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ANIMAL GENETICS AND GENOMICS

Comparison of performance of F1 Romanov crossbred ewes with wool and hair breeds during fall lambing and body weight and longevity through six production years

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Abstract

The objective of this study was to evaluate wool (Dorset and Rambouillet) and hair (Dorper, Katahdin, and White Dorper) breeds for their ability to complement Romanov germplasm in an annual fall lambing system by estimating direct maternal grandsire and sire breed effects on economically important lamb and ewe traits. After 3 yr of evaluation under spring lambing, ewes of the five F1 types were transitioned to spring mating, exposed to composite terminal sires, and evaluated under a barn lambing system at 4, 5, and 6 yr of age. A total of 527 first generation crossbred (F1) ewes produced 1,151 litters and 2,248 lambs from 1,378 May exposures. After accounting for differences in dam age, birth type, and sex, lamb survival to weaning was unaffected by maternal grandsire breed ($P = 0.30$). However, lambs born to 50% Dorset (16.8 ± 0.21 kg) or 50% White Dorper ewes (16.8 ± 0.28 kg) were heavier at weaning than those born to 50% Katahdin dams (13.8 ± 0.32 kg; $P < 0.001$). Additionally, lambs born to 50% Dorset ewes were heavier than those born to 50% Rambouillet (16.0 ± 0.22 kg) and 50% Dorper ewes (15.7 ± 0.33 ; $P \leq 0.03$), but no other pairwise maternal grandsire breed differences were observed ($P \geq 0.06$). Ewe body weight ($n = 3,629$) was recorded prior to each of six possible mating seasons and, across ages, was greatest for Dorset- and Rambouillet-sired ewes (56.7 ± 0.44 and 56.5 ± 0.45 kg, respectively), intermediate for Dorper- and White Dorper-sired ewes (54.7 ± 0.78 and 54.1 ± 0.64 kg, respectively), and least for Katahdin-sired ewes (51.5 ± 0.45 kg). Fertility after spring mating (0.80 ± 0.03 to 0.87 ± 0.02), litter size at birth (1.46 ± 0.09 to 1.71 ± 0.07), and litter size at weaning (1.25 ± 0.06 to 1.46 ± 0.06) were not impacted by sire breed ($P \geq 0.16$). Ewe longevity, assessed as the probability of being present after 6 production years, was also not affected by sire breed (0.39 ± 0.03 to 0.47 ± 0.03 ; $P = 0.44$). Rambouillet-sired ewes weaned more total weight of lamb (21.5 ± 0.94 kg) than Katahdin-sired ewes (17.8 ± 0.94 kg; $P = 0.05$), but no other sire breed differences were detected ($P \geq 0.07$). Results demonstrated that incorporating the Romanov into a crossbreeding system is a practical means of improving out-of-season ewe productivity.

Key words: ewe productivity, fertility, hair breeds, lamb survival, out-of-season mating, wool breeds

Abbreviations

BW	body weight
BW ₀	lamb birth weight
BW ₈	lamb 56 d adjusted weaning weight
FR	ewe fertility
LS ₀	litter size at parturition per ewe exposed
LS ₈	litter size at weaning per ewe exposed
LW ₈	litter weaning weight per ewe exposed
SURV ₈	lamb survival to weaning

Introduction

More than 85% of the U.S. lambs are born from January to May (USDA APHIS, 2014a), which can have negative downstream effects on carcass quality and value if domestic harvest is to remain relatively constant throughout the year. In extensive production systems, this seasonal bottleneck is due to both biological constraints and producer husbandry to optimize neonatal survival and synchronize ewe nutritional demands with forage quality. However, out-of-season or accelerated lambing systems may improve a producer's ability to capture increased market value due to holiday demand or seasonal supply constraints. Although light control and exogenous hormone treatments have improved ewe fertility in suboptimal mating seasons (Chemineau et al., 1992; Abecia et al., 2012), exploiting genetic variation across and within breeds is a less intensive yet permanent approach (Lamberson and Thomas, 1982; Asadi-Fozi et al., 2020). A more comprehensive evaluation of breeds and crossbreeding systems is warranted to provide producers with different options to impact the seasonal variation in fertility that constrains the U.S. lamb production.

Out-of-season lamb production has been improved by crossing domestic white-face wool breeds to prolific breeds such as the Finnsheep and Romanov. In direct purebred and crossbred comparisons, Romanov ewes had greater spring fertility than Finnsheep ewes (Stanford et al., 1998; Casas et al., 2005). Meanwhile, the proportion of hair sheep within the U.S. industry has grown (USDA APHIS, 2014b), yet few studies have investigated their complementarity with the Romanov in crossbreeding systems. Freking and Murphy (2020) evaluated 50% Romanov ewes sired by wool (Dorset and Rambouillet) or hair breeds (Katahdin, Dorper, or White Dorper) in intensive and extensive spring lambing systems through their first three parities. The objective of the present study was to compare the maternal performance of these

F1 ewes through three additional parities in an annual fall lambing system.

Materials and Methods

The U.S. Meat Animal Research Center (USMARC) Institutional Animal Care and Use Committee approved the experiment following the recommendations of the Federation of Animal Science Societies (FASS, 2010).

Experimental design

The present experiment was the second phase of a breed evaluation conducted at USMARC (Clay Center, NE; 40°31' N). A description of the first phase of this experiment that generated one-half Romanov F1 ewes was detailed by Freking and Murphy (2020). Briefly, MARC Romanov ewes were bred to Dorset, Rambouillet, Katahdin, Dorper (i.e., black-headed variant), or White Dorper rams each fall from 2000 to 2002. Replacement F1 ewe lambs were born the following springs (2001 to 2003), assigned to intensive or extensive spring lambing treatments, and exposed to terminal sires for the first time at ~7 mo of age. Crossbred ewes remained in their spring lambing treatment and service sire breed group for three parities before being evaluated in the fall lambing system of the present study for up to three additional parities. The breeding season transition was accomplished by withholding ewes from a fourth fall mating, then exposing them to rams the following spring as 4 yr olds.

Prior to spring mating, vasectomized and intact MARC Composite III rams (one-half Columbia, one-fourth Hampshire, and one-fourth Suffolk; Leymaster, 1991) were managed in a light-controlled enclosure with 8 h of light and 16 h of dark per day for an average of 38 and 56 d, respectively. Both vasectomized and intact rams were semen tested to ensure sterility and breeding soundness, respectively. Vasectomized rams were introduced to F1 ewes at an average ratio of 1:25 for a period of 14 d. Intact rams were joined to ewes in multiple-sire groups for 35 d. Mating was initiated the first week of May (2005 to 2009) with an average ram-to-ewe ratio of 1:20. All ewes and rams were placed in one breeding pen in 2005 and 2009 but randomly allocated to one of two breeding pens (each with approximately the same number of rams) in 2006, 2007, and 2008.

Table 1 describes the number of F1 ewes that entered the present study by sire breed. Major differences in ewe and lamb husbandry between the systems evaluated in Freking and Murphy (2020) and the present study are outlined in Table 2. Ewes in the present study were managed in drylot in late gestation and provided a corn silage-based total-mixed ration. All ewes were required to rear their entire litter unless lamb nutritional status was observed to be failing, in which case affected lambs were transferred to the nursery for artificial

Table 1. The numbers of 50% Romanov ewes exposed and resulting lamb production through three production years in a fall lambing system

Sire breed	No. of sires	No. of F1 ewes	No. of exposures	No. of litters	No. of lambs born
Dorset	18	141	363	298	607
Rambouillet	18	125	338	294	583
Katahdin	18	131	334	273	525
Dorper	9	52	139	118	232
White Dorper	9	78	204	166	301
Total	72	527	1,379	1,151	2,248

Table 2. Description of husbandry and data collection differences in 50% Romanov ewes in Freking and Murphy (2020) and the present study

Study	Lambing season	Management system ¹	Ewe age, yr	Litter size reduced ²	Lamb weaning age, wk	Lamb BW collected, wk
Freking and Murphy (2020)	Spring	Intensive	1 to 3	Yes	8	Birth, 8, 12, and 24
	Spring	Extensive	1 to 3	No	12	8, 12, and 24
Present	Fall	Intensive	4 to 6	Dependent	8	Birth, 8

¹Intensive, ewes were provided with harvested feed through late gestation/lactation, lambed in drylot, and were transferred to single bonding pens with their lamb(s). Lambs were provided with a total-mixed creep diet beginning at 2 wk and through weaning; Extensive, ewes were not provided with supplemental feed through late gestation/lactation and lambed on pasture with little human interference. Lambs were not provided creep feed.

²Yes, litters were reduced to a maximum of two lambs shortly after parturition. Excess lambs were transferred to the nursery and provided ad libitum milk replacer and creep feed until ~4 to 5 wk of age then managed with their dam-reared contemporaries until weaning; No, ewes were required to rear their entire litter and lambs were not transferred to the nursery; Dependent, ewes were required to rear their entire litter unless lamb health status was observed to be failing, in which case lambs were transferred to the nursery and managed as outlined above.

rearing (2.3 ± 2.7 d of age). Nursery-reared lambs were offered ad libitum milk replacer until 4 to 5 wk of age (32.2 ± 3.8 d) and then were remixed with their dam-reared contemporaries after weaning. Ram lambs were castrated at ~2 wk of age, and all lambs were offered a total-mixed creep diet (18% crude protein) beginning at ~2 wk of age. Dam- and nursery-reared lambs were removed from ewe pens at ~8 wk (58.7 ± 3.2 d).

Barren ewes were not culled, and all ewes present at spring mating had the opportunity to lamb in the fall. Ewes were only removed from the present study if they died or became functionally unsound. Primary culling reasons were mastitis, respiratory disease, overall health, and poor milk production.

Lamb and ewe traits

Lamb traits included BW at birth (BW_0 , $n = 2,248$), 56 d adjusted weaning BW (BW_8 , $n = 1,771$), and survival to weaning (0 or 1; $SURV_8$, $n = 2,077$). Records from nursery-reared lambs were included in the analysis of BW_0 but not BW_8 or $SURV_8$. Ewe fertility (FR) was expressed as whether she lambed in the fall after being exposed in the spring (0 or 1). Litter size at parturition (LS_0) included all lambs born dead or alive. Ewes were credited with the performance of their nursery-reared lambs in the calculation of litter size and weight at 8 wk (LS_8 and LW_8 , respectively). All annual productivity traits were expressed on a per ewe exposed basis ($n = 1,378$). Body weight was recorded on ewes that were present at mating in each year of Freking and Murphy (2020) as well as the current study ($n = 3,629$). The longevity of each ewe was calculated as presence or absence (0 or 1) in the flock after six potential weaning events.

Statistical analyses

Lamb traits were analyzed in mixed models with fixed effects of maternal grandsire breed (Dorset, Rambouillet, Katahdin, Dorper, or White Dorper), age of dam at breeding (4, 5, or 6 yr), lamb birth year (2005 to 2009), birth type class (1, 2, or 3+), and sex along with the random effect of dam (nested within maternal grandsire breed). Lamb BW and $SURV_8$ were analyzed in SAS (v. 94.; SAS Institute Inc., Cary, NC) using the MIXED and GLIMMIX procedures, respectively. Lamb $SURV_8$ was modeled as a binary variable and least-squares means (\pm SE) were back-transformed to the original scale.

Models for annual ewe productivity traits and BW were analyzed as repeated measures with fixed effects of ewe birth year (2001, 2002, or 2003), sire breed, and ewe age at breeding. Additionally, a random effect of sire (nested within sire breed and ewe birth year) was fit and a compound symmetric covariance structure with heterogeneous variance across age

was assumed for the ewe (nested within sire, sire breed, and birth year) effect. Ewe FR was analyzed as a binary variable in the GLIMMIX procedure, while litter size and weight traits were analyzed in the MIXED procedure. Ewe longevity was analyzed as a binary variable in the GLIMMIX procedure with fixed effects of ewe birth year and sire breed and the random effect of sire (nested within sire breed and ewe birth year). All cross-classified two-way interactions in the aforementioned models for lamb and ewe traits were fit.

Results

Lamb BW and survival

Least-squares means for the main effects on lamb BW and survival are displayed in Table 3. The maternal grandsire breed \times birth type interaction effect was significant in the analysis of lamb BW_0 ($P = 0.03$). Within twin litters, lambs born to 50% Katahdin dams were lighter (4.35 ± 0.06 kg; $P < 0.01$) than those born to 50% Rambouillet (4.67 ± 0.05 kg) or 50% White Dorper dams (4.71 ± 0.07 kg). However, no grandsire breed differences were detected within single or triplet born lambs ($P \geq 0.07$). As a main effect, lambs born to 50% Rambouillet dams had greater BW_0 ($P < 0.01$) than lambs born to 50% Katahdin dams, but no other pairwise grandsire breed differences were detected ($P \geq 0.17$). Age of dam did not affect lamb BW_0 ($P = 0.37$) but lamb BW_0 decreased with increasing birth type, and males were heavier than females ($P < 0.01$).

Similar to BW_0 , BW_8 was greater for males than females ($P < 0.01$), decreased with increasing birth type ($P < 0.01$), and was not affected by age of dam ($P = 0.24$). Lambs born to 50% Dorset or 50% White Dorper ewes had similar BW_8 ($P > 0.99$), but both were heavier than those born to 50% Katahdin ($P \leq 0.03$). Additionally, lambs born to 50% Dorset ewes were heavier than those born to 50% Rambouillet and 50% Dorper ewes ($P \leq 0.03$), but no other pairwise maternal grandsire breed differences were observed ($P \geq 0.06$). The only main effect to impact $SURV_8$ was birth type, where triplet-born lambs had lower survival ($P < 0.001$) than twin- and single-born lambs that were not different from each other ($P = 0.95$).

F1 ewe annual productivity

The ewe birth year \times age at spring breeding interaction effect was significant in the analyses of all annual ewe productivity traits ($P \leq 0.01$) except for LW_8 ($P = 0.12$). However, the main effects or interaction effects involving ewe birth year are not discussed since annual variation in performance is expected

Table 3. Least-squares means (\pm SE) for the main effects of maternal grandsire breed, dam age, birth type, and sex on lamb BW₀, BW₈, and SURV₈

Effect	Level	Trait		
		BW ₀ , kg	BW ₈ , kg	SURV ₈
Grandsire breed	Dorset	4.58 \pm 0.05 ^{ab}	16.8 \pm 0.21 ^a	0.89 \pm 0.02
	Rambouillet	4.71 \pm 0.05 ^a	16.0 \pm 0.22 ^b	0.90 \pm 0.02
	Katahdin	4.46 \pm 0.05 ^b	15.4 \pm 0.22 ^{bc}	0.85 \pm 0.02
	Dorper	4.50 \pm 0.08 ^{ab}	15.7 \pm 0.33 ^b	0.88 \pm 0.03
	White Dorper	4.61 \pm 0.08 ^{ab}	16.8 \pm 0.28 ^{ab}	0.89 \pm 0.03
Dam age, yr	4	4.55 \pm 0.05	16.0 \pm 0.20	0.89 \pm 0.02
	5	4.55 \pm 0.04	16.3 \pm 0.17	0.90 \pm 0.02
	6	4.62 \pm 0.05	16.1 \pm 0.21	0.86 \pm 0.02
Birth type, n	1	5.36 \pm 0.05 ^a	19.9 \pm 0.23 ^a	0.91 \pm 0.02 ^a
	2	4.55 \pm 0.03 ^b	15.4 \pm 0.13 ^b	0.92 \pm 0.01 ^a
	3+	3.81 \pm 0.05 ^c	13.1 \pm 0.21 ^c	0.79 \pm 0.03 ^b
Sex	Female	4.44 \pm 0.03 ^b	16.4 \pm 0.15 ^a	0.89 \pm 0.01
	Male	4.70 \pm 0.03 ^a	15.8 \pm 0.15 ^b	0.88 \pm 0.02

^{a-c}Means within an effect and column with no superscripts in common are different ($P \leq 0.03$).

Table 4. Least-squares means (\pm SE) for the main effects of ewe age at spring mating and sire breed on 50% Romanov ewe spring FR, LS₀ and LS₈, and total LW₈ in a fall lambing system

Effect	Level	Trait ¹			
		FR	LS ₀ , n	LS ₈ , n	LW ₈ , kg
Sire breed	Dorset	0.81 \pm 0.03	1.64 \pm 0.07	1.38 \pm 0.06	21.3 \pm 0.91 ^{ab}
	Rambouillet	0.87 \pm 0.02	1.71 \pm 0.07	1.46 \pm 0.06	21.5 \pm 0.94 ^a
	Katahdin	0.80 \pm 0.03	1.55 \pm 0.07	1.25 \pm 0.06	17.8 \pm 0.94 ^b
	Dorper	0.83 \pm 0.04	1.64 \pm 0.10	1.34 \pm 0.10	18.8 \pm 1.46 ^{ab}
	White Dorper	0.81 \pm 0.04	1.46 \pm 0.09	1.28 \pm 0.08	20.6 \pm 1.24 ^{ab}
Age, yr	4	0.87 \pm 0.02 ^a	1.69 \pm 0.04 ^a	1.44 \pm 0.04 ^a	22.3 \pm 0.63 ^a
	5	0.81 \pm 0.02 ^b	1.60 \pm 0.05 ^{ab}	1.37 \pm 0.04 ^a	20.7 \pm 0.67 ^a
	6	0.79 \pm 0.02 ^b	1.50 \pm 0.05 ^b	1.21 \pm 0.05 ^b	17.0 \pm 0.71 ^b

¹Litter size and weight traits are expressed on a per ewe exposed basis.

^{a,b}Means within an effect and column with no superscripts in common are different ($P \leq 0.05$).

but difficult to attribute to specific biological or environmental factors. Least-squares means for main effects on ewe FR, LS₀, LS₈, and LW₈ are displayed in Table 4. Age at breeding affected FR and was greater in 4-yr-old ewes ($P = 0.02$) than 5- and 6-yr-old ewes that were not different ($P = 0.33$). Four-year-old ewes had greater LS₀ and LS₈ ($P < 0.01$) than 6-yr-old ewes, and LS₈ was greater for 5-yr-old than 6-yr-old ewes ($P = 0.01$). However, sire breed did not affect ewe FR, LS₀, or LS₈ ($P \geq 0.15$).

The sire breed \times age at spring breeding interaction effect was significant in the analysis of LW₈ ($P = 0.01$). No differences in LW₈ were detected among ages within Dorset-, Rambouillet-, and White Dorper-sired ewes ($P \geq 0.06$). However, within Katahdin- and Dorper-sired ewes, LW₈ was greater at 4 yr (21.5 \pm 1.18 and 23.1 \pm 1.86 kg, respectively) than 6 yr of age (14.8 \pm 1.35 and 13.8 \pm 2.10 kg, respectively; $P \leq 0.01$). As a main effect, 4- and 5-yr-old ewes had similar LW₈ but were both greater than 6-yr olds ($P < 0.001$). Rambouillet-sired ewes had greater LW₈ than 50% Katahdin ewes ($P = 0.05$), but no other sire breed differences were detected ($P \geq 0.07$).

F1 ewe BW at breeding and longevity

The ewe birth year \times age and sire breed \times age interaction effects were significant in the analysis of ewe BW at breeding ($P < 0.01$). The interaction of sire breed \times ewe age was mostly due to the changes in magnitude between sire breeds rather

than re-ranking among them. No sire breed differences were detected among BW at first mating ($P \geq 0.31$). Within second and later matings, both Dorset- and Rambouillet-sired ewes were heavier ($P < 0.01$) than Katahdin-sired ewes. Dorset-sired ewes were heavier than White Dorper-sired ewes at fourth breeding ($P = 0.02$) but no other pairwise differences among breeds were observed within ewe ages ($P \geq 0.08$). Least-squares means for the main effects on mating BW are displayed in Table 5. Mating BW increased through 4 yr and decreased thereafter and was different ($P < 0.01$) between all ages except 3 and 6 yr ($P = 0.07$). Katahdin-sired ewes were the lightest at mating ($P \leq 0.01$). Dorset- and Rambouillet-sired ewes were heavier than 50% White Dorper ewes ($P \leq 0.02$) but had similar BW to each other and Dorper-sired ewes ($P \geq 0.15$). Ewe longevity, assessed as the probability of being present after six production years, was not affected by sire breed ($P = 0.44$), and their least-squares means ranged from 0.39 \pm 0.03 to 0.47 \pm 0.03.

Discussion

The seasonal nature of reproductive activity in sheep is mainly regulated by photoperiod, a characteristic that likely evolved to ensure late gestation and lactation coincide with environmental conditions that favor offspring survival and forage growth (Lincoln and Short, 1980). On the large U.S. sheep operations (500

Table 5. Least-squares means (\pm SE) for the main effects of ewe age and sire breed on 50% Romanov ewe BW at breeding

Effect	Level	BW, kg
Sire breed	Dorset	56.7 \pm 0.44 ^a
	Rambouillet	56.5 \pm 0.45 ^a
	Katahdin	51.5 \pm 0.45 ^c
	Dorper	54.7 \pm 0.78 ^{a,b}
	White Dorper	54.1 \pm 0.64 ^b
Age, yr	1	36.8 \pm 0.23 ^e
	2	50.0 \pm 0.26 ^d
	3	57.4 \pm 0.29 ^c
	4	64.9 \pm 0.33 ^a
	5	60.9 \pm 0.35 ^b
	6	58.3 \pm 0.40 ^c

^{a-e}Means within an effect with no common superscript are different ($P \leq 0.02$).

or more ewes), most of the lambs are born in spring (April to June; ~50%) or winter months (December to March; ~40%), and very few are born in fall months (October and November; ~10%; USDA APHIS, 2014a). The seasonality of lamb supply can be reduced by increasing the number of fall born lambs, which has been identified as a priority by the U.S. sheep industry. However, ewe fertility and prolificacy are generally lower in spring than fall mating flocks (Fogarty and Mulholland, 2013). Therefore, it is essential to evaluate mating strategies that can contribute to improved ewe productivity in suboptimal mating seasons.

The length of the seasonal anestrus period varies among sheep breeds but generally becomes shorter as breed origin transitions from temperate to tropical latitudes (Rosa and Bryant, 2003). The Dorset and Rambouillet are both derived from the Spanish Merino and have traditionally been used to improve out-of-season lamb production in domestic flocks. The proportion of ovulating Dorset ewes in Australia (34°27' S) was low from October to December (23% to 30%) but considerable in September (73%) and January (80%; Hall et al., 1986). Wiggins et al. (1970) reported that 44% to 77% of Rambouillet ewes exhibited estrus from March to June in Alabama (32°35' N). The effects of Rambouillet ewe origin (TX vs. Northwest [MT and WY]) and management location (TX = 31°25' N vs. ID = 44°10' N) on estrus activity were evaluated by Hulet et al. (1974). Within the first year of their study, the proportion of ewes ovulating in March to June was greater for TX-TX (38% to 88%) and TX-ID ewes (33% to 100%) than Northwest-TX (0% to 50%) and Northwest-ID ewes (5% to 100%).

In 2011, most of the U.S. sheep inventories was classified as white-faced fine (44%) or medium wool breed background (18%) and contained fewer individuals of black-faced wool (14%) or hair breeding (11%; USDA APHIS, 2014b). Still, the proportion of hair sheep has grown substantially from earlier estimates in 2001 (1.2%) and 1996 (0.4%). The Katahdin and variants of the Dorper are the most popular composite hair breeds among the U.S. sheep producers and originate from Maine and South Africa, respectively. Burke (2005) evaluated Katahdin and Dorper ewes in Arkansas (35°8' N) and reported that ultrasound pregnancy rates 30 d post April to May breeding were low at <1 yr of age (<20%) but considerable at >2 yr of age (~75%). However, fetal losses thereafter were evident in ewes <1 yr of age as the proportion that lambled the following fall (~5%) was reduced.

Traits associated with seasonality and out-of-season lamb production would seem to be logical targets where the use of marker-assisted selection could have a substantial biological

and economic impact, since the traits are lowly heritable, sex limited, and expressed late in life, providing significant challenges for conventional selection practices (Notter and Cockett, 2005). Variation associated with the melatonin receptor 1A (MTNR1A) has had conflicting results as a significant contributor influencing seasonal reproductive responses (Notter and Cockett, 2005; Posbergh et al., 2019), highlighting the difficulty of tracking the genetic architecture for these phenotypes. Clock genes and their associated genetic variations have been implicated in multiple mammalian species to influence these seasonal responses through calendar cells in the pituitary that respond to and are influenced by melatonin secretions (King and Takahashi, 2000). New comprehensive genomic and bioinformatic approaches have shed additional light on the key target genes that drive seasonal breeding responses (Lomet et al., 2020). This most recent modeling effort suggests that Kiss1 neurons and their responses to estrogen and thyroid hormone are pivotal to the long-recognized seasonal switch in the ability of estrogen to exert negative feedback to drive seasonal breeding. These additional genes would make inviting candidates for investigation into the genetic control of seasonality in different sheep populations.

Currently, there are a total of 43 quantitative trait loci (QTL; not all independent as overlap of same position between traits) reported to be associated with aseasonal reproduction or their component traits in sheep dispersed across most of the autosomes as well as the X chromosome (<https://www.animalgenome.org/cgi-bin/QTLdb>). Among those QTL, many were identified from recent genome-wide association study data using a variety of sheep breeds including Dorset and Polypay and 600K chip analyses that have led to the identification of genes involved with eye development, reproductive hormones, and neuronal changes being the most promising for influencing the ewe's ability to lamb year-round (Posbergh et al., 2019). Integration of all these suggested targets could be evaluated using the approach suggested by Heaton et al. (2017) to scan these target genes in most of the U. S. populations including Romanov. The performance of Romanov and Finnsheep crossbred ewes would also seem to support the concept that a large number of loci contribute to these traits each with small additive effects.

Experimental results suggest that most of the purebred sheep populations commonly reared in the United States are not sufficiently aseasonal for consistent out-of-season lamb production. Although the Finnsheep and Romanov originate from regions near 60°N, they are among the least seasonal breeds. Österberg (1981) evaluated Finnsheep ewes exposed to a vasectomized ram year-round in Finland (61°41' N) and reported the mean dates for first and last occurrence of behavioral estrus were October 9 and May 27, respectively. In Canada (49°42' N), Stanford et al. (1998) placed mature Finnsheep and Romanov ewes under a vasectomized ram and exogenous hormone protocol prior to April and May breeding and reported considerable fall lambing rates (81% to 95%). As stated previously, 50% Romanov ewes have outperformed 50% Finnsheep ewes in direct comparisons for litter size and total weight of lamb at weaning (Thomas, 2010), hence their utilization in the present study.

Notter (2002) suggested that substantial heterosis for duration of breeding season is unlikely. Therefore, improved spring fertility in Finnsheep or Romanov crossbred ewes appears to be more heavily dependent on the additive effect of prolific breeds than interactive effects among other contributing breeds. While Casas et al. (2005) observed an interaction

between sire breed (Dorset, Montadale, Texel, Finnsheep, and Romanov) and dam breed (Composite III and northwestern whiteface) on USMARC F1 ewe spring fertility, least-squares means for Finnsheep- and Romanov-sired ewes (82% and 91%, respectively) were much greater than the other sire breeds (70% to 73%). Similarly, no sire breed differences were detected in the present evaluation of spring fertility, and all F1 Romanov cross ewes performed respectably (80% to 87%). Asadi-Fozi et al. (2020) estimated that, although the heritability of spring fertility was low (0.07 to 0.15) in a composite population of 50% Rambouillet, 25% Dorset, and 25% Finnsheep ewes, single-trait selection over 17 yr was effective. Furthermore, no major antagonisms with other economically important traits were reported, and mean fertility of adult ewes in the spring was approximately 88% near the end of the experiment (Asadi-Fozi et al., 2020). Therefore, incorporating a proportion of prolific germplasm into crossbred/composite sheep populations and applying selection thereafter seems to be the most logical strategy to substantially reduce the duration of seasonal anestrus in ewes.

The first phase of this experiment evaluated F1 ewes in two spring lambing environments through their first three parities (Freking and Murphy, 2020). In both phases of this experiment, ewe prolificacy was analyzed on a per ewe exposed basis and was not impacted by sire breed. For completeness, prolificacy on a per ewe lambing basis was 1.95 ± 0.62 lambs in the present study. In Freking and Murphy (2020), 50% White Dorper ewes accounted for greater weight of lamb marketed than 50% Rambouillet and Katahdin ewes. However, in the present study, 50% Rambouillet ewes had heavier LW_8 than 50% Katahdin ewes. It is possible the inconsistency of the sire breed effect on the total weight of lamb produced between the two experimental phases could be dependent upon interactive effects among specific ewe ages, mating seasons, or service sire breeds. For example, the productivity advantages of White Dorper \times Romanov ewes may be limited to early parities, during fall breeding, and/or when exposed to Suffolk or Texel rams. Conversely, Rambouillet \times Romanov ewes may be the most productive only in later parities, during spring breeding, and/or when exposed to Composite III rams. However, because ewe ages and service sire breeds were not cross classified across mating season, the design of the current experiment does not allow a formal test of this. Nevertheless, results from the two experimental phases are in general agreement with others and suggest ewe productivity can be greatly improved in a variety of production systems by developing crossbred or composite sheep flocks with an optimal proportion of prolific breeding.

Acknowledgments

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Conflict of interest statement

The authors declare no real or perceived conflicts of interest.

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