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Sex of Littermate Twin Affects Lifetime Ewe Productivity[3]

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Summary

Ewe productivity is synonymous with annual litter-weight weaned (LWW) per ewe exposed to rams for breeding, and LWW is largely a function of number of lambs born (NLB) and weaned (NLW). Selecting for LWW should increase litter size and numbers of ewe-ram co-twins. Thus, we used historical records to determine whether sex of co-twin affected lifetime productivity of twinborn ewes. United States Sheep Experiment Station (USSES) lambing records (n = 8,650) from 1991 through 1997 were queried to identify twinborn ewes that were reared with their biological dams and retained in the breeding flock (n = 1,628; Columbia, 383; Polypay, 536; Rambouillet, 383; and Targhee, 326). Corresponding records for lifetime-cumulative counts of lambs born (stillborn and live-born) with recorded birth weights and weaned with recorded-weaning weights, cumulative weight of lambs weaned, lifetime count of lambing events, and age at first lambing (1 yr, 2 yr, or 3 yr) were evaluated using PROC GLM and PROC MIXED methods. Alpha was set at 0.10. Only the main effects of sex of co-twin, ewe-weaning weight, ewe breed, and ewe-birth year were significant. Per-ewe exposed to rams, but not per-ewe lambing, cumulative-lifetime weaning weight (P = 0.03) and numbers of lambs born (P = 0.07) and weaned (P = 0.04) were greater for ewes with a ram co-twin than for ewes with a ewe co-twin. Sex of co-twin did not affect number of lifetime-lambing events or age at first lambing for ewes exposed (P = 0.14 and P = 0.59, respectively) or ewes lambing (P = 0.67 and P = 0.27, respectively). Ewe-weaning weight affected cumulative-lifetime weaning weights (P = 0.0003), lifetime numbers of lambs born (P = 0.001) and weaned (P = 0.02), and lifetime-lambing events (P = 0.001), but not age at first lambing (P = 0.44) per-ewe exposed. Productivity of Polypay and Rambouillet ewes generally exceeded that of Columbia and Targhee ewes, although breed ranking was not constant among productivity traits of twinborn ewes. Based on the data, we concluded that ewes born co-twin to a ram had an advantage over ewes born co-twin to a ewe. This advantage amounted to 15.55 kg in lifetime litter-weight weaned per-ewe exposed. We believe that sex of co-twin should be evaluated further to determine whether it is a useful environmental adjustment, beyond lamb sex and type of birth and rearing, for lamb weights and traits related to ewe productivity.

Key Words: Sheep, Production, Efficiency, Reproduction

Introduction

Ewe productivity, typically synonymous with annual litter-weight weaned (LWW) per ewe exposed to breeding, is a key determinant of net-economic return per ewe (Ercanbrack and Knight, 1998; Snowder, 2002; Snowder and Fogarty, 2009). Ewe prolificacy (i.e., number of lambs born; NLB) accounted for approximately 37 percent of the genetic improvement in LWW (Ercanbrack and Knight, 1998). The weighted mean genetic correlation between LWW and NLB was 0.60 and between LWW and number of lambs weaned (NLW) was 0.80 (Snowder and Fogarty, 2009). Also, the genetic correlation between the NSIP Maternal Wool Breeds Index was 0.40 for NLB and 0.94 for NLW (Notter, 2014). Thus, selecting for LWW should increase litter size (Ercanbrack and Knight, 1998) and, as a consequence, "competition in utero between twin lambs" (Donald and Purser, 1956) and endocrinological disparities between ewe-ram fetal twins (Padula, 2005). However, the effect of competition in utero on reproductive performance and overall productivity of ewes has received little attention. The few reports in refereed journals indicated that sex of co-twin had little effect on subsequent reproductive performance of the ewes (Meredith and Keisling, 1996; Avdi and Driancourt, 1997; Casellas and Caja, 2014), although first-year survival, and thus breeding success, was less for unmanaged Soay ewes born co-twin to a ram (Korsten et al., 2009). By contrast, rodent and swine studies indicate that in utero proximity of a female to a male fetus can, for example, affect that female's age at first estrus (von Saal, 1981) and reproductive capacity (vom Saal and Finch, 1988; Drickamer et al., 1997). Because of the economic importance of ewe productivity, and its relationship to NLB and NLW, we used historic United States Sheep Experiment Station (USSES) records to test the null hypothesis that sex of co-twin does not affect ewe productivity.

Materials and Methods

Animals

This research was conducted with records extracted from a database and did not involve animal experimentation. Thus, Institutional Animal Care and Use Committee approval was not required. Lambing records (n = 8,650) from the United States Sheep Experiment Station were queried to identify twin-born ewes, which were born from 1991 through 1997 and with production years from 1992 to 2008, reared with their biological dams, and retained in the breeding flock (n = 1,628; Columbia, 383; Polypay, 536; Rambouillet, 383; and Targhee, 326). These ewes represented the most recent set of lifetime records, based on a typical, 8-yr-flock lifespan, at the time the data were queried. Single-born-single-reared ewes were not included in the dataset because the objective focused on the relationship only between co-twins. The dataset contained approximately twice as many records for ewes from ewe-ewe co-twin pairs than for ewes from ewe-ram co-twins because each ewe was considered a record and ram-ram co-twin data were not used. Corresponding lifetime-production records were extracted from the database for analyses.

Ewes were managed in a rangeland production system and mated annually with Columbia, Polypay, Rambouillet, and Targhee rams respective to breed. Lambs were born in mid-March through late April and reared with their biological dams on spring and summer ranges until weaning in August, when ram lambs were separated from ewe lambs. Flock sizes ranged from 600 to 1,100 mature ewes. Independent culling criteria for ewe lambs at weaning were based on body weights, wool blindness, fleece characteristics, jaw malformations, and various health issues. From the time of separation at weaning until breeding, ewes and ewe lambs grazed separate pastures. In mid-October, ewes and ewe lambs were moved to drylot pens for a 35-d breeding period. Ewes were single-sire mated, and ewe lambs were bred to either purebred or crossbred rams. Age of ewe and mating experience of rams varied across years. After breeding, ewes were returned to range until approximately February 1 each year and then placed in drylots through lambing. Ewe lambs remained in drylots throughout the winter and lambing. Generally, ewes were culled for debilitating disease, poor udder score, poor lambing history, or at greater than 8 yr of age. Even though rams had passed breeding soundness examinations, some rams had poor breeding success during the breeding period. Thus, only data from ewes that were exposed to fertile rams were considered.

Measurements and Statistical Methods

To determine the effect of co-twin sex on ewe productivity, lifetime-cumulative counts of lambs born (stillborn and live-born) with recorded birth weights and weaned with recorded weaning weights, cumulative weight of lambs weaned, lifetime count of lambing events, and age at first lambing (1, 2, or 3 yr) were evaluated. To include or exclude differences in fertility, cumulative weaning weight, lifetime counts of lambs born and weaned, lifetime count of lambing events, and age at first lambing were expressed as ewes exposed to rams for breeding and ewes that lambed. Records for ewes that did not lamb were excluded from calculations on a per-ewe-lambing basis. Lifetime-ewe productivity was measured as cumulative-weaning weight per ewe exposed to rams for breeding. Cumulative weights were determined using a calculated 120-d weaning weight (birth weight + [120 d × preweaning ADG]). The PROC GLM procedure in SAS (SAS Inst., Inc., Cary, N.C.) was used and included co-twin sex, age of dam in years (1 to 8), offspring sex (i.e., ewe or ram), sire breed, lambing year, birth-litter count (1, 2, or 3 lambs), and method of rearing (dam-reared or nursery-reared).

Ten ewes produced stillborn lambs and were given a value of 0 for birth weight and weaning weight. Ewes that were missing either birth-weight or weaning-weight data were excluded from the analyses. The effects of sex of co-twin on defined traits were analyzed using mixed models (PROC MIXED; SAS Inst., Inc.). The model included breed (Columbia, Polypay, Rambouillet, and Targhee), co-twin sex (male or female), breed × co-twin sex, ewe birth year (1991 to 1997), ewe-recorded-birth weight, and ewe-recorded-weaning weight, as fixed effects, and sire of the ewe as the random effect. The PROC GLM, Type III sums of squares were used to calculate percentage of the total sums of squares for each source of variation in the model to explain differences in ewe productivity, and we interpreted this as the relative importance of each effect. Quantitative data are shown as least-squares means and SEM. Alpha was set at 0.10.

Results

Only the main effects of sex of co-twin, ewe breed, ewe-weaning weight, and ewe-birth year were significant. The breed × co-twin sex interaction was not significant for any trait. Ewe weaning weight and ewe-birth weight, with one exception, accounted for the greatest proportions of the total variability, and sex of littermate always accounted for the smallest proportion; ewe-birth year and ewe breed, with one exception, were intermediate (Table 1). However, even when all main effects were taken into account in the analysis, co-twin differences were still apparent for most production traits.

Co-twin Effects

Cumulative-lifetime weaning weight was greater ($P = 0.03$) per ewe exposed from ewe-ram twins than for ewes from ewe-ewe twins, but the trait was not significant on a per-ewe-lambing basis ($P = 0.20$; Table 2). The ewe-ram advantage in cumulative-lifetime weaning weight for ewes exposed was 15.55 kg, averaging 1.94 kg/yr over a typical 8-yr flock lifespan. Per-ewe exposed, lifetime counts of lambs born and lambs weaned were greater for ewes born co-twin to a ram ($P = 0.07$ and $P = 0.04$, respectively) than for ewes born co-twin to a ewe (Table 3). However, per-ewe lambing, sex of co-twin did not affect the number of lambs born or weaned ($P > 0.20$). Ewes with a ram co-twin gave birth to an average of 1.57 lambs/yr and weaned an average of 1.44 lambs/yr, whereas ewes with a ewe co-twin gave birth to an average of 1.52 lambs/yr and weaned 1.38 lambs/yr. Sex of co-twin did not affect lifetime counts of lambing events or age at first lambing for ewes exposed ($P = 0.14$ and $P = 0.59$, respectively) or ewes lambing ($P = 0.67$ and $P = 0.27$, respectively; Table 3).

Effects of Birth Weight and Weaning Weight

On a per-ewe-exposed basis and a per-ewe-lambing basis, ewe birth weight was not a significant source of variation for any trait evaluated. However, ewe weaning weight was significant for cumulative lifetime weaning weights ($P = 0.0003$), lifetime numbers of lambs born ($P = 0.001$) and weaned ($P = 0.02$), and lifetime lambing events ($P = 0.001$), but not for age at first lambing ($P = 0.44$) per ewe exposed. Weaning weight per ewe lambing affected ($P < 0.09$) all traits, except lifetime counts of lambs weaned ($P = 0.22$).

Breed Effects

Cumulative-lifetime weaning weights (Table 2), on a per-ewe-exposed and on a per-ewe-lambing basis, were greater for Polypay than for Columbia ($P < 0.001$ and 0.0001, respectively), Rambouillet ($P = 0.01$ and 0.006, respectively), and Targhee ewes ($P = 0.003$ and 0.004, respectively). Rambouillet did not differ from Targhee ewes ($P = 0.30$), but both Rambouillet ($P = 0.003$ and 0.002, respectively) and Targhee exceeded ($P = 0.02$ and 0.007, respectively) Columbia ewes, which averaged 46.0 kg/yr less than the other three breeds.

Per-ewe exposed and per-ewe lambing, lifetime number of lambs born (Table 4) was greater for Polypay ($P = 0.0001$ and 0.0001, respectively),

Table 1. Type III sums of squares for main effects to show the relative importance of each source of variation for explaining differences in lifetime ewe productivity.

Source of variation	Cumulative lifetime weaning weight[a]	Lifetime born[a]	Lifetime weaned[a]	Lifetime counts of lambing events[a]	Age at first lambing[a]
Per ewe exposed (n = 1,628)					
Sex of littermate	67,907.24	53.05	50.31	11.91	0.34
Ewe birth year	327,692.47	424.61	322.66	122.06	12.38
Ewe breed	520,464.66	435.43	203.27	30.59	28.82
Ewe weaning weight	1,958,823.37	2,291.95	1,426.20	621.79	45.47
Ewe birth weight	1,294,931.41	1,575.31	1,070.34	477.75	60.39
Total sums of squares	24,131,731.40	30,249.46	22,159.38	8,703.94	1,059.44
Per ewe lambing (n = 1,277)					
Sex of littermate	14,066.11	3.20	9.99	0.21	0.75
Ewe birth year	337,223.57	397.54	267.35	83.87	8.65
Ewe breed	343,302.59	252.54	76.80	20.77	21.39
Ewe weaning weight	1,213,041.55	1,374.95	828.40	293.85	54.02
Ewe birth weight	910,981.44	1,156.90	791.30	301.67	16.02
Total sums of squares	15,971,570.45	20,295.62	14,312.07	4,884.97	422.70

[a] Cumulative lifetime weaning weight = cumulative weight of lambs weaned in kilograms; Lifetime born = cumulative count of recorded birth weights; Lifetime weaned = cumulative count of recorded weaning weight; Lifetime counts of lambing events = cumulative count of lambing events; Age at first lambing = age ewe first lambed (1, 2, or 3 yr of age). Ewes were produced in an autumn-breeding management system.

Table 2. Effect of sex of co-twin or breed on lifetime productivity of all ewes exposed and lambing[a].

	n	Cumulative lifetime weaning weight, kg
Per ewe exposed		
Co-twin[b]		
Ewe	1,090	113.20 ± 7.20
Ram	538	128.75 ± 8.74
Breed[c]		
Columbia	383	86.79 ± 10.30
Polypay	536	152.92 ± 8.90
Rambouillet	383	127.87 ± 9.95
Targhee	326	116.32 ± 10.24
Per ewe lambing		
Co-twin[d]		
Ewe	826	150.59 ± 7.00
Ram	451	160.24 ± 8.69
Breed[c]		
Columbia	309	121.06 ± 10.21
Polypay	433	186.11 ± 8.59
Rambouillet	297	158.15 ± 10.18
Targhee	238	156.33 ± 10.42

[a] Values are least-squares means ± SEM from SAS, PROC MIXED analyses.
[b] Cumulative lifetime weaning weight for ewes from ewe-ram co-twin births was greater ($P = 0.03$) than that of ewes from ewe-ewe co-twin births.
[c] On per-ewe-exposed and per-ewe-lambing basis, cumulative lifetime weaning weights were greater for Polypay than for Columbia ($P < 0.001$ and 0.0001, respectively), Rambouillet ($P = 0.01$ and 0.006, respectively), and Targhee ($P = 0.003$ and 0.004, respectively) ewes. Per ewe exposed and per ewe lambing, cumulative lifetime weaning weights for Rambouillet ($P = 0.003$ and 0.002, respectively) and Targhee ($P = 0.02$ and 0.007, respectively) were greater than those for Columbia ewes, but the values did not differ ($P > 0.30$) between Rambouillet and Targhee ewes.
[d] Sex of littermate did not affect ($P = 0.20$) cumulative lifetime weaning weights.

Rambouillet ($P = 0.0001$ and 0.0006, respectively), and Targhee ($P = 0.03$ and 0.01, respectively) than for Columbia ewes. The number was greater ($P = 0.006$) for Polypay than for Targhee, but not greater ($P > 0.20$) than for Rambouillet. Rambouillet and Targhee did not differ ($P > 0.10$).

Lifetime numbers of lambs weaned (Table 4), on per-ewe-exposed and per-ewe-lambing bases, were greater for Polypay ($P = 0.0002$ and 0.005, respectively) and Rambouillet ($P = 0.0003$ and 0.01, respectively) than for Columbia ewes. Polypay ewes exposed and lambing weaned more lambs in a lifetime than did Targhee ($P = 0.0007$ and 0.03, respectively), but not more than Rambouillet ewes ($P = 0.90$ and 0.60, respectively). On both bases, lifetime numbers of lambs weaned did not differ between Columbia and Targhee ewes ($P = 0.20$ and 0.44, respectively). Rambouillet ewes exposed weaned a greater number of lambs than did Targhee ewes exposed ($P = 0.02$), but Rambouillet and Targhee ewes lambing did not differ ($P = 0.10$).

For lifetime counts of lambing events per ewe exposed (Table 4), Rambouillet exceeded Columbia ($P = 0.01$) and Targhee ($P = 0.07$), but not Polypay ewes ($P = 0.54$). Counts were greater for Polypay than Columbia ($P = 0.04$), and counts for Targhee did not differ from Columbia ($P = 0.49$) or Polypay ($P = 0.15$). Per-ewe lambing, lifetime counts of lambing events for Rambouillet exceeded Columbia ($P = 0.07$) and Polypay ($P = 0.09$), but not Targhee ewes ($P = 0.17$). Counts did not differ

Table 3. Effect of sex of co-twin on prolificacy, lifetime number of lambs weaned, cumulative years lambing, and age at first lambing for ewes exposed and ewes lambing[a].

	n	Lifetime born[b]	Lifetime weaned[b]	Lifetime counts of lambing events	Age at first lambing
Per ewe exposed					
Ewe co-twin	1,090	4.06 ± 0.25	3.64 ± 0.21	2.64 ± 0.13	1.20 ± 0.05
Ram co-twin	538	4.49 ± 0.29	4.10 ± 0.26	2.83 ± 0.16	1.23 ± 0.06
Per ewe lambing[c]					
Ewe co-twin	826	5.24 ± 0.25	4.81 ± 0.21	3.49 ± 0.12	1.63 ± 0.04
Ram co-twin	451	5.43 ± 0.30	5.06 ± 0.26	3.55 ± 0.15	1.60 ± 0.04

[a] Values are least-squares means ± SEM from SAS, PROC MIXED analyses.
[b] Per ewe exposed, lifetime born and lifetime weaned were greater ($P < 0.08$) for ewes from ewe-ram co-twin births than for ewes from ewe-ewe co-twin births.
[c] Per ewe lambing, sex of co-twin did not affect ($P > .70$) any of the traits.

Table 4. Effect of breed on prolificacy, total number of lambs weaned, lifetime counts of lambing events, and age of first lambing for ewes exposed and ewes lambing[a].

	n	Lifetime born[b]	Lifetime weaned[c]	Lifetime counts of lambing events[d]	Age of first lambing[e]
Per Ewe Exposed					
Breed					
Columbia	383	3.18 ± 0.35	3.09 ± 0.31	2.46 ± 0.19	1.34 ± 0.07
Polypay	536	5.10 ± 0.31	4.42 ± 0.27	2.88 ± 0.18	1.34 ± 0.06
Rambouillet	383	4.71 ± 0.34	4.38 ± 0.31	2.99 ± 0.19	1.11 ± 0.07
Targhee	326	4.13 ± 0.35	3.57 ± 0.31	2.62 ± 0.19	1.06 ± 0.07
Per Ewe Lambing					
Breed					
Columbia	309	4.28 ± 0.35	4.42 ± 0.30	3.40 ± 0.17	1.86 ± 0.05
Polypay	433	6.04 ± 0.30	5.37 ± 0.26	3.46 ± 0.15	1.63 ± 0.04
Rambouillet	297	5.64 ± 0.34	5.25 ± 0.30	3.74 ± 0.17	1.52 ± 0.05
Targhee	238	5.38 ± 0.36	4.71 ± 0.31	3.48 ± 0.18	1.46 ± 0.05

[a] Values are least-squares means ± SEM from SAS, PROC MIXED analyses. Lifetime born = cumulative count of recorded birth weights; Lifetime weaned = cumulative count of recorded weaning weights; Lifetime counts of lambing events = cumulative count of lambing events; Age of first lambing = age ewe first lambed (1, 2, or 3 yr of age). Ewes were produced in an autumn-breeding management system.

[b] Per ewe exposed: Polypay, Rambouillet, and Targhee > Columbia ($P = 0.0001$, $P = 0.001$, $P = 0.03$, respectively); Polypay > Targhee ($P = 0.006$) but not different from Rambouillet ($P > 0.20$); and Rambouillet not different from Targhee ($P > 0.10$). Per ewe lambing: Polypay, Rambouillet, and Targhee > Columbia ($P = 0.0001$, $P = 0.0006$, $P = 0.01$, respectively); Polypay > Targhee ($P = 0.07$) but not different from Rambouillet ($P > 0.20$); and Rambouillet not different from Targhee ($P > 0.50$).

[c] Per ewe exposed: Polypay and Rambouillet > Columbia ($P = 0.0002$ and $P = 0.0003$, respectively); Columbia not different from Targhee ($P = 0.20$); Polypay > Targhee ($P = 0.007$) but not different from Rambouillet ($P > .90$); and Rambouillet > Targhee ($P = 0.02$). Per ewe lambing: Polypay and Rambouillet > Columbia ($P = 0.005$ and $P = 0.01$, respectively); Columbia not different from Targhee ($P = 0.44$); Polypay > Targhee ($P = 0.03$) but not different from Rambouillet ($P > .60$); and Rambouillet not different from Targhee ($P = 0.10$).

[d] Per ewe exposed: Rambouillet > Columbia ($P = 0.01$) and Targhee ($P = 0.07$) but not different from Polypay ($P = 0.54$); Polypay > Columbia ($P = 0.04$) but not different from Targhee ($P = 0.15$); and Columbia not different from Targhee ($P = 0.49$). Per ewe lambing: Rambouillet > Columbia ($P = 0.07$) and Polypay ($P = 0.09$) but not different from Targhee ($P = 0.17$); Columbia not different from Targhee ($P = 0.72$) and Polypay ($P = 0.75$); and Targhee not different from Polypay ($P = 0.92$).

[e] Per ewe exposed: Rambouillet and Targhee < Columbia ($P = 0.001$ and 0.0005, respectively) and Polypay ($P = 0.0001$ and 0.003, respectively); Rambouillet not different from Targhee ($P > 0.30$); and Columbia not different from Polypay ($P = 0.99$). Per ewe lambing: Rambouillet and Targhee < Columbia ($P = 0.001$ for both) and Polypay ($P = 0.003$ and 0.04, respectively); and Polypay < Columbia ($P = 0.0001$).

between Columbia and Targhee ($P = 0.72$), Columbia and Polypay ($P = 0.75$), or Targhee and Polypay ewes ($P = 0.92$).

On per-ewe-exposed and per-ewe-lambing bases, age at first lambing (Table 4) was less ($P < 0.004$) for Rambouillet and Targhee than for Columbia and Polypay ewes. Per ewe exposed, age at first lambing did not differ between Columbia and Polypay ($P = 0.99$) or between Rambouillet and Targhee ewes ($P > 0.40$). Per ewe lambing, Polypay were younger ($P = 0.0001$) at first lambing than Columbia ewes. Seventy percent of the Rambouillet and 60.5 percent of the Targhee ewes lambed as yearlings, whereas 54.4 percent and 52.7 percent, respectively, of the Columbia and Polypay ewes lambed for the first time as 2 yr olds.

Discussion

Sex of co-twin affected lifetime productivity of twinborn ewes. We used litter weight weaned per-ewe exposed to rams for breeding as the definition of ewe productivity because this is the typical expression of ewe productivity and consistent with management practices in extensive sheep production systems (Ercanbrack and Knight, 1998; Snowder, 2002; Snowder and Fogarty, 2009). Data were also expressed on a per-ewe-lambing basis to determine whether sex of co-twin affected that subset of ewes. The environmental effect of sex of co-twin was primarily limited to measures that were calculated on a per-ewe-exposed, rather than on a per-ewe-lambing, basis. There is no clear explanation for this difference, but we speculate that sex of co-twin could have affected the ability of ewes to become pregnant and lamb and to wean more lambs over a lifetime of exposures to rams for breeding. In rodents and swine, sex of adjacent littermate(s) in utero was associated with differences in timing of puberty (vom Saal and Finch, 1988), duration of estrous cycles (vom Saal and Bronson, 1980b), age at first estrus (vom Saal, 1981), and reproductive capacity (vom Saal and Finch, 1988; Drickamer et al., 1997). In the present study, marking harnesses were not used to identify ewes as bred and ultrasonography for pregnancy determination was not used as management tool, so it is possible that a greater percentage of ewes with a female co-twin did not become pregnant or had greater rates of fertilization failure or embryonic or fetal mortality than those with a male co-twin. Co-twin effects on embryonic loss in sheep has been assessed (Avdi and Driancourt, 1997), but loss was determined between ovulation and lambing, not taking into account potential fertilization failure in ewes exposed to rams for mating or late embryonic or fetal loss. In rodents and swine, sex of adjacent littermate(s) in utero was associated with differences in sexual behavior (vom Saal and Bronson, 1978; Kinsley et al., 1986a; Rohde Parfet et al., 1990) and attractiveness to males (vom Saal, 1989), so it may be possible that ewes with a male co-twin were more sexually attractive to rams or had more proceptive behavior than ewes with a female co-twin and became pregnant at a greater rate.

Per-ewe exposed, the cumulative-lifetime-weaning weight advantage for ewes born co-twin to a ram was substantial and considerably greater than the expected-annual-genetic increase in litter weight weaned of 0.69 kg/yr (Ercanbrach and Knight, 1998) for Columbia, Polypay, Rambouillet, and Targhee sheep and 0.61 kg/yr for Polypay sheep (Notter, 2014). Improvements in genetic merit for litter weight weaned were attributed to approximately 37 percent prolificacy, 27 percent to percentage of lambs weaned, 17 percent to lamb weaning weight, 12 percent to fertility, and 7 percent to ewe viability (Ercanbrack and Knight, 1998). Indeed, the weighted-mean genetic correlation between litter-weight weaned and number of lambs born was 0.60 and between litter-weight weaned and number of lambs weaned was 0.80 (Snowder and Fogarty, 2009).

In the present study, the environmental effect of ewes born co-twin to a ram improved, on a per-ewe-exposed basis, lifetime counts of lambs born (i.e., prolificacy) and lambs weaned. In addition, lifetime numbers of lambs born and weaned increased as ewe-weaning weight increased. Thus, the environmental "benefit" to a ewe born co-twin to a ram was perhaps due to a greater number of ewes born co-twin to a ram becoming pregnant and lambing, explaining the increased prolificacy, lambs weaned, and lifetime ewe-weaning weight in ewes exposed to rams for breeding and why effects of co-twin were not seen in these variables in ewes lambing. However, the benefit of having a male co-twin did not increase lifetime counts of lambing events or decrease the age at first lambing. This is somewhat surprising because ewe lambs with heavier weaning weights were more likely to lamb at 1 yr of age, and this relationship was primarily environmental, rather than genetic (Kirschten et al., 2015).

Data from the present study contrast with previous data in refereed journals. The data in those reports on sheep indicate that sex of co-twin did not have important effects on fertility (Slee, 1963), embryonic development (Avdi and Driancourt, 1997), timing of puberty (Meredith and Keisling, 1996), or number of lambs born per ewe (Casellas and Caja, 2014). However, first-year survival and breeding success were less for unmanaged Soay ewes born co-twin to a ram (Korsten et al., 2009).

Too little is known about the interaction of ewe-ram co-twins in utero and between birth and weaning to offer an unequivocal explanation for the effects of co-twin sex in the present study. Also, the events in utero and between birth and weaning were confounded and cannot be separated with the dataset used for this study. Nevertheless, a large percentage of ewe-ram co-twins may share chorioallantoic circulation, and the endocrine environment of ewes from ewe-ram co-twins should be expected to differ from that of ewes from ewe-ewe co-twins (Wilkes et al., 1978); this is possibly associated with variation in placental size, function (Alexander, 1964), and circulatory systems (Valdes Cruz et al., 1977). Shared chorioallantoic circulation between male and female fetuses leads to freemartinism in cattle (Parkinson et al., 2001). At least 90 percent of the female calves from female-male co-twins are freemartins, and freemartin females are anestrus and sterile (Parkinson et al., 2001). By contrast, only a small percentage, perhaps less than 5 percent (Brace et al., 2008; Martinez-Royo et al., 2009), of ewes from ewe-ram co-twins are freemartins, which are also anestrus and sterile.

In the present study, androgens and other biochemical factors from ram lambs were conceivably transferred to their ewe co-twins during critical periods of prenatal development, and this could have affected reproductive development and function after birth (Short, 1975; Clarke et al., 1976; Wood and Foster, 1998). Treating fetal sheep with large doses of testosterone will disrupt, but not enhance, reproductive functions of ewes in postnatal life (Padmanabhan and Veiga-Lopez, 2014), and neither fetal-testosterone treatment nor factors related to freemartinism can explain the response of ewes that were naturally born co-twin to rams in the present study.

Ewe-birth weight in the present study did not affect any of the traits that were evaluated. This is consistent with a recent report of a large study indicating that absolute-birth weight did not affect litter size of Ripollesa ewes from twin births, but in contrast to data from the same study indicating that relative-birth weight (i.e., weight difference between twins) affected litter size of ewes from twin births (Casellas and Caja, 2014). Reproductive ability, measured as litter size, of twinborn ewes that were >600 g lighter than their co-twins was less than that of ewes with smaller disparities in birth weights (Casellas and Caja, 2014).

However, in the present study, weaning weight of ewes exposed affected lifetime number of lambs born and weaned, lifetime-lambing events, and cumulative-weaning weights, but not age at first lambing. These results should be expected because the heritability estimate was 0.14 for 120-d weaning weight and 0.15 for probability of lambing as a yearling, and the phenotypic and genetic correlations between the two traits were 0.18 and 0.23, respectively (Kirschten et al., 2015). Also, the positive relationship between weaning weight and various reproductive traits has been recognized for many years (Burfening et al., 1971; Dickerson and Laster, 1975; Stobart et al., 1987). Moreover, the relationships between ewe-weaning weight, degree of maturity at weaning, number of lambs born, number of lambs weaned, and lamb weaning weight were all positive (Stobart et al., 1987).

Breed effects were expected in the present study, and most of the effects were consistent with various published studies of Columbia, Polypay, Rambouillet, and Targhee sheep and ewes with Finnsheep breeding (Dickerson, 1977; Ercanbrak and Knight, 1985; Lewis and Burfening, 1988; Notter and McClaughtery, 1991; Nawaz et al., 1992; Inman and Slyter, 1993; Ercanbrack and Knight, 1998; Leeds and Lewis, 2006; Taylor et al., 2009). In general, productivity of Polypay and Rambouillet ewes exceeded that of Columbia and Targhee ewes, although breed ranking was not constant among productivity traits. Particularly important were the Polypay and Rambouillet advantages, compared with Columbia and Targhee, in cumulative lifetime weaning weights, lifetime numbers of lambs born, and lifetime numbers of lambs weaned. For age at first lambing, breed ranking was not consistent with a previous study of United States Sheep Experiment Station Columbia, Polypay, Rambouillet, and Targhee sheep (Leeds and Lewis, 2006). Based on between 3,802 and 4,990 records per breed, 45.7 percent, 81.3 percent, 58.8 percent and 49.9 percent of the Columbia, Polypay, Rambouillet, and Targhee ewes, respectively, lambed at approximately 1 yr of age (Leeds and Lewis, 2006). The differences in age at first lambing between the present and previous reports may reflect how the data were sampled and the differences in sizes of the datasets: 1,628 records in the present study and 17,798 records in Leeds and Lewis (2006).

Conclusion

Ewe productivity, defined as litter-weight weaned per ewe exposed to rams for breeding, is considered the key determinant of net-economic-return per ewe. Based on the results of this study, ewes with a ram co-twin were more productive than ewes with a ewe co-twin, regardless of breed and birth weight. We do not have a mechanistic explanation for the environmental "benefit" to a ewe born co-twin to a ram and, thus, suggest that cause-and-effect studies are warranted to explore this phenomenon in depth. Also, we believe that sex of co-twin should be further evaluated to determine whether it is a useful environmental adjustment, beyond lamb sex and type of birth and rearing, for lamb weights and traits related to ewe productivity.

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