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# JOURNAL OF ANIMAL SCIENCE

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# Genetic evaluation of days to harvest in crossbred lambs<sup>1</sup>

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**ABSTRACT:** Days to harvest (DTH) is the number of days a lamb is fed before reaching a target level of fatness. Although economically relevant, this trait has not been thoroughly evaluated in sheep. Most lambs harvested in the United Kingdom are crossbreds sired by purebred terminal sires, with Charollais, Suffolk, and Texel most commonly used. Sires from these breeds were selected on an index designed to increase lean growth while constraining fat. The purpose of this research was to 1) evaluate the effects of index selection in terminal sires on DTH and 2) evaluate the feasibility of incorporating DTH into genetic evaluation programs. Charollais, Suffolk, and Texel sheep had participated in sire referencing schemes where genetic links among flocks were established by sharing rams. Rams with high or low index scores were chosen from these schemes and mated to crossbred ewes at 3 farms in the United Kingdom. Lambs were harvested at a target 11% subcutaneous fat. Records on DTH from 6,350 lambs were analyzed in 2 ways: 1) as time to harvest fitting a survival model and 2) as a normally dis-

tributed variable in a bivariate analysis with weight at harvest. The survival analysis was stratified by rearing type (single or twin). In both approaches, sires were fitted using a multivariate normal distribution with a relationship matrix. Regardless of model fitted, sire index did not affect DTH ( $P > 0.10$ ). However, Texel-sired lambs reached harvest faster ( $P < 0.01$ ) than either Charollais- or Suffolk-sired lambs although DTH in those 2 breed types did not differ ( $P > 0.1$ ). Ewe lambs reached harvest faster than wethers ( $P < 0.01$ ). Lambs from older ewes were harvested faster ( $P < 0.001$ ). The heritability of DTH was 0.21 from the survival model and 0.20 from the bivariate model. Rank correlation of sire EBV between methods was 0.9, suggesting strong agreement. The use of high or low index sires did not extend DTH in lambs harvested at a target fatness. Importantly, there is no antagonism between improving carcass merit and extending the grazing season. Furthermore, DTH is moderately heritable. If economically justified within a breeding program, it could be reduced through genetic selection.

**Key words:** crossbred lambs, days to harvest, genetic evaluation, index selection, survival analysis

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## INTRODUCTION

Days to harvest (DTH) is an economically relevant trait (Golden et al., 2000) that measures how many days a lamb is fed before reaching a target level of fatness. Longer finishing periods often can increase costs because of the need to provide supplementary feed after the end of the normal grazing season. Given that this trait may substantially affect the efficiency of production systems, a thorough investigation and genetic analysis of DTH is appropriate. Although growth rate has been extensively

studied in sheep (e.g., Safari et al., 2005) and influences DTH, DTH has not been evaluated.

We investigated 2 approaches to genetic evaluation of DTH. In our first approach, our intent was to quantify the risk, or probability, that a lamb would be harvested at a given time. Survival analysis (Kalbfleisch and Prentice, 2002) provides a method for doing so. By considering DTH as a time to an event, we determined whether the probability that lambs were harvested at a given age differed among sires. Survival analysis has been used previously in sheep to model traits such as lamb survival time (e.g., Leeds et al., 2012) but not time to a harvest endpoint. Therefore, this application is unique.

However, there are disadvantages to survival analysis. It is difficult to conduct a multivariate analysis to account for correlations with other traits and potential bias from selection for those traits. For this reason, our second approach was to fit a bivariate model of DTH, in which it was assumed to be normally distributed, and weight at harvest.

Given the likely economic importance of DTH, the objectives of this study were 2-fold: 1) to evaluate the effects of index selection and terminal sire breed on DTH and 2) to ascertain whether genetic evaluation of DTH is feasible in terminal sire sheep using either survival analysis or bivariate methods.

## MATERIALS AND METHODS

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

### Data Description

Lambs were reared on pasture and from 10 wk of age were assessed for harvest condition every 2 wk. The DTH was defined as the number of days between a lamb's birth and its harvest at a subjective target condition score of 3L, corresponding to approximately 11% subcutaneous fat by visual evaluation (Kempster et al., 1986). To score for body condition, lambs were restrained and assessed for fatness by palpation of the vertebral process and ribs. Lambs were reared to a common fatness level to compare them at the same physiological maturity. Further details of husbandry and mating have been given previously (Márquez et al., 2012, 2013).

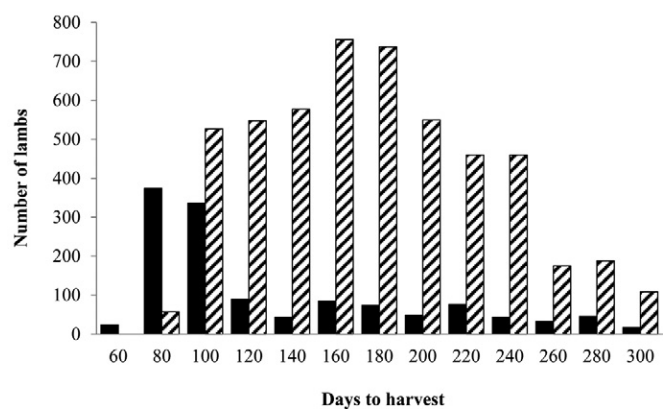
Records of DTH were obtained on 6,350 lambs born from 1999 to 2002. Lambs were from matings of Scottish and Welsh Mule ewes with Charollais, Suffolk, and Texel terminal sires, as previously described (van Heelsum et al., 2003; Márquez et al., 2012). Terminal sire breeding accounts for 70% of lambs harvested in the

United Kingdom, and the most widely used breeds are Charollais, Suffolk, and Texel (Pollott and Stone, 2004). The rams used were obtained from their breed's sire referencing schemes (Simm et al., 2001). Selection was based on a lean growth index designed to increase carcass lean growth while constraining fat growth at a constant age end point (Simm and Dingwall, 1989). After approximately a decade of sire referencing, rams from the top and bottom 5% of these schemes were chosen. High index rams differed by  $198 \pm 8$  index points (4.6 SD) from low index rams and had higher live weight and ultrasonic muscle depth EBV and lower ultrasonic fat depth EBV than low index rams (Márquez et al., 2012). Most rams were used for 2 breeding seasons and were moved between 3 farms in the United Kingdom (in England, Scotland, and Wales). Genetic links among farms and years were created by relocating rams to different farms after 1 breeding season. In total, 94 rams were used for mating, approximately half from each index category. Each of the 3 terminal sire breeds contributed approximately one-third of the rams.

### Statistical Modeling

The distribution of DTH was highly skewed, and no suitable transformations were found to approximate normality. We attempted to fit a generalized linear model to these data using Weibull, Gamma, and Poisson distributions. In all cases, based on the Anderson-Darling goodness of fit test (Anderson and Darling, 1952), the fit was poor ( $P < 0.01$ ). This finding was confirmed by visual assessment of the fit of these distributions. A zero inflated Poisson regression, setting the earliest DTH as zero, was also attempted; the fit was again poor ( $P < 0.01$ ).

Underlying these distributional issues was the fact that single- and twin-reared lambs differed substantially in DTH (Fig. 1). Single-reared lambs reached harvest fatness earlier than twin-reared lambs but over a wider



**Figure 1.** Histogram of days to harvest in single- and twin-reared lambs. Twin-reared lambs are represented by dashed black bars and single-reared lambs by solid black bars.

age range. There were 1,274 lambs reared as singletons and 5,076 lambs reared as twins.

**Survival Analysis.** The DTH is a measure of time to an event (harvest), which can be analyzed using a survival model. Formally, the survival function is the probability that an animal  $i$  survives to time  $t$  (Kachman, 1999). We estimated the survival function with a Kaplan-Meier survival curve (Kaplan and Meier, 1958), which quantifies the probability of surviving to a point in time given the cumulative probability of surviving in the preceding time intervals. It also accounts for censoring. However, because all lambs had a harvest date, there was no censoring in these data.

The hazard can be modeled in several ways although the Cox (Cox, 1972) and Weibull (Kalbfleish and Prentice, 2002) proportional hazards models are most commonly used. The Cox model is semiparametric: it makes no distributional assumption on the hazard function. The Weibull model assumes that the hazard function has a Weibull distribution. We investigated the appropriateness of the Weibull model and found that the fit to the data was poor. Therefore all analyses were performed using the Cox proportional hazards model.

The Cox proportional hazards models were fitted with the Survival Kit v6.0 (Ducrocq et al., 2010). The model fit was

$$h(t, \mathbf{X}, \mathbf{Z}) = h_{o_g}(t) \exp(\mathbf{X}'\beta + \mathbf{Z}'\mathbf{u}),$$

in which  $\mathbf{X}$  is an incidence matrix for fixed effects,  $\beta$  are fixed effects coefficients,  $\mathbf{Z}$  is an incidence matrix for random effects, and  $\mathbf{u}$  is a vector of random coefficients. The baseline hazard,  $h_{o_g}(t)$ , was stratified by rearing type (the  $o$  subscript designates the baseline hazard and  $g$  designates the rearing type, single or twin). This was done because baseline hazards of each group were different, as evident from their distributions (Fig. 1).

Fixed effects in the model were sire index category, sire and dam breed, age of dam, sex of lamb, birth year, farm, and birth year–farm interaction. Both dam breeds were represented in all farms, avoiding confounding of dam breed with farm. Estimated subcutaneous fat percentage at harvest, based on condition score, was fitted as a covariate. Other 2-way interactions, including sire breed by index category, were tested but were unimportant ( $P > 0.1$ ).

Sire was fitted as a random effect with a multivariate normal distribution with mean zero and variance  $\mathbf{A}\sigma_s^2$ , in which  $\sigma_s^2$  is the sire variance and  $\mathbf{A}$  is the relationship matrix among sires. The pedigree used to form the relationship matrix included the 94 sires of the crossbred lambs, along with 75 paternal grandsires and 94 paternal granddams. There was no relatedness between sires of different breeds; within a breed, sires of different index

categories also were not related. The  $\mathbf{A}$  matrix therefore comprised disconnected subpopulations characterizing the genetic relatedness within the 6 breed-index category sire groups.

The feasibility of combining the sire index-breed groups was evaluated with a likelihood ratio test. The 6 groups formed independent samples and were analyzed separately with the proportional hazard model described earlier to obtain their log-likelihood. The sum of the 6 log-likelihoods was tested against the log-likelihood of the combined analysis. No difference was found ( $P > 0.1$ ), indicating that the combined analysis was equivalent to separate analyses of each index-breed group. Furthermore, the estimates of sire variances for each subset were similar to that obtained from the combined analysis. We therefore combined the data.

The inclusion of rearing dam as a random effect was tested with a likelihood ratio test, which suggested that it should be added to the model. Rearing dam was assumed to follow a log- $\gamma$  distribution, with shape and scale parameter taken to be equal. The use of the log- $\gamma$  distribution is mathematically convenient, and tends to a log-normal distribution when parameter estimates are large (Ducrocq, 1997).

Estimates of moments of the posterior distributions of random effects (mean, standard deviation, and skewness) were obtained according to Ducrocq and Casella (1996). An approximate estimate of the heritability ( $h^2$ ) on a nonlogarithmic scale was obtained according to Yazdi et al. (2002) as

$$h^2 = 4\sigma_s^2 / (\sigma_s^2 + \sigma_d^2 + 1),$$

in which  $\sigma_d^2$  is the variance due to rearing dam, calculated as the tri- $\gamma$  function evaluated at the posterior mode of the variance of the rearing dam effect. This heritability can be interpreted similarly to heritabilities in standard linear mixed models (Yazdi et al., 2002).

Estimates of sire effects ( $\hat{s}$ ) were obtained and approximate accuracies (acc) were calculated as

$$\text{acc} = \left\{ n / \left[ n + (4 - h^2) / h^2 \right] \right\}^{1/2},$$

in which  $n$  is the number of observations on a sire. Estimated breeding values of sires were first expressed as a hazard ratio (HR), which is obtained by exponentiating the sire solution. The HR can be thought of as the risk of an event to occur for a certain level of a fixed effect compared to another level of that fixed effect. A higher HR indicates higher risk of an event occurring, in this case harvest of the lamb. In addition, EBV were expressed as genetic standard deviations units ( $\hat{s} / \sigma_s$ , in which  $\sigma_s$  is the square root of the sire variance) and as expected median DTH of progeny.

**Table 1.** Mean days to harvest of different categories

	No.	Days to harvest $\pm$ SE	Median	Minimum	Maximum
<b>Sire index</b>					
High	3,167	179.3 $\pm$ 1.0	179	69	325
Low	3,183	176.1 $\pm$ 1.0	173	73	325
<b>Sire breed</b>					
Charollais	2,276	181.9 $\pm$ 1.6	181	75	314
Suffolk	1,968	181.1 $\pm$ 1.3	178	75	319
Texel	2,106	169.9 $\pm$ 1.3	164	69	325
<b>Dam breed</b>					
Scottish Mule	3,020	176.0 $\pm$ 1.1	173	69	325
Welsh Mule	3,330	179.2 $\pm$ 1.0	177	73	319
<b>Rearing type</b>					
Single	1,274	143.1 $\pm$ 1.7	113	69	325
Twin	5,076	186.4 $\pm$ 0.7	183	81	325

Expected survival curves for sires with different EBV were calculated (HR of 0.8 to 1.2, at 0.1 increments). Median DTH were obtained for all permutations of fixed effects for each HR and then averaged. This approach provided expected median DTH for progeny of sires with different EBV.

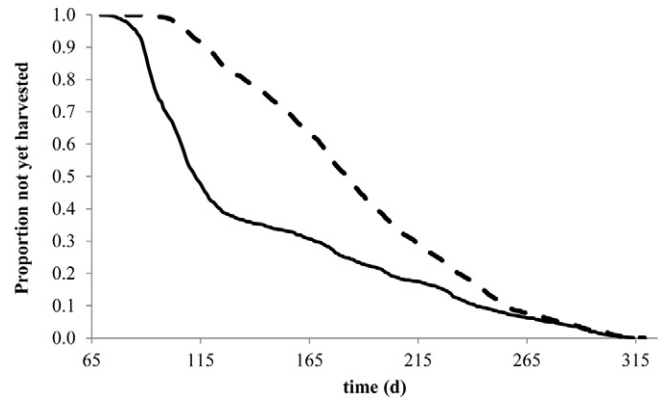
**Bivariate Model.** Our second approach was to fit a bivariate linear-linear model. The response variables were weight at harvest (HWT) and DTH. The rams used were selected on their lean growth index. Because index scores are not computed for crossbred lambs, HWT rather than index score was used as the response variable. Because BW is a main component of the index, HWT is correlated with it. Both HWT and DTH were considered to be normally distributed, and the peculiarity in distributions of single- and twin-reared lambs was ignored.

The fixed effects fitted for both traits were the same as that for the survival model with the addition of rearing type. Subcutaneous fat depth was also still included as the covariate. Similar to the survival model, random effects were sire, rearing dam, and residual. The model was fitted and variances and covariances were estimated with ASReml (Gilmour et al., 2009). Convergence was assumed when the log-likelihood changed less than 0.002 times the current iteration number, and the estimates of variances changed by less than 1%.

Solutions from the survival and bivariate model were compared by obtaining rank correlations between sire EBV obtained from the 2 methods.

## RESULTS

The raw means of DTH for different categories of interest are shown in Table 1. The overall mean of DTH was 178 (SD 57) d, and the median DTH was 175 d; the minimum and maximum DTH were 69 and 325 d, respectively. The wide range of DTH was due



**Figure 2.** Kaplan-Meier estimate of survival function. Twin-reared lambs are represented by the dashed black line. Single-reared lambs are represented by the solid black line.

in part to the long-tailed distribution of single-reared lambs. Table 1 and Fig. 1 show that twin- and single-reared lambs reached DTH following different trajectories, which were not proportional (i.e., not constant over time). The median DTH (estimated from Kaplan Meier survival curve) was 112 for single- and 182 d for twin-reared lambs (Fig. 2). Seventy-five percent of single- and twin-reared lambs were harvested by 181 and 224 d and 90% by 241 and 256 d, respectively.

## Survival Analysis

**Design Variables Hazard Ratios.** For the survival analysis, differences between groups were estimated in terms of HR. In our study a higher HR is favorable because those animals reached harvest condition in fewer days than the others. Table 2 shows estimates of HR for categories of interest. There were no differences in HR for lambs sired by high versus low index sires ( $P = 0.5$ ). Suffolk-sired lambs were chosen as the reference level for sire breed. Texel-sired lambs had a greater hazard than Suffolk- and Charollais-sired lambs ( $P < 0.001$ ) and therefore reached harvest condition earlier than lambs of the other breeds. There was no difference between Charollais- and Suffolk-sired lambs in DTH.

Lambs from Scottish or Welsh ewes did not differ in DTH ( $P = 0.8$ ; Table 2). Lambs from younger ewes took longer to reach harvest condition, but there were no differences between lambs from 4- and 5-yr-old dams ( $P > 0.1$ ). Ewe lambs reached harvest condition earlier than wether lambs ( $P < 0.001$ ). There was a strong farm  $\times$  birth year interaction but no clear pattern was observed to disentangle its likely cause.

**Variance Component Estimates.** The mean and the mode of the posterior distribution of the sire variance were 0.065 and 0.061, respectively. Its SD was 0.014. The rearing dam variance component was calculated as the tri- $\gamma$  function evaluated at the estimated shape-

**Table 2.** Hazard ratios under Cox proportional hazards model of different categories

	Hazard ratio	95% confidence interval		P-value
		Lower	Upper	
Sire index				
Low versus high	0.958	0.850	1.080	0.5
Sire breed				
Charollais versus Suffolk	1.020	0.876	1.187	0.8
Texel versus Suffolk	1.440	1.242	1.671	<0.001
Dam breed				
Scottish versus Welsh	1.054	0.989	1.124	0.1
Sex				
Ewe versus wether	1.130	1.070	1.194	<0.001
Age of dam, yr				
3 versus 2	1.291	1.193	1.397	<0.001
4 versus 2	1.310	1.182	1.452	<0.001
5 versus 2	1.374	1.188	1.589	<0.001
Subcutaneous fat	1.025	0.976	1.125	0.4

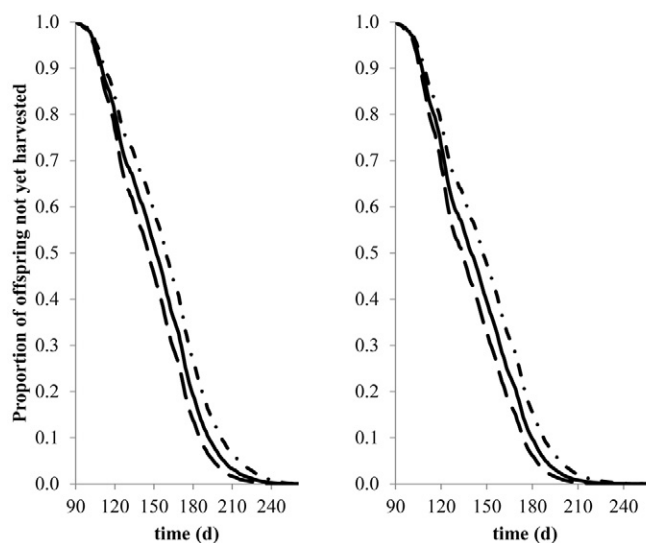
scale of the log- $\gamma$  distribution. The mean and mode were 0.137 and 0.138, respectively. Its SD was 0.017. The heritability of DTH was estimated as 0.21.

The mean HR for sires with EBV in the top and bottom 10% of the population was 1.17 and 0.84, respectively, which corresponded with genetic standard deviation units of 2.41 and  $-2.68$ . For a HR of 1.17, the expected median DTH for single-reared lambs was 114 d and for twin-reared lambs was 167 d. For a HR of 0.84, these values were 123 and 178 d. Approximate accuracies ranged from 0.26 to 0.92.

As an illustration of the consequence of sire genetic differences in survival rate, expected survival curves for Suffolk and Texel sires were calculated. These are shown for twin ewe offspring from a contemporary group born in 2003 to Scottish Mule dams in Scotland (Fig. 3). Sire HR of 0.8, 1.0, and 1.2 were assumed. As expected, DTH decreased with increasing sire HR. The median DTH for Suffolk sires with a HR of 0.8 was 159 d, with a HR of 1.0 was 151 d, and with a HR of 1.2 was 145 d. For Texel rams, the median DTH was 147 d with a HR of 0.8, 139 d with a HR of 1.0, and 133 d with a HR of 1.2.

### Bivariate Model

**Design Variable Solutions.** In the bivariate model there were no differences between high- and low-index sired lambs for DTH ( $P = 0.17$ ). Index differences were observed for HWT, with high index sired lambs being 0.46 kg heavier than low index sired lambs. There were no differences between Suffolk- and Charollais-sired lambs in DTH ( $P > 0.10$ ) although Texel-sired lambs reached harvest condition on average 12 d faster than Suffolk- or Charollais-sired lambs ( $P < 0.01$ ). At finishing, Suffolk-



**Figure 3.** Expected survival curves of Suffolk (left) and Texel (right) sires with hazard ratios of 1.2 (dashed line), 1.0 (solid line), and 0.8 (dashed and dotted line). The illustrations are for twin ewe offspring of these sires from a contemporary group born in 2003 to Scottish Mule dams in Scotland.

sired lambs were heavier than Charollais- and Texel-sired lambs. Charollais-sired lambs were heavier than Texel-sired lambs. These results are similar to those reported in Márquez et al. (2013) for the same data.

Breed of dam defined a significant amount of variation for both traits, with Scottish mules rearing lambs on average 2.2 kg heavier than Welsh mules. Lambs from Scottish mules reached harvest 1.6 d later than those from Welsh mules. The age of the dam also influenced both traits, with older ewes rearing heavier lambs in fewer days ( $P < 0.01$ ).

**Variance Component Estimates.** The genetic correlation between DTH and HWT was  $0.58 \pm 0.10$ , and the residual correlation was  $0.45 \pm 0.01$ . The heritability of DTH was  $0.20 \pm 0.04$  and for HWT  $0.19 \pm 0.04$ . The rank correlation between sire EBV for DTH obtained from the survival and bivariate analyses was 0.9. Among the 5 highest ranking rams (approximately 5%), 4 were the same in both methods.

## DISCUSSION

**Model Selection.** Modeling DTH data was challenging because of its highly skewed and nonnormal distribution. Attempts were made to transform and to fit alternative distributions to these data (e.g., Gamma, zero inflated Poisson). All of these provided a very poor fit. Because DTH reflects a time to an event (harvest), a survival model was deemed appropriate. Still, there are drawbacks of survival analysis. There are larger computation requirements, which make fitting large animal models difficult. It is not straightforward to include maternal additive effects in the model fitted or to do multivariate analyses.

To account for possible selection for a correlated trait, an alternative to the survival model was to fit DTH as a normally distributed variable in a bivariate analysis. A drawback to this approach is that differences in the distributions of DTH in single- and twin-reared lambs were not intimately modeled.

The nonnormality in the distribution of DTH stemmed from the differences between single- and twin-reared lambs (Fig. 1). There are biological reasons for these differences: single-reared lambs have more resources from their dams whereas twins have to compete for these resources to grow. Previous studies (e.g., Tosh and Kemp, 1994) have identified litter size as a factor affecting growth: competition between multiple-reared lambs keeps them from realizing their full genetic potential before weaning. Therefore, single-reared lambs have an advantage in growth over twin-reared lambs. There was a wide range of DTH in these lambs, as can be observed from the long tail in the distribution of DTH for single-reared lambs. This result suggests that some single-reared lambs either lacked the genetic potential to take advantage of their favorable environment or simply were unthrifty. This skewness was not year or site specific but general for all lambs. The distribution of DTH for twin-reared lambs more nearly approached normality but still exhibited some skewness.

### ***Index and Breed Comparisons***

Lambs were finished to a fixed fat level so they would be at comparable physiological maturity at harvest. Ideally, animals should be compared at a fixed maturity level because different body tissues grow at different rates (Butterfield, 1988). Under nonlimiting conditions, animals will follow a genetically determined path towards maturity: growth rates of bone tissue followed by lean tissue would be higher earlier in this trajectory. After reaching maturity, the animals primarily are depositing fat tissue (Lewis et al., 2002a). Therefore, comparing animals at fixed levels of physiological maturity, as approximated by fatness, is more equitable than comparisons at fixed ages or weights (Parks, 1982).

The lack of differences in DTH between lambs sired by high and low index rams in either evaluation model is favorable. Rams were selected on an index that constrained fat growth (Simm and Dingwall, 1989). Therefore it could be expected that lambs sired by leaner (high index) rams would require more time to reach a fixed harvest fatness level than those sired by fatter (low index) rams. Because this was not the case, terminal sire breeders selecting on the lean growth index do not have to be concerned about deleterious consequences on DTH. Likewise, selection for improved carcass merit does not extend the grazing period or potentially require additional feeding after grazing is exhausted, with risk

of increasing production costs. This selection index has been used in the United Kingdom with favorable results in growth and carcass traits (Lewis et al., 1996, 2002b).

In both models, Charollais- and Suffolk-sired lambs did not differ in DTH whereas Texel-sired lambs reached harvest fatness earlier than either. At harvest, Suffolk- and Texel-sired lambs did not differ in ultrasonic fatness whereas Charollais-sired lambs were fatter; in the bivariate analysis, Suffolk-sired lambs were heaviest followed by Charollais and then Texel-sired lambs, similar to results in Márquez et al. (2013). Some research (Cameron and Drury, 1985; Kempster et al., 1987) suggests that breeds with lighter mature weights tend to reach a level of subcutaneous fat more quickly.

Ewe breed did not define variation in DTH in the survival model. Although significant when DTH was considered normally distributed in the bivariate model, the difference between ewe breeds was small (1.6 d). Such small differences between ewe breeds in DTH are favorable. Maternal heritabilities for growth at and after weaning have been found to be low (Safari et al., 2005), indicating a waning maternal influence at harvest. However, Fogarty et al. (2000) found that the breed of dam is influential in determining the age at which lambs reach harvest condition. That study used Merino and Merino cross ewes, and the authors hypothesized that this reflects the differences in the sizes of the ewes. Our results indicate that United Kingdom sheep producers likely have flexibility in choosing Mule (crossbred) ewe types to mate to terminal sires, particularly with regards to DTH.

### ***Genetic Evaluation***

Our estimates of genetic parameters using either model show that there is variation in DTH. Heritability estimates were moderate, which was expected because it effectively resembles growth rate, with heritability estimates of a similar magnitude. The estimates were also very similar between the 2 analytical approaches: 0.21 for survival analysis and 0.20 for the bivariate analysis. Safari et al. (2005) reviewed estimates of genetic parameters of sheep and reported heritabilities for weight gain of  $0.17 \pm 0.01$ . These results indicate that there is potential for genetic improvement if DTH was incorporated into a selection program.

Genetic variation in DTH exists among sire breeds, as evidenced by the differences in median DTH of different breeds (Fig. 3) and, in the survival model, by the HR of sire breeds (Table 2). There was a difference of 14 d between median DTH of sires with HR of 0.8 and 1.2, indicative of a range in the finishing period depending on the sire's breeding value. The ranking of sire breeds in DTH was similar in the bivariate analysis, substantiating that differences in harvest periods could be expected across breed types.



The method used for genetic evaluation of DTH influenced sire solutions. The rank correlation of sire EBV of 0.9 obtained from the survival and bivariate analyses indicated that rerankings of sires will be present although they may not be substantial. Both methods have advantages and drawbacks. Survival analysis may better account for differences in rearing types of lambs but is currently restricted to univariate applications. Although less able to model distributional differences between rearing types, multivariate evaluations of normally distributed traits is common in genetic evaluations. Although any selection bias was likely small in these data—all lambs were harvested—it can be addressed with a multivariate approach. Linear models are known to be robust to departures from normality stemming from the central limit theorem. Given the size of these data, the large correlation between EBV may reflect that robustness.

### *Economic Relevance*

A considerable amount of the cost associated with finishing an animal is related to the days it spends on feed to reach a desired harvest endpoint. Golden et al. (2000) suggest that DTH is an economically relevant trait in beef cattle and that genetic evaluation in terms of EBV for this trait would simplify comparing the costs of finishing progeny of different sires (Garrick and Enns, 2003). Still, an economic evaluation of the profitability of selecting for reduced DTH in sheep systems is needed, given that this has not been done previously.

Days to harvest EBV have been developed for beef cattle and could be developed for sheep breeding programs. The justification for doing so, however, depends on this trait's economic relevance with respect to other traits affecting growth and harvest attributes. Still, if warranted, the best way to incorporate a DTH EBV would be as part of a selection index that considers these and other components of the breeding objective. The different harvest endpoints used in commercial production would need to be considered in the design of such an index. In the United States, the Gelbvieh beef breed publishes a carcass value index that incorporates estimates of genetic merit for carcass weight, DTH, marbling, and rib eye area. These are adjusted to a constant fat endpoint (American Gelbvieh Association, 2011).

From these results we conclude that selection on the lean growth index does not have negative effects on the number of days required for lambs to reach a target level of fatness. Differences between terminal sire breeds exist and can be exploited by producers to select the best rams for their production system. These and previous results (Márquez et al., 2012, 2013) lead us to recommend wider uptake of index-based selection as a permanent

and cost-effective way to improve sheep in the United Kingdom and elsewhere.

Furthermore, genetic evaluation of DTH using either survival analysis or a bivariate model is computationally feasible. Heritability estimates were similar in both methods and the correlation between sire EBV was high. We are better able to model nonnormality and differences in the distribution of single- and twin-reared lambs with the survival analysis. However, if there is selection for other traits, biases cannot be directly addressed. It therefore may be more pragmatic to include DTH as a normally distributed variable in genetic evaluation programs.

Because DTH was moderately heritable, improvement through genetic selection can be expected. If economically justified, DTH could be incorporated into an index to facilitate reducing the costs of finishing lambs in pasture-based systems.

### LITERATURE CITED

- American Gelbvieh Association. 2011 Gelbvieh adds value when feeding cattle. [www.gelbvieh.org/communication/news.html?dt=092011](http://www.gelbvieh.org/communication/news.html?dt=092011). (Accessed November 13 2012).
- Anderson, T., and D. Darling. 1952. Asymptotic theory of certain "goodness-of-fit" criteria based on stochastic processes. *Ann. Math. Stat.* 23:193–212.
- Butterfield, R. M. 1988. *New concepts of sheep growth*. University of Sydney, Australia.
- Cameron, N. D., and D. J. Drury. 1985. Comparison of terminal sire breeds for growth and carcass traits in crossbred lambs. *Anim. Prod.* 40:315–322.
- Cox, D. 1972. Regression models and life-tables. *J. R. Stat. Soc. Series B Stat. Methodol.* 34:187–220.
- Ducrocq, V. 1997. Survival analysis, a statistical tool for longevity data. In: *Proc. 48th Annu. Meet. Eur. Assoc. Anim. Prod., Vienna, Austria*. p. 1–14.
- Ducrocq, V., and G. Casella. 1996. A Bayesian analysis of mixed survival models. *Genet. Sel. Evol.* 28:505–529.
- Ducrocq, V., J. Sölkner, and G. Mészáros. 2010. Survival Kit v6 – A software package for survival analysis. In: *Proc. 9th World Congr. Genet. Appl. Livest. Prod., Leipzig, Germany*. p. 232–235.
- Fogarty, N. M., D. L. Hopkins, and R. van der Ven. 2000. Lamb production from diverse genotypes. 1. Lamb growth and survival and ewe performance. *Anim. Sci.* 70:135–145.
- Garrick, D. J., and R. M. Enns. 2003. How to best achieve genetic change? In: *Proc. Beef Improvement Federation 35th Annual Res. Symp. and Annual Meet.*, Lexington, KY. p. 48–50.
- Gilmour, A. R., B. J. Gogel, B. R. Cullis, and R. Thompson. 2009. *ASReml user guide release 3.0*. VSN International Ltd., Hemel Hempstead, UK.
- Golden, B. L., D. J. Garrick, S. Newman, and R. M. Enns. 2000. Economically relevant traits. A framework for the next generation of EPDs. In: *Proc. 32nd Beef Improvement Federation 32nd Annual Res. Symp. and Annual Meet.*, Wichita, KS. p. 2–13.
- Kachman, S. D. 1999. Applications in survival analysis. *J. Anim. Sci.* 77(Suppl. 2):147–153.
- Kalbfleish, J., and R. Prentice. 2002. *The statistical analysis of failure time data*. J. Wiley & Sons, Hoboken, NJ.

- Kaplan, E., and P. Meier. 1958. Nonparametric estimation from incomplete observations. *J. Am. Stat. Assoc.* 53:457–481.
- Kempster, A. J., G. L. Cook, and M. Grantley-Smith. 1986. National estimates of the body composition of British cattle, sheep and pigs with special reference to trends in fatness. A review. *Meat Sci.* 17:107–138.
- Kempster, A. J., D. Croston, D. R. Guy, and D. W. Jones. 1987. Growth and carcass characteristics of crossbred lambs by ten sire breeds, compared at the same estimated carcass subcutaneous fat proportion. *Anim. Prod.* 44:83–98.
- Leeds, T. D., D. R. Notter, K. A. Leymaster, M. R. Mousel, and G. S. Lewis. 2012. Evaluation of Columbia, USMARC-Composite, Suffolk, and Texel rams as terminal sires in an extensive rangeland production system: I. Ewe productivity and crossbred lamb survival and preweaning growth. *J. Anim. Sci.* 90:2931–2940.
- Lewis, R. M., G. C. Emmans, W. S. Dingwall, and G. Simm. 2002a. A description of the growth of sheep and its genetic analysis. *Anim. Sci.* 74:51–62.
- Lewis, R. M., G. C. Emmans, and G. Simm. 2002b. Effects of index selection on the carcass composition of sheep given either ad libitum or controlled amounts of food. *Anim. Sci.* 75:185–195.
- Lewis, R. M., G. Simm, W. S. Dingwall, and S. V. Murphy. 1996. Selection for lean growth in terminal sire sheep to produce leaner crossbred progeny. *Anim. Sci.* 63:133–142.
- Márquez, G. C., W. Haresign, M. H. Davies, G. C. Emmans, R. Roehe, L. Bünger, G. Simm, and R. M. Lewis. 2012. Index selection in terminal sires improves early lamb growth. *J. Anim. Sci.* 90:142–151.
- Márquez, G. C., W. Haresign, M. H. Davies, R. Roehe, L. Bünger, G. Simm, and R. M. Lewis. 2013. Index selection in terminal sires improves lamb performance at finishing. *J. Anim. Sci.* 91:38–43.
- Parks, J. R. 1982. *A theory of feeding and growth of animals*. Springer-Verlag, Berlin, Germany.
- Pollott, G. E., and D. G. Stone. 2004. *The breeding structure of the British sheep industry 2003*. Department for Environment Food and Rural Affairs, London, UK.
- Safari, E., N. M. Fogarty, and A. R. Gilmour. 2005. A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. *Livest. Prod. Sci.* 92:271–289.
- Simm, G., and W. S. Dingwall. 1989. Selection indices for lean meat production in sheep. *Livest. Prod. Sci.* 21:223–233.
- Simm, G., R. M. Lewis, J. E. Collins, and G. J. Nieuwhof. 2001. Use of sire referencing schemes to select for improved carcass composition in sheep. *J. Anim. Sci.* 79:E255–E259.
- Tosh, J. J., and R. A. Kemp. 1994. Estimation of variance components for lamb weights in three sheep populations. *J. Anim. Sci.* 72:1184–1190.
- van Heelsum, A. M., R. M. Lewis, M. H. Davies, and W. Haresign. 2003. Growth and carcass characteristics in wether lambs of a crossbred dam line. *Anim. Sci.* 76:45–53.
- Yazdi, M. H., P. M. Visscher, V. Ducrocq, and R. Thompson. 2002. Heritability, reliability of genetic evaluations and response to selection in proportional hazard models. *J. Dairy Sci.* 85:1563–1577.

## References

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