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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[1,2]

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ABSTRACT: A 3-yr study was conducted to comprehensively evaluate Columbia, Suffolk, USMARC-Composite (Composite), and Texel breeds as terminal sires in an extensive rangeland production system. The objective was to estimate breed-of-ram effects on ewe fertility, prolificacy, and dystocia, and sire breed effects on lamb survival and growth until weaning at approximately 132 d of age. Data were from 22 Columbia, 22 Composite, 21 Suffolk, and 17 Texel rams with 957 exposures to 574 adult Rambouillet ewes (3- to 7-yr-old at lambing), 908 lambings, and 1,834 lambs. Ram breed did not affect ewe fertility (mean = 94.9%; P = 0.73), total number born per ewe lambing (mean = 2.02 lambs; P = 0.20), number born alive per ewe lambing (mean = 1.90 lambs; P = 0.24), or number weaned per ewe lambing (mean = 1.45 lambs, P = 0.94). Dystocia rates were different (P = 0.01) for ewes mated to Columbia (12.2%), Composite (13.5%), Suffolk (25.7%), and Texel rams (31.9%) during 1 yr of the study, but differences among ram breeds were not repeatable ($P \geq 0.38$) during the other 2 yr. Suffolk-sired lambs were heavier ($P \leq 0.02$) at birth (5.5 kg) and weaning (40.3 kg) than lambs sired by the other breeds, which did not differ ($P \geq 0.34$) for birth weight (mean = 5.3 kg). Texel-sired lambs (37.4 kg) were lighter ($P \leq 0.02$) at weaning than Columbia- (38.8 kg) and Composite-sired (38.4 kg) lambs, which did not differ (P = 0.40) for weaning weight. Sire breed effect approached significance (P = 0.06) for lamb survival to weaning; estimated survival probabilities were 0.87 (Columbia), 0.89 (Composite), 0.93 (Suffolk), and 0.86 (Texel) for lambs reared by their birth dam. Interaction between sire breeds and birth weight affected (P < 0.001) lamb survival and revealed that lightweight Columbia- and Suffolk-sired lambs had a greater risk of death than lightweight lambs sired by Composite and Texel rams, but risk of death did not increase substantially for heavyweight lambs from any of the breeds. When mated to adult Rambouillet ewes in an extensive rangeland production system, the use of Suffolk rams is warranted to improve preweaning growth of market lambs and is not predicted to affect ewe fertility, ewe prolificacy, dystocia, or lamb survival compared with the other sire breeds we tested.

Key words: breeds, dystocia, ewe productivity, growth, lamb survival, sheep

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INTRODUCTION

Extensive diversity among sheep (*Ovis aries*) breeds, production environments, and management systems requires systematic and comprehensive breed evaluations to allow producers to identify breeds that are best suited for their production system. Nearly 50% of the U.S. breeding sheep inventory is located in 11 western states (NASS, 2010) where sheep are primarily grazed on rangelands. Well-adapted ewes with moderate prolificacy and primarily Rambouillet

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ancestry are commonly mated to Suffolk and Columbia rams for commercial lamb production. The favorable growth and leanness of the Suffolk breed have been well documented. However, producers have criticized the fitness of Suffolk-sired lambs, and experimental data have supported this criticism (e.g., Smith, 1977). Columbia is traditionally considered to be a dual purpose meat-wool breed, is well-adapted to extensive rangeland production systems, and has experienced a significant increase in body size as a result of selection. Comparative data for other terminal sire breeds in extensive rangeland production are lacking in the literature.

A 3-yr study was conducted at the U.S. Sheep Experiment Station (Dubois, ID) to comprehensively evaluate Columbia, Suffolk, USMARC-Composite (**Composite**), and Texel breeds as terminal sires in an extensive rangeland production system. Traits characterized included mating ewe productivity, crossbred progeny performance from birth to market BW, and carcass merit. The Composite was developed in the 1970s, has 50% Columbia, 25% Hampshire, and 25% Suffolk ancestry (Leymaster, 1991), and is less extreme in adult size than currently-available rams of these breeds. The Texel breed originated in the Netherlands, has a moderate body size with desirable muscularity, and is used extensively as a terminal sire breed in Europe, Australia, and New Zealand. This manuscript describes breed-of-ram effects on ewe productivity and dystocia and sire breed effects on lamb survival and growth until weaning.

MATERIALS AND METHODS

The U.S. Sheep Experiment Station (**USSES**) Institutional Animal Care and Use Committee (Dubois, ID) reviewed and approved all husbandry practices used in this study.

General Experimental Design

Columbia (n = 22), Suffolk (n = 22), and Texel (n = 20) rams were sampled from 11, 11, and 10 industry flocks, respectively, and from USSES Columbia and Suffolk flocks. Fifty percent and 27% of Suffolk and Columbia rams, respectively, were acquired from flocks (n = 6 and 3, respectively) participating in the U.S. National Sheep Improvement Program (**NSIP**); no Texel flocks participated in NSIP. Texel rams were primarily descendants of sheep imported into the United States from Denmark and Finland in 1985 (Leymaster and Jenkins, 1993). All Composite rams (n = 22) were sampled from the U.S. Meat Animal Research Center (Clay Center, NE) flock.

Yearling rams were preferred and accounted for 88% (76 of 86) of the rams used in the study. However, logistical considerations and limited availability of yearling Texel rams resulted in the use of a few older rams and ram lambs. Purchased rams were transported to the USSES in early summer, isolated from USSES flocks for 6 to 8 wk, and monitored for evidence of disease.

Ewes were sampled from the USSES Rambouillet flock, which has been selected for increased BW of the weaned litter since 1976 (Ercanbrack and Knight, 1998). Ewes were selected each year from approximately 700 available ewes based on age and average annual BW of lambs weaned. Young ewes (1 or 2 yr old at lambing) and the highest-ranking ewes were assigned to matings with purebred Rambouillet rams and were thus excluded from the current study, whereas lower-ranking adult ewes (3 to 7 yr old at lambing) were assigned at random within ewe age and sire to be mated to 1 of the 4 terminal sire breeds.

The experimental design specified that approximately 10 Rambouillet ewes would be mated to each of 8 or 9 rams per sire breed each autumn (2005, 2006, and 2007), resulting in approximately 330 matings per year. Most rams were used for only 1 yr, but at least 2 rams per sire breed were retained and mated in the subsequent year to provide genetic linkages across years. All rams were tested and confirmed to have acceptable libido (Stellflug et al., 2006) before commencement of each mating season. However, 3 Texel rams in 2005 and 1 Suffolk ram in 2007 failed to sire any lambs. Subsequent semen testing and behavioral observation indicated that the 3 Texel rams were sterile and that the Suffolk ram consistently failed to achieve vaginal intromission. Our objective was to evaluate sire breeds using only fertile rams; therefore, data from these rams were removed from the dataset. Table 1 summarizes numbers of rams, matings, and total lambs born by sire breed and year.

Flock Management

Each year, rams were exposed to ewes in single-sire breeding pens for a 21-d period beginning mid-October. After mating, ewes were herded as a single contemporary group on shrub-dominated winter range. Six Suffolk cleanup rams were herded with the ewes on winter range for approximately 21 d to mate with any ewes that had not conceived to the planned mating sire. Ewes remained on the winter range until mid- to late-January and then were maintained in a drylot and fed to meet or exceed NRC requirements (NRC, 1985). Ewes were shorn and vaccinated against clostridial diseases (Covexin 8; Intervet/Schering-Plough Animal Health, Whitehouse Station, NJ) in mid-February.

Ewes lambed in March and early April (2006, 2007, and 2008) in outdoor lots under frequent surveillance (i.e., ewes were observed once every 1 to 2 h), and ewes exhibiting signs of dystocia were assisted. After lambing, ewes and their lambs were moved to individual, indoor claiming pens for approximately 48 h. Within 24 h after birth, lambs were

Table 1. Numbers of rams[1], matings[2], and lambs born by ram breed and year

	Ram breed											
	Columbia			USMARC-Composite			Suffolk			Texel		
Year	Rams	Matings	Lambs	Rams	Matings	Lambs	Rams	Matings	Lambs	Rams	Matings	Lambs
2005/2006	8	79 (76)	139	8	80 (79)	152	8	79 (78)	157	8[3]	80 (50)	96
2006/2007	9 (2)	88 (86)	173	9 (2)	88 (86)	174	9 (2)	88 (86)	171	9 (4)	96 (95)	181
2007/2008	9 (2)	85 (83)	153	9 (2)	85 (84)	159	9[4] (2)	85 (73)	123	9 (2[5])	85 (81)	156
Total[6]	22	252 (245)	465	22	253 (249)	485	22	252 (237)	451	20	261 (226)	433

[1]Numbers in parentheses are the numbers of rams that were used in the previous mating year.

[2]Numbers in parentheses are the numbers of matings from which data were used in the study. Ewes mated to the 4 rams that did not sire any lambs and ewes that died before lambing were excluded from all analyses.

[3]Three Texel rams in 2005 were sterile and were excluded from the study.

[4]One Suffolk ram in 2007 did not sire any lambs and was excluded from the study.

[5]One ram was used in the 2 previous mating years.

[6]Total given for rams is the number of rams initially sampled for the study.

given unique identification using ear tags, and elastrator bands were used to dock tails at the distal end of the caudal tail fold and to castrate ram lambs. During the initial claiming period, lambs were orphaned or cross-fostered as needed based on subjective evaluations of the ability of the ewe to rear the litter (e.g., milking ability and general health) and the viability of the lamb (e.g., birth weight, abomasal fill, and vigor). Most ewes giving birth to 3 or more lambs were limited to rearing no more than 2 lambs; however, 6 ewes were given the opportunity to rear 3 lambs.

After the claiming period, ewes and litters were commingled in outdoor lots, and ewes were fed to meet or exceed NRC requirements (NRC, 1985) for approximately 1 mo. Ewes and litters were herded as a single contemporary group on sagebrush-steppe range beginning late April or early May and subalpine range beginning early July. Lambs were weaned in early August at approximately 132 d of age.

Traits and Data

Ram size and Conformation. In July or August of each year, yearling rams used as sires in this study were weighed and evaluated for BCS, shoulder height and width, hip width, heart girth, body length, canon bone circumference, scrotal circumference, and ultrasonic backfat thickness and LM area (Leeds et al., 2008) between the 12th and 13th ribs.

Ewe Productivity. Ewe fertility was recorded as 0 for open ewes (i.e., nonpregnant) and 1 for ewes that lambed. Ewe prolificacy was recorded as total number of live plus stillborn lambs (**TNB**) and number born alive (**NBA**). Numbers of lambs removed from the litter (i.e., orphaned or cross-fostered lambs) and weaned were also recorded for all ewes that lambed. Records of ewes mated to the 4 rams that did not produce any lambs (n = 40 ewes) and ewes that died or became missing during the period between mating and lambing (n = 5, 7, and 9 ewes mated in 2005, 2006, and 2007, respectively) were removed from the dataset. Date of lambing, and lamb color when appropriate (i.e., for all sire breeds except Suffolk), were used to discriminate between ewes that conceived to the planned mating sire and ewes that conceived to a cleanup sire. Lamb records for ewes that conceived to a cleanup sire were removed from the dataset and these ewes were considered open.

Dystocia. In 2006, dystocia scores were assigned as 1 = normal, no assistance; 2 = normal, but lamb was palpated in birth canal to check status; 3 = assistance due to malpresentation of leg(s); 4 = assistance due to malpresentation of head; 5 = assistance, breech; 6 = assistance due to other reasons; and 7 = assistance due to severe difficulty. Explanations of the nature of the lambing difficulty were recorded for scores of 6 and 7. This system did not record dystocia scores for individual lambs, but instead characterized dystocia of the entire litter based on the lamb with the largest score, and did not specifically address dystocia associated with lambs having heavy birth weight.

The dystocia scale was modified for 2007 and 2008, and scores were assigned to individual lambs instead of the entire litter to characterize the association between dystocia and birth weight. Scores 1 through 5 remained unchanged; 6 = assistance due to lack of cervical dilation; 7 = assistance due to other reasons (with explanation); and 8 = assistance due to large lamb. Furthermore, shepherds in 2007 and 2008 were strongly discouraged from providing lambing assistance that was not clearly indicated. Throughout the study, shepherds did not have advanced knowledge of the ram breed mated to each ewe.

Lamb Performance. Birth weight was recorded for all stillborn lambs and lambs born alive. Lamb BW were recorded in late April or early May (mean age = 36.8 d; SD = 7.2 d) before grazing sagebrush steppe range (2007 and 2008 only), in late June (mean age = 97.7 d; SD = 6.0 d) before grazing subalpine range, and at weaning in early August (mean age = 132.1 d; SD = 6.3 d).

Lamb survival was recorded as age (d) at death or censoring, and the birth date was considered d 1 of age. A total of 241 lambs were stillborn or died before weaning. Survival records were censored when a lamb was orphaned (n = 212), cross-fostered (n = 33), or weaned (n = 1,314). The experimental design specified that ewes and lambs would be maintained each year in a single contemporary group. However, 18 ewes were removed from the contemporary group, either accidentally or due to poor health of the ewe, and records of their 24 lambs were censored at 3 d of age. Ten lambs became missing while being herded on the rangelands, and their records were censored at the oldest age at which their own BW was recorded.

Statistical Analyses

Ram Conformation Traits. Data for conformation traits of 76 yearling rams were described with a linear model using PROC GLM (SAS Inst. Inc., Cary, NC) to provide a general characterization of the rams as they arrived at the USSES. Because of the diversity in origin of these rams, breed was the only effect included in the model.

Ewe Productivity. Data for ewe productivity traits were described using PROC GLIMMIX (SAS Inst. Inc.) with a model including fixed effects of ram breed, year, ewe age, and ram breed × yr interaction, and random effects of ram (nested within year and ram breed) and ewe. Nesting of ram effects within year and ram breed resulted in estimation of year-specific constants for the 17 rams used in multiple years. The numbers of ewes used for 1, 2, or all 3 yr of the study were 283, 199, and 92, respectively.

Ewe fertility was analyzed as a binomial variable. Ewe prolificacy, number of lambs removed from the litter, and number of lambs weaned were analyzed as ordered multinomial variables using only data from ewes that lambed. Data from open ewes were included in a subsequent analysis of number of lambs weaned to express this trait on a per-ewe-joined basis. The GLIMMIX procedure does not provide back-transformed least-squares means for ordered multinomial variables, so means for fixed-effect variables were approximated assuming a normal distribution.

Dystocia. Frequencies of dystocia scores ≥ 3 ranged from 0 to 6.7% among years and thus were too small to permit statistical analysis of the different types of dystocia. Furthermore, only 11 lambs (n = 4 Columbia-, 4 Composite-, 1 Suffolk-, and 2 Texel-sired), all born in 2008, had a dystocia score of 8, giving no indication of sire breed differences in dystocia associated with large lambs. Thus, litter- and lamb-based dystocia scores were reclassified as "normal" (score = 1 or 2) and "assisted" (score ≥ 3). To allow direct comparison of frequencies of dystocia across all 3 yr, litter-based dystocia classifications were derived for ewes lambing in 2007 and 2008 to mimic the scoring system used in 2006.

Differences among sire breeds for frequency of dystocia on either a litter basis or lamb basis (2007 and 2008 only) were tested within years by χ^2 analysis. The overall effect of sire breed after adjusting for year effects was tested using the Cochran-Mantel-Haenszel general association statistic (Cochran, 1954; Mantel and Haenszel, 1959; Mantel, 1963; Birch, 1965; Landis et al., 1978) in PROC FREQ (SAS Inst. Inc.).

Lamb Growth. Birth weight data were described with a mixed-effects linear model using PROC MIXED (SAS Inst. Inc.). The initial (full) model included fixed effects of sire breed, year, TNB, ewe age, lamb gender, and all 2-way interactions with sire breed, and random effects of sire (nested within year and sire breed) and ewe. Lambs born as quadruplets (n = 16) were grouped with triplet-born lambs for the analysis. All design variables (sire breed, year, and ewe age) remained in the model regardless of significance level. Interaction terms were removed sequentially from the model based on significance level, and only interaction terms with $P \leq 0.05$ remained in the final model. The Satterthwaite option was used to approximate denominator degrees of freedom for tests of fixed effects. Data from stillborn lambs and lambs born alive were included in the analysis, with the exception that BW of lambs born prematurely (n = 33) were excluded. Eight lambs had missing birth wight data.

The model for BW recorded in late April or early May, late June, and at weaning in early August was similar to that for birth wight except that lamb age at the time of the BW measurement was included as a linear covariate, and a variable for type of birth and rearing (**TBR**) replaced TNB. The TBR variable grouped lambs according to the TNB and total number reared in the litter and had 5 classes (1-1, 2-1, 2-2, 3-1, and 3-2). Due to small counts, lambs with TBR of 1-2 were grouped with 2-2, and lambs with TBR of 3-3, 4-2, and 4-3 were grouped with 3-2. A ewe was deemed to have reared a lamb if the lamb was present with the litter at $\geq$14 d of age.

Lamb Survival. Survival data were described with a Weibull survival model using PROC LIFEREG (SAS Inst. Inc.). The initial (full) model included effects of sire breed, year, TNB (1, 2, or 3+ lambs), ewe age, lamb gender, linear and quadratic effects of birth weight, and all 2-way interactions with sire breed, including covariates. Birth weights were expressed as deviations from the respective sire breed mean in the analysis; thus, breed differences in survival include effects of mean differences in birth weight. All design variables (sire breed, year, and ewe age) remained in the model regardless of significance level. Interaction terms and non-design variables were removed sequentially from the model based on significance level, and only terms with $P \leq 0.05$ remained in the final model. Survival functions were estimated as $S_i(t) = \exp\{-[t_i e^{-\beta x_i}]^{1/\sigma}\}$, where $S_i(t)$ is the probability that the ith lamb survives to age t, $\boldsymbol{\beta}$ is a vector of regression coefficients associated with explanatory variables with design vector $\mathbf{x}$ for the ith lamb, and σ is a scale parameter (Allison, 1995). If $\sigma > 1$, the hazard is decreasing over time; if $\sigma < 1$, the hazard is increasing over time. Wald χ^2 statistics were calculated as $(\beta_1 - \beta_2) \div [\mathrm{var}(\beta_1) + \mathrm{var}(\beta_2) - 2 \times \mathrm{cov}(\beta_1\ \beta_2)]$, where β_1 and β_2 are sire breed solutions, to test differences among sire breeds (Allison, 1995). Records of 36 lambs (all stillborn) with missing birth weight or gender information were excluded from the analysis.

RESULTS

Ram Size and Conformation

Least-squares means for yearling ram conformation traits are shown in Table 2. Breed differences are confounded with flock of origin, thereby limiting inferences that can be drawn from Table 2, especially for Composite rams, which came from a single flock and were developed on a lower plane of nutrition than that anticipated in industry seedstock flocks. However, differences among Columbia, Suffolk, and Texel rams are generally considered representative of those observed in the industry. Columbia and Suffolk rams were similar in BW ($P = 0.41$) and heavier than Composite and Texel rams ($P \leq 0.001$), which likewise did not differ in BW ($P = 0.14$). Differences among breeds for conformation traits were generally consistent with differences observed for BW. However, Composite rams were taller at the shoulder ($P = 0.003$) and longer-bodied ($P < 0.001$) than Texel rams despite similar BW. Texel rams, despite lighter BW, did not differ from Columbia rams for shoulder width ($P = 0.46$), from Suffolk rams for hip width ($P = 0.99$), or from either breed for ultrasonic backfat thickness ($P \geq 0.35$). No differences were detected among the breeds for BCS ($P = 0.20$).

Table 2. Breed least-squares means for conformation traits measured on 76 yearling rams[1]

	Breed				
Trait	Columbia	USMARC-Composite	Suffolk	Texel	Pooled SE
BW, kg	128.3[a]	94.9[b]	135.5[a]	83.9[b]	3.4
BCS	5.5	5.1	5.4	5.7	0.2
Shoulder height, cm	92.8[a]	76.7[b]	93.0[a]	71.6[c]	1.0
Shoulder width, cm	32.5[ab]	30.4[c]	33.8[a]	31.7[bc]	0.4
Hip width, cm	33.4[a]	29.3[b]	32.4[ab]	28.8[b]	0.9
Heart girth, cm	123.0[a]	108.5[b]	120.3[a]	104.4[b]	1.6
Body length, cm	96.1[a]	82.8[b]	95.2[a]	73.4[c]	1.3
Canon bone circumference, cm	13.7[a]	12.2[b]	13.5[a]	11.8[b]	0.3
Ultrasonic backfat thickness, mm	3.5[ab]	2.7[a]	4.2[b]	3.2[ab]	0.4
Ultrasonic LM area, cm^2	25.0[a]	20.9[b]	27.8[a]	21.5[b]	0.8
Scrotal circumference, cm	36.9[ab]	34.9[c]	38.6[a]	35.0[bc]	0.5

[a-c]Means within a row with different superscripts differ ($P \leq 0.05$). Mean separation tests were adjusted for multiple comparisons using the Tukey-Kramer option in PROC GLM (SAS Inst. Inc., Cary NC).

[1]Least-squares means are not adjusted for BW differences among breeds.

Ewe Productivity

Inferences from this study were made using data from 957 exposures of 574 ewes to 82 rams, 908 lambings, and 1,834 lambs. Estimates of ram breed effects on ewe productivity traits are shown in Table 3. During the study, 94.9% of ewes lambed, and TNB and NBA for ewes that lambed averaged 2.02 and 1.90 lambs, respectively. An average of 0.27 lamb per litter (14.2% of NBA) was orphaned or cross-fostered. Number of lambs weaned per ewe joined and per ewe lambing averaged 1.37 and 1.45, respectively. Ram breed effects were not detected ($P \geq 0.14$) for any ewe productivity trait. However, the ram breed × year interaction approached significance for TNB ($P = 0.09$), NBA ($P = 0.08$), and number of lambs removed from the litter ($P = 0.09$). Across years, rams of the larger breeds (i.e., Columbia and Suffolk) tended to have more variation in TNB than Composite and Texel rams. Means for TNB ranged from 1.89 to 2.14 lambs for Columbia rams and 1.87 to 2.12 lambs for Suffolk rams but were quite consistent for Composite (range = 2.04 to 2.09 lambs) and Texel rams (range = 2.03 to 2.05 lambs). More Suffolk- and Composite-sired lambs tended to be removed from the litter in 2006 than Columbia- and Texel-sired lambs, whereas differences among the sire breeds were smaller in 2007 and 2008 (data not shown).

Dystocia

Percentages of ewes and lambs requiring lambing assistance are given by sire breed and year in Table 4. In 2006, ewes mated to Suffolk and Texel rams had a greater frequency of dystocia than ewes mated to Columbia and Composite rams. However, this difference was not observed in 2007 or 2008 on either a litter or individual lamb basis. The χ^2 analysis of 3-way frequency tables (yr

Table 3. Estimates of ram breed effects on traits of ewe productivity

	Ram breed					
Trait	Columbia	USMARC-Composite	Suffolk	Texel	Pooled SE	*P*-value
Ewe fertility, %	96.1	96.4	97.6	95.6	1.3	0.73
TNB[1]	2.00	2.06	2.00	2.04	0.04	0.20
NBA[2]	1.88	1.97	1.89	1.88	0.04	0.24
Lambs removed from litter,[3] n	0.23	0.33	0.28	0.23	0.04	0.14
Lambs weaned per ewe lambing, n	1.45	1.48	1.46	1.44	0.05	0.94
Lambs weaned per ewe joined, n	1.38	1.40	1.39	1.36	0.05	0.91

[1]Total number of stillborn lambs plus lambs born alive per ewe that lambed.

[2]Number of lambs born alive per ewe that lambed.

[3]Lambs orphaned or cross-fostered per litter per ewe lambing.

Table 4. Percentages of ewes and lambs requiring lambing assistance by year and sire breed and significance tests for sire breed effects

	Sire breed				
Year	Columbia	USMARC-Composite	Suffolk	Texel	*P*-value[2]
2006	12.2	13.5	25.7	31.9	0.01
2007[1]	11.1 (6.9)	6.0 (2.9)	12.9 (7.0)	13.5 (8.8)	0.38 (0.13)
2008[1]	12.8 (8.5)	10.3 (8.8)	11.9 (6.5)	7.8 (4.5)	0.76 (0.42)
All years	12.0	9.7	16.8	15.5	0.08

[1]Percentages of lambs that required lambing assistance are given in parentheses.

[2]Differences among sire breeds within year were tested using χ^2. Differences among sire breeds across years were tested using a Cochran-Mantel-Haenszel general association test after adjustment for year effects.

× dystocia class × survival) indicated that lambs born in litters with dystocia were 1.9 to 4.4 times more likely to die by 14 d of age ($P < 0.001$; 20.5 vs. 4.7% mortality in 2006, 9.0 vs. 4.7% mortality in 2007, and 18.5 vs. 7.6% mortality in 2008). This analysis assumed that orphaned lambs, which were removed from the litter within a few days of birth, survived to 14 d. Exclusion of orphaned lambs from the analysis increased the predicted overall likelihood of death slightly, to 4.8, 1.9, and 2.5 times that of lambs born to ewes that did not require assistance in 2006, 2007, and 2008, respectively. Across all classification variables, mean BW at birth for dystocial (5.08 ± 0.10 kg) and normal-birth lambs (5.08 ± 0.03 kg) did not differ ($P = 0.98$; 2007 and 2008 data only), and this lack of difference was consistent within sire breeds ($P \geq 0.83$; data not shown) and TNB ($P \geq 0.22$; data not shown).

Lamb BW

Suffolk-sired lambs were heavier ($P \leq 0.02$) at birth, in late June (mean age = 97.7 d), and at weaning (mean age = 132.1 d), but not in late April/early May (mean age = 36.8 d; $P = 0.22$; 2007 and 2008 data only) than lambs from the other sire breeds (Table 5). Suffolk-sired lambs averaged 5.1% heavier in late April/early May than lambs sired by the other 3 breeds, and this relative size advantage was intermediate to those observed at birth and in late June (4.6 and 6.1%, respectively), suggesting that the smaller number of observations may have prevented detection of a significant sire breed effect in late April/early May. Columbia- and Composite-sired lambs had similar BW at all ages between birth and weaning ($P \geq 0.40$). Texel-sired lambs had similar birth weight compared with Columbia- and Composite-sired lambs ($P \geq 0.34$), but were lighter than Columbia-sired lambs in late June ($P = 0.03$) and were lighter than lambs from both sire breeds at weaning ($P \leq 0.02$). The sire breed × lamb gender interaction approached significance for BW in late June ($P = 0.11$) and at weaning ($P = 0.08$), but sire breed did not interact ($P \geq 0.12$) with other variables at any age to affect lamb BW. Male lambs from Columbia, Composite, and Suffolk sires ranged from 0.81 ± 0.50 to 1.39 ± 0.51 kg heavier at weaning than female lambs of the respective breeds, but Texel-sired male lambs averaged 2.66 ± 0.54 kg heavier at weaning than Texel-sired female lambs, and this pattern was consistent across years ($P = 0.58$ for sire breed × lamb gender × year interaction; data not shown).

Male lambs were heavier ($P \leq 0.003$) than female lambs at all ages, birth weight decreased ($P \leq 0.001$) as TNB increased, and lambs reared as singles were heavier ($P \leq 0.001$) at all ages than lambs reared as twins or triplets (data not shown). Dam age affected lamb BW at birth ($P < 0.001$; data not shown), but not at later ages ($P \geq 0.13$).

Lamb Survival

Percentages of lambs that died before weaning (including stillborn lambs) were 15.3, 11.5, 10.4, and 15.5 for Columbia, Composite, Suffolk, and Texel sires, respectively. Relative to TNB, 72.7, 71.3, 72.3, and 70.2% of lambs were weaned and 12.0, 17.1, 17.3, and 14.3% of lambs had records censored before weaning for Columbia, Composite, Suffolk, and Texel sires, respectively.

Sire breed effects interacted with effects of ewe age ($P = 0.04$) and the linear effect of birth weight ($P < 0.001$) to affect lamb survival. Further examination of survival functions for the sire breed × ewe age interaction revealed no consistent changes in rankings or magnitude of differences among sire breeds across ewe ages (see online-only data supplement; http://journalofanimalscience.org), and inferences about sire breed effects on lamb survival were made with the sire breed × ewe age interaction excluded from the model. The sire breed × gender interaction approached

Table 5. Sire breed least-squares means for lamb BW from birth to weaning

		Sire breed				
Trait	Mean age, d (SD)	Columbia	USMARC-Composite	Suffolk	Texel	*P*-value
Birth BW, kg	–	5.33 ± 0.05[b]	5.28 ± 0.05[b]	5.50 ± 0.05[a]	5.26 ± 0.06[b]	< 0.01
BW in April/May,[1] kg	36.8 (7.2)	13.19 ± 0.21	13.39 ± 0.22	13.64 ± 0.21	13.21 ± 0.21	0.22
BW in late June, kg	97.7 (6.0)	31.17 ± 0.31[b]	31.02 ± 0.31[b,c]	32.12 ± 0.31[a]	30.41 ± 0.31[c]	< 0.001
Weaning BW, kg	132.1 (6.3)	38.77 ± 0.36[b]	38.43 ± 0.36[b]	40.25 ± 0.36[a]	37.41 ± 0.37[c]	< 0.001

[a-c]Means within a row with different superscripts differ ($P \leq 0.05$).

[1]Data from 2007 and 2008 only.

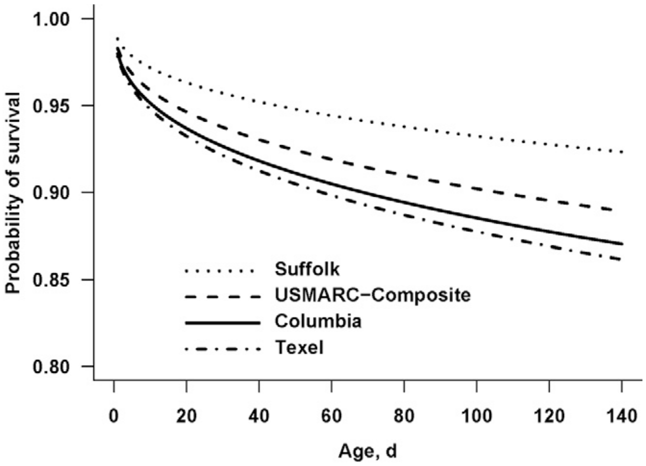

Figure 1. Plots of survival functions from birth to weaning for 4 sire breeds (Columbia, USMARC-Composite, Suffolk, and Texel) adjusted to a lamb born in 2006 to a 3-yr-old ewe. Survival functions did not differ (P = 0.06) among the sire breeds.

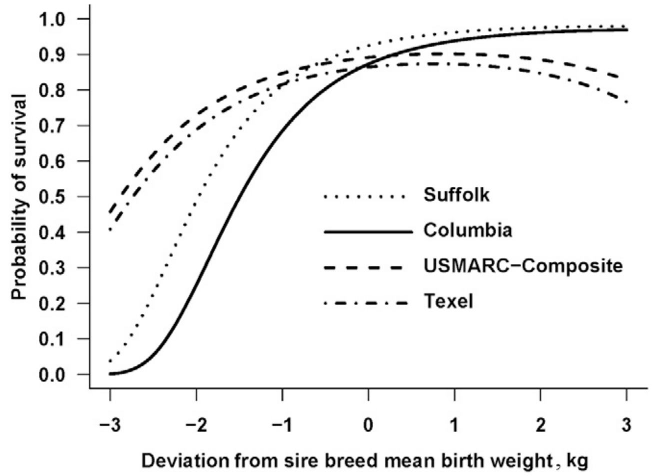

Figure 2. Plots of survival functions for the sire breed × birth BW interaction ($P < 0.001$) adjusted to a lamb born in 2006 to a 3-yr-old ewe.

significance ($P = 0.06$) but was likewise excluded from the final model. Suffolk- and Composite-sired female lambs tended to have a survival advantage over male lambs of the respective breeds, whereas Columbia- and Texel-sired male lambs tended to have a survival advantage over female lambs of the respective breeds (data not shown). Gender did not affect lamb survival ($P = 0.41$).

Sire breed effects on lamb survival from the final model with additional effects of year, ewe age, linear and quadratic effects of birth weight, and the interaction between sire breed and birth weight (linear) approached significance ($P = 0.06$). Figure 1 shows plots of survival functions for the 4 sire breeds, expressed relative to lambs born in 2006 to 3-yr-old ewes (i.e., levels with median estimates of survival probability). Suffolk-sired lambs tended to have a greater probability of survival (0.925) to weaning at 132 d than Columbia- (0.873) and Texel-sired lambs (0.864), and a similar probability of survival compared with Composite-sired lambs (0.892). Censored data from orphaned and cross-fostered lambs represented a nonrandom sample, thus survival probabilities have inference only to lambs kept with their dam and may be greatly affected by management practices. The scale parameter (σ) estimate was 2.57, indicating a decreasing hazard over time.

Survival functions comparing effects of birth weight on survival for each sire breed (Figure 2) reveal that lightweight lambs sired by rams of the larger breeds (i.e., Columbia and Suffolk) had a greater risk of death than did lightweight Composite- and Texel-sired lambs ($P < 0.001$ for sire breed × birth weight interaction). By contrast, survival did not decrease substantially for heavyweight lambs from any of the sire breeds. Linear and quadratic effects of birth weight ($P \leq 0.01$) seemed to explain the effect of TNB on lamb survival; TNB had a significant effect ($P < 0.01$) without birth weight in the model, but was not important ($P = 0.88$) when birth weight was included.

Year effects were important ($P < 0.01$; data not shown) for lamb survival. Effects of dam age approached significance ($P = 0.07$); lambs reared by 3-, 4-, and 5-yr-old ewes tended to survive better than lambs reared by older ewes.

DISCUSSION

The choice of terminal sire breed affects crossbred lamb BW from birth to weaning, but not traits of ewe productivity or lamb survival, when rams are mated to mature Rambouillet ewes in an extensive rangeland production system. Suffolk is the primary terminal sire breed in the United States because of its favorable growth rate and leanness, and the superior preweaning growth of Suffolk-sired lambs in the current study was, thus, largely anticipated. Suffolk-sired crossbred lambs were generally heavier at birth and weaning than Columbia-sired crossbred lambs in previous studies (Leymaster and Smith, 1981; Nugent and Jenkins, 1991; Ali et al., 2005), although Jenkins (1986) did not detect a difference between these sire breeds for BW at weaning. In some studies, Texel-sired crossbred lambs were similar to Suffolk-sired crossbred lambs for BW at birth and weaning (Latif and Owen, 1979; Leymaster and Jenkins, 1993; Ali et al., 2005). However, all of these studies used ewes with Finnsheep ancestry, and in most cases lambs were markedly smaller at birth across all sire breeds, which may partly explain discrepancies with the current study.

The sampling of flocks, and of rams within flocks, is invariably an issue in studies designed to compare breeds. Representative samples are desired, but acquisition of such samples is not trivial. If all breeds actively participate in national genetic evaluation programs, adjustments for sampling bias is possible (Notter and Cundiff, 1991). In the current study, however, only the Columbia and Suffolk breeds participate in NSIP.

The estimated sampling bias for NSIP Suffolk rams used in the current study was substantial. Means for 60-d weaning and 120-d postweaning weight EPD for all NSIP Suffolk lambs in the 2009 genetic evaluation were 0.2 and 0.5 kg, respectively, whereas corresponding EPD of NSIP Suffolk rams used in this study averaged 1.0 and 2.1 kg. Rams from NSIP flocks sired 56% of the Suffolk crossbred lambs evaluated in this study, which means that adjustment for nonrandom sampling within NSIP flocks may thus reduce the least-squares mean for weaning weight of Suffolk-sired lambs (40.3 kg) by 0.4 to 0.9 kg relative to that expected for NSIP Suffolk rams sampled at random. However, Suffolk-sired lambs would still be significantly heavier than lambs produced by rams of the other 3 breeds. This hypothetical adjustment does not, however, address possible sampling effects among or within non-NSIP Suffolk flocks or other breeds, or the relationship between NSIP EPD and actual performance in this extensive range environment. The latter issue, however, can be considered in future analyses.

No meaningful sampling effect was apparent for NSIP Columbia rams. Only 27% of Columbia rams used in this study came from NSIP flocks, and their 60-d weaning and 120-d postweaning weight EPD averaged 0.2 and 0.8 kg, respectively, compared with means of 0.2 and 0.6 kg for all Columbia lambs in the most recent genetic evaluation. Little, if any, sampling bias was anticipated for Composite and Texel rams because 1) Composite rams were sampled effectively at random from the only source flock and 2) the number of Texel flocks in the United States is relatively small, and genetic relationships among Texel flocks are relatively large because of their recent importation (Leymaster and Jenkins, 1993).

This study was conducted, in part, because of concerns regarding poor survival of Suffolk-sired crossbred lambs (Bradford et al., 1960; Fahmy et al., 1972; Carter and Kirton, 1975; Smith, 1977). Few studies have directly compared the terminal sire breeds evaluated herein, and no studies have assessed the relative survival of Composite-sired crossbred lambs. In contrast to our findings, Leymaster and Jenkins (1993) reported that Texel-sired crossbred lambs had better survival than Suffolk-sired crossbred lambs. Leymaster and Smith (1981) did not detect a difference in survival between Suffolk- and Columbia-sired crossbred lambs, and Ali et al. (2005) did not detect differences in survival among Suffolk-, Columbia-, and Texel-sired crossbred lambs. However, in the latter study, the survival rate of Suffolk-sired lambs (80.3%) was numerically much larger than those of Columbia- (67.2%) and Texel-sired lambs (68.2%). Nugent and Jenkins (1991) reported better survival of Suffolk-sired crossbred lambs than Columbia-sired crossbred lambs.

Studies by Leymaster and Smith (1981), Nugent and Jenkins (1991), Leymaster and Jenkins (1993), and Ali et al. (2005) all used ewes with some, but varying, degrees of prolific (Finnsheep) ancestry (approximately 12.5 to 100%), whereas a less prolific ewe type (Rambouillet) was used in the current study. Despite apparent discrepancies among studies in relative rankings of sire breeds, these studies collectively reveal a consistent pattern and suggest the presence of an important sire breed × dam breed interaction, whereby relative survival rates of Suffolk-sired crossbred lambs decreased as the proportion of prolific ancestry in the dam increased. This purported interaction is supported by the decreased survival of Suffolk-sired lambs born to one-half Finnsheep ewes compared with one-quarter Finnsheep ewes reported in Notter and Copenhaver (1980). However, studies by Hohenboken et al. (1976), Smith (1977), Leymaster and Smith (1981), Nugent and Jenkins (1991), and Freking and Leymaster (2004) did not detect significant sire breed × dam breed interactions on crossbred lamb survival within the scope of sire and dam breeds that were tested.

The linear and quadratic effects of birth weight on lamb survival observed in this study are generally consistent with other literature reports and demonstrate negative effects of below-average birth weight on lamb survival (Smith, 1977; Notter and Copenhaver, 1980; Kleemann et al., 1990; Gama et al., 1991; Casellas et al., 2007; Hatcher et al., 2009; Speijers et al., 2010). Some increases in lamb mortality were observed at > 1 SD above the mean birth weight in those studies, but appreciable increases only occurred near the upper limit of the data and may have been artifacts of the linear and quadratic curve fitting rather than biologically-meaningful effects. These scientists, thus, concluded that lamb survival is maximized at an intermediate, optimum birth weight. Birth weight of crossbred lambs in the current study ranged from 2.3 to 8.5 kg and, thus, were typical of ranges reported by others, but our data do not suggest an appreciable risk of death for lambs with heavier-than-average birth weight born to adult Rambouillet ewes. The survival analysis used in this study is expected to be superior to polynomial regressions in terms of goodness of fit, and an analysis of Polypay lamb survival data from the USSES (Borg, 2007) using a Weibull proportional hazards model likewise did not detect an appreciable increase in the risk of death for lambs with heavy birth weight (i.e., > 6 kg compared with the mean birth weight of 3.95 kg).

The greater risk of death for lightweight Columbia- and Suffolk-sired lambs compared with lightweight Composite- and Texel-sired lambs in the current study, and the effects of dam breed and prolificacy on crossbred lamb birth weight (Smith, 1977; Leymaster and Smith, 1981), are consistent with the purported sire breed × dam breed interaction on lamb survival described above. Furthermore, Taylor (1985) summarized data from a wide range of mammalian species and strains within species and concluded that, among species, comparable physiological endpoints (e.g., birth and puberty) are generally achieved at similar proportions of adult BW and that time (d) required to reach a fixed proportion of adult BW is approximately proportional to the 0.27 power of adult BW. These predictions also hold in large measure among breeds within a species, but gestation length is a notable exception, with negligible differences in gestation length among breeds that differ widely in adult BW. In the current study, yearling BW of Columbia and Suffolk rams averaged 47.5% greater than those of Composite and Texel rams, leading to an estimated difference in BW of 23.75% (i.e., one-half of 47.5%) between crossbred yearling offspring of these 2 sets of rams assuming the rams are mated to ewes with yearling BW equivalent to the mean yearling BW of the Composite and Texel rams (i.e., 89.4 kg). This estimated difference would necessarily increase as the size of the dam breed decreases. However, Columbia- and Suffolk-sired lambs were, on average, only 2.8% larger at birth than were Composite- and Texel-sired lambs. Even if part of the observed differences in yearling ram BW were environmental rather than genetic in origin, birth weight of Suffolk- and Columbia-sired lambs clearly represent a substantially smaller proportion of predicted adult BW than do birth weight of Composite- and Texel-sired lambs. This reduced degree of maturity at birth would be further accentuated in lightweight lambs or, potentially, in smaller lambs produced by younger or more prolific ewes and may be a source of increased risk of neonatal mortality in offspring of large sire breeds. Effects of maternal and paternal imprinting of genes involved in fetal growth, though, for example, IGF2 and its receptor (Thomsen, 2007), may also be involved in downregulation of sire breed differences in lamb birth weight and merit further study.

An increased incidence of dystocia can partially offset the increased productivity that is anticipated from terminal crossbreeding systems because dystocial lambs require more labor inputs and have a greater risk of death (Smith, 1977; Scales et al., 2000; Holst et al., 2002; Speijers et al., 2010). The mean incidence of dystocia in the current study (13.4%; litter basis) was intermediate of those reported from other studies that compared terminal sire breeds (Smith, 1977; Hinch et al., 1986; Scales et al., 2000; Holst et al., 2002; Matheson et al., 2010; Speijers et al., 2010), and dystocial lambs had a significantly greater risk of death than did normal-birth lambs. Differences among sire breeds for dystocia have been reported (Scales et al., 2000) and have been consistent with differences in mean birth weight (Speijers et al., 2010). In 2006, ewes mated to Suffolk and Texel rams had a greater incidence of dystocia than ewes mated to Columbia and Composite rams, but the sire breeds did not differ in 2007 or 2008. Other studies have similarly reported substantial year-to-year variation in dystocia rates (Smith, 1977; Hinch et al., 1986), and the lack of consistency across years in the current study may be partly explained by the more liberal lambing assistance provided by shepherds in 2006 compared with 2007 and 2008. The current data do not suggest that fetopelvic disproportion (i.e., large lamb relative to the maternal pelvic size) should be a concern when rams from these 4 terminal sire breeds are mated to mature ewes that frequently give birth to ≥ 2 lambs (84% in the current study), nor that dystocia rate should be an important factor when selecting among these 4 terminal sire breeds. Several scientists concur that the benefits associated with terminal crossbreeding systems outweigh potential detrimental effects of increased dystocia (Smith, 1977; Scales et al., 2000; Speijers et al., 2010).

The lack of breed-of-ram effects on ewe fertility and prolificacy in this study is generally consistent with data from studies comparing dual-purpose or terminal-type ram breeds mated in the autumn (Bradford et al., 1960; Fahmy et al., 1972; Carter and Kirton, 1975; Hohenboken et al., 1976; Freking et al., 2000; Speijers et al., 2010). Ewe fertility and prolificacy did not differ among Columbia, Suffolk, and Texel rams in studies reported by Latif and Owen (1979), Leymaster and Smith (1981), Leymaster and Jenkins (1993), and Ali et al. (2005). Nugent and Jenkins (1991) did not detect a difference in ewe fertility between Columbia and Suffolk rams in an annual spring-lambing production system, but reported an advantage of 0.25 lambs born per ewe lambing for Columbia rams. Comparative data for Composite rams are not available in the literature. Collectively, results from the current and previous studies suggest that ewe fertility and prolificacy are not likely to be important criteria when selecting among ram breeds to be used in a terminal crossbreeding production system. Although the ewe:ram ratio of 10:1 used in the current study is within the range of ratios used in the studies referenced herein, results may differ when sires from these breeds are exposed to a much greater number of ewes (e.g., ewe:ram ratio $\geq$ 50:1). Furthermore, the increased incidence of infertile Texel rams in the first year of this study highlights the need for comprehensive assessment of breeding soundness and semen quality in prospective rams.

In conclusion, the use of Suffolk rams to improve preweaning growth of market lambs in extensive production systems is warranted, and is not predicted to affect ewe fertility, prolificacy, or lamb survival compared with the other sire breeds tested when rams are mated to adult Rambouillet ewes. The increased dystocia rates observed for Suffolk- and Texel-sired lambs in the first year of the study were not repeatable. Thus, we cannot conclude that important differences exist among the sire breeds for dystocia in the production system studied. Data for postweaning growth, muscling, and fatness (Notter et al., 2012), carcass composition (Mousel et al., 2012), feed efficiency, and product quality from this study are reported in companion papers in this series.

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