maniatis and Pollott, 2002; Safari et al., 2005; Riggio et al., 2008). Litter size and rearing type were a significant source of variation in all traits studied. The BWT of triplet and quadruplet born lambs was not significantly different, but single-born lambs were heaviest, followed by twin-born lambs (results not shown). These results agree with previous estimates from the literature (Peeters et al., 1996; Fogarty et al., 2005): ewes with single lambs have significantly more resources to dedicate to their lambs, which were heavier at all ages.

The age and parity of ewes also exerts significant influence on lamb BW. Peeters et al. (1996) found that lambs of 1-yr-old ewes had significantly lighter birth weight and decreased postnatal growth rate compared with lambs of multiparous ewes, in accordance with other literature (Freetly and Leymaster, 2004; Alvarez et al., 2010). Similar results were found presently, with older ewes producing heavier lambs. In the current study, increases in lamb BW over the years were related in part to ewe age and parity. In 2000 all ewes were primiparous and had not yet reached full maturity. The mean age of the flock increased over the duration of the study, with the consequence that BW and ADG of lambs increased overall. Concurrently, the Bluefaced Leicester sires of the Mule ewes were being selected on an index that included increased BW as part of its goal (van Heelsum et al., 2003, 2006; Mekkawy et al., 2009). Therefore the Mule ewes were better every year. This is reflected in the current results: regardless of sire index, lambs from ewes of the same age improved every year, in part because their dams improved.

Two different ewe genotypes were used in the current study. The Scottish Mules were heavier at birth, 10 wk, and 16 wk than the Welsh Mules (van Heelsum et al., 2003), which is to be expected because their Scottish Blackface dams are generally larger than Welsh Speckled Face dams. It has been reported that animals from larger mature size breeds grow more rapidly than those from smaller mature size breeds (Bradford, 2002). Other studies have also found differences in BWT of lambs from different dam breeds (Johnston et al., 1999; Fogarty et al., 2000). The profitability of using larger or smaller ewe genotypes depends on the production system and on the resources available for ewes because larger ewes will require more inputs than smaller ewes, but may produce heavier lambs.

As part of model selection, an interaction between dam and sire breed was tested. Because none was found, it was not fitted in the final analytical model. This result is in accordance with at least some literature (Cameron and Drury, 1985; Freking et al., 2000). On the other hand, Kempster et al. (1987) found the interaction to be significant. The sire and dam breeds used were not the same as those used in the current study, which differed appreciably. Because no interaction was detected even in this case, different levels of heterosis from specific breed crosses would seem unlikely. It would appear that dam breed will not necessarily be important when comparing progeny of sires from different breeds.

Environmental Influences

The influence of farm and year, and their interaction, was significant for all measures. Lambs reared in Scotland were always heavier with greater ADG, followed by those in England and Wales, which only differed in BWT. The heavier BW in Scotland may be explained by environmental conditions. Because the early season climate is harsher in Scotland, the lambing season began approximately 2 wk later than in the more southern farms. In addition, mid-summer rainfall tends to be less in England and Wales, which, combined with different soil types, results in a temporary decrease in DM yield not observed in Scotland at the time that requirements for lambs are increasing. The day length in mid-summer Scotland is longer than in England and Wales; this also has a positive effect on the DMI of lambs.

On average the 5WT and 10WT of lambs increased most years because of ongoing selection in the sires of both the dams and lambs. A decrease in 5WT, 10WT, and ADG was observed in 2001, which may reflect 2 conditions in that year. First, many ewes were primiparous, thus producing lighter offspring than in later years as ewes aged. Second, and probably of most importance, 2001 was the year of the foot and mouth disease outbreak in the United Kingdom. Although the project ewes were not directly affected by the disease, differences in weights were site specific, with 5WT decreasing in Wales and England, but not Scotland, and 10WT and ADG decreasing across all sites. The constraints in animal movement were put in place earlier in England and Wales than in Scotland, which limited the ability of those farms to provide better forage and increased the incidence of parasitism.

Conclusions

Based on our results, selection on the lean growth index in TS breeds can bring about improvements in the growth of their commercial offspring reared on grass. Because TS breeds have a large influence on the production of market lambs in the United Kingdom, index selection therefore offers an effective way of improving meat production. Its utility has been observed for growth (e.g., Lewis et al., 2002; Lewis and Emmans, 2007) and carcass (e.g., Cameron and Bracken, 1992; Simm et al., 2001; Lewis et al., 2004; Conington et al., 2006) traits. Importantly, an advantage of index selection is that genetic changes are permanent, cumulative, and cost effective (Simm and Dingwall, 1989). Our results support the wider uptake of this methodology as a means for improving the efficacy of sheep production systems.

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