Divergent planes of nutrition in mature rams influences birth characteristics of offspring but not growth performance or ewe reproductive productivity

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The objective of the current study was to characterize the effects of divergent planes of nutrition in mature rams on lambing and weaning rates, as well as offspring postnatal characteristics. While sire nutritional status prior to conception did not influence lambing or weaning rates and growth in offspring, birth weight and several body measurements were impacted, suggesting an effect of paternal diet on in utero development.

Summary

Twenty-four mature Rambouillet rams (initial mean body weight [BW] = 183.0 ± 6.4 lb) were randomly assigned to be managed on either a positive (gain 12% of initial BW; POS), maintenance (maintain initial BW; MAINT), or negative (lose 12% of initial BW; NEG) plane of nutrition over 84 days. Following the feeding period, rams were placed with 10 ewes each for a 28-day breeding season. Ewes were managed similarly throughout gestation. At lambing, birth weights and body measurements were recorded. Weights, body measurements, and scrotal circumference were recorded at weaning (approximately 60 days of age). All lambs were raised similarly throughout the growth period and final weights were recorded at approximately 220 days of age. Adjusted weaning weights and pre- and post-weaning average daily gain (ADG) were calculated. Lambing and weaning rates, as well as the number of lambs born and weaned per ewe lambed, were similar among treatments ($P > 0.34$). Lambs sired to NEG rams had greater birth weights, chest circumference, and shoulder-hip length than MAINT lambs ($P < 0.04$). These differences were not observed at weaning ($P > 0.23$), and pre-weaning ADG and adjusted weaning weights were similar among sire treatments ($P > 0.40$). While male offspring weighed more at day 160 and had a greater post-weaning ADG compared to female offspring ($P < 0.001$), no effects of sire treatment were observed for growth performance or scrotal circumference ($P > 0.36$). These findings provide insight on the effects of paternal nutrition on reproductive performance and offspring physiology, which could contribute to improved long-term managerial decisions for producers.

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Introduction

There are dramatic changes in body weight and plane of nutrition that occur throughout the production year for sires in livestock species as a result of differences in nutrient availability and workload. Previous research has demonstrated a link between male fertility and nutrition, representing an opportunity to optimize reproductive performance. Inadequate nutrition (both over- and undernutrition) has been associated with poor reproductive performance in bulls and rams, including reduced sperm production and motility, hormone concentrations, and libido (Brown, 1994). Based on producer preferences and available feedstuffs, there is variation in the rate of gain for sires leading up to the breeding season, which may not only affect reproductive performance, but also offspring development.

Recent studies in humans and mice have shown that changes in paternal nutrition prior to conception is linked to differences in offspring development and physiology and may contribute to metabolic diseases such as obesity and type II diabetes (Fullston et al., 2013). This occurs due to exposure of the developing sperm to altered concentrations of hormones and nutrient availability. This can result in sperm with alterations in nucleic acid composition and structure (known as epigenetic modifiers [i.e., DNA methylation patterns, histone modifications, RNA transcripts, etc.]), which are transferred to the embryo at the time of fertilization. The developing embryo and subsequent fetus may then experience differences in growth and development during pregnancy, leading to potential alterations in postnatal outcomes. Understanding the effects of paternal programming has several implications for improving livestock efficiency, thus the objective of this study was to characterize the effects of paternal plane of nutrition on ewe reproductive productivity, offspring body measurements and growth performance.

Procedures

A summary of procedures and characterization of the model are described by Bochantin et al., (2022). Briefly, mature Rambouillet rams (n = 24; BW = 183.0 ± 6.4 lb) from the Hettinger Research Extension Center (HREC; Hettinger, ND) were transported to NDSU (Fargo, ND) for this study. Rams were individually housed and randomly assigned to one of three treatments; a positive (gain 12% of initial BW [**POS**]; n = 8), maintenance (maintain initial BW [**MAINT**]; n = 8), or negative (lose 12% of initial BW [**NEG**]; n = 8) plane of nutrition. The feeding period was 84 days, corresponding to the length of two spermatogenic cycles in rams and ensuring that all sperm developed during the experimental period were exposed to the dietary treatment. Rams were fed a common diet and weighed on a weekly basis, after which dietary allotments were adjusted to achieve the targeted BW. The subsequent changes in body weight, composition, hormone and metabolite concentrations, and semen characteristics in response to divergent planes of nutrition are summarized by Bochantin et al. (2022).

Following the feeding period, rams were transported to HREC and each ram was placed in a pen with 10 ewes of similar age and body weight for a 28-day breeding season. After breeding, ewes were turned out to graze mixed native prairie pasture and managed similarly throughout gestation. Two weeks prior to lambing, ewes were brought to the lambing facilities and fed a common diet (Table 1). Lamb sex, birth type (singleton, twins, etc.), birth weight, lamb vigor, and body measurements at approximately 6 to 12 hours after birth were recorded. Body measurements included: crown-rump length (**CRL**; cm), shoulder-hip length (**SHL**; cm), chest circumference (**CC**; cm), and biparietal distance (**BPD**; cm; Table 2). Ewe and lamb cohorts were managed similarly through weaning, which occurred at approximately 60 days of age. Body weight and measurements, as well as scrotal circumference (cm), were recorded at weaning, and pre-weaning average daily gain (ADG) was calculated. Throughout the growth period, all lambs were fed a starter diet, consisting of a commercially available starter pellet (70%) and oat hay (30%). End weights were recorded at approximately 220 days of age and used to calculate post-weaning ADG. Scrotal circumference was also measured for ram lambs.

Data were analyzed with the MIXED procedure of SAS 9.4 (SAS Inst. Inc., Cary, NC), with ram serving as the experimental unit. Differences among treatments were considered significant at $P \leq 0.05$ and tendencies at $0.05 < P \leq 0.10$.

Results and Discussion

Sire treatment did not influence the proportion of ewes that lambed, nor the number of lambs born per ewe exposed or per ewe lamb ($P > 0.77$; Table 3). Additionally, there were no differences among sire treatments in the total weight of lamb birthed per ewe exposed or per ewe lambed ($P > 0.34$; Table 3). In terms of ewe productivity variables before weaning, there were no differences among sire treatments, including the number of lambs weaned per ewe exposed nor per ewe lambed ($P > 0.54$). Additionally, the weight of lambs weaned per ewe exposed and per ewe lambed were not affected by sire treatment ($P > 0.54$), which also was observed at the end timepoint ($P > 0.65$). Collectively, sire dietary treatment did not affect the number of ewes bred or offspring born, indicating minimal effects on ram reproductive performance; however, the number of ewes per ram in the current experiment is lower than that of typical commercial production, so further evaluation is needed to better understand the extent of sire nutrition on reproductive performance.

There were no treatment × sex interactions observed for any of the variables recorded through the experiment. Interestingly, birth weight was influenced by sire treatment and sex of the lamb ($P < 0.03$). While male offspring weighed more than females ($P < 0.001$), lambs sired by NEG rams had greater birth weights than

Table 1. Ingredient list and inclusion rate of ingredients fed to gestating/lambing ewes and lamb offspring.

Ingredient, % DM	Inclusion, %	CP, %	TDN, %
Gestating & lambing ewes			
Ground hay	80.0	15.0	63.1
Oats	20.0	13.0	75.0
Lambs prior to weaning			
Creep feed	100.0	18.0	80.0
Lambs after weaning			
Grower pellet	75.0	16.0	80.0
Oats	25.0	13.0	75.0

Table 2. Weight and body measurements at lambing and weaning of offspring sired by rams managed on divergent planes of nutrition.

Item	Treatment[1]				Sex			*P*-value[3]		
	POS	MAINT	NEG	SEM	Male	Female	SEM	TRT	Sex	TRT × Sex
Birth Measurements										
Weight, lb	8.6^{x}	8.4^{ax}	9.3^{by}	0.22	9.2b	8.5^{a}	0.17	0.03	0.001	0.98
CRL, cm	45.9	45.9	46.7	1.81	46.3	46.0	1.79	0.18	0.36	0.91
CC, cm	37.6^{ab}	37.4^{a}	38.4^{b}	0.41	37.9	37.7	0.35	0.05	0.34	0.80
SHL, cm	20.2^{ab}	19.9^{a}	20.7^{b}	1.73	20.2	20.4	1.72	0.04	0.43	0.89
Hip Width, mm	53.9	53.5	53.9	0.53	54.4^{b}	53.2^{a}	0.45	0.72	0.001	0.94
BPD, mm	58.9^{x}	59.3^{xy}	60.1^{y}	2.06	60.1^{b}	58.8^{a}	20.4	0.09	< 0.001	0.86
Weaning Measurements										
Weight, lb	26.0	27.1	28.4	7.01	27.1	26.9	6.94	0.40	0.93	0.90
Pre-Weaning ADG, lb/d	0.24	0.26	0.24	0.08	0.24	0.26	0.08	0.58	0.40	0.99
CRL, cm	70.5	70.6	70.7	4.51	70.1	71.1	4.48	0.98	0.23	0.62
CC, cm	53.7^{a}	54.8^{ab}	56.1^{b}	4.09	54.4	55.3	4.06	0.04	0.23	0.75
SHL, cm	31.8	31.9	31.6	2.50	31.6	31.9	2.50	0.89	0.52	0.66
BPD, mm	72.7	72.1	72.9	3.05	72.1^{x}	73.0y	3.03	0.57	0.08	0.15
Scrotal circumference, cm	11.2	11.6	11.2	0.33	-	-	-	0.66	-	-
Post-Weaning Measurements										
End weight, lb	111.6	114.4	116.1	3.39	125.9^{b}	102.1^{a}	2.93	0.36	< 0.001	0.44
Post-weaning ADG, lb/d	0.46	0.49	0.49	0.02	0.53^{b}	0.39^{a}	0.02	0.41	< 0.001	0.31
Scrotal circumference, cm	30.9	31.1	30.7	1.00	-	-	-	0.88	-	-

[1]Rams were managed on one of three treatments: to gain 12% of initial BW (POS), maintain initial BW (MAINT), or lose 12% of initial BW (NEG) during an 84-day feeding period.
[2]Measurements recorded included weight, crown-rump length (CRL), chest circumference (CC), shoulder-hip length (SHL), hip width, biparietal distance (BPD), average daily gain (ADG), and scrotal circumference (SC).
[3]Significance was set at $P < 0.05$ and tendency at $0.05 < P \le 0.10$ and included the effects of sire treatment (TRT), sex, and their interaction (TRT × Sex).
[ab]Means within a row for each main effect column (TRT or Sex) lacking a common superscript differ ($P < 0.05$).
[xy]Means within a row for each main effect column (TRT or Sex) lacking a common superscript tended to differ ($0.05 < P \le 0.10$)

Table 3. Lambing, weaning, and rearing weights of offspring sired by rams managed on divergent planes of nutrition.

Item	Treatment[1]				
	POS	MAINT	NEG	SEM	*P*-value
Lambing[2]					
Ewes lambed per ewes exposed, %	77.3	73.2	70.1	14.2	0.88
Average day of lambing interval	12.7	12.9	12.9	3.8	0.99
No. born per ewe exposed	1.48	1.36	1.35	0.21	0.77
No. born per ewe lambed	1.78	1.81	1.79	0.09	0.96
Weight of lamb birth per ewe exposed, lb	13.9	12.3	13.2	1.57	0.78
Weight of lamb birth per ewe lambed, lb	16.5	16.8	17.9	0.68	0.34
Weaning					
No. weaned per ewe exposed	0.97	0.77	0.89	0.131	0.55
No. weaned per ewe lambed	1.14	0.99	1.14	0.114	0.54
Weight of lamb weaned per ewe exposed, lb	36.6	29.8	36.4	5.36	0.64
Weight of lamb weaned per ewe lambed, lb	42.3	37.7	44.9	4.65	0.54
Rearing					
No. at end of experiment per ewe exposed	0.86	0.70	0.79	0.12	0.65
No. at end of experiment per ewe lambed	1.00	0.90	1.02	0.113	0.71
Weight of lamb per ewe exposed, lb	94.8	80.5	90.4	13.38	0.74
Weight of lamb per ewe lambed, lb	110.0	103.2	116.4	12.48	0.76

[1]Rams were managed on one of three treatments: to gain 12% of initial BW (POS), maintain initial BW (MAINT), or lose 12% of initial BW (NEG) during an 84-day feeding period.
[2]Rams were placed in an outdoor pen facility with 10 ewes each for a 28-day breeding period following the feeding period. Lambing characteristics were calculated for each ram exposed to the 10 ewes.

MAINT-sired lambs ($P = 0.04$) and tended to have greater birth weights than lambs sired by POS rams ($P = 0.08$). Furthermore, chest circumference and shoulder-hip length, were influenced by sire treatment, where NEG lambs had greater values than MAINT lambs ($P < 0.05$). Additionally, NEG lambs tended to have greater biparietal distance than POS lambs at birth ($P = 0.09$), while male lambs exhibited a greater biparietal distance than female lambs ($P < 0.001$). Interestingly, the majority of these differences in birth measurements were not observed in the weaning measurements. At weaning, NEG lambs had a greater chest circumference than POS lambs ($P < 0.04$), while female lambs tended to have greater biparietal distance than male lambs ($P = 0.08$). There were no differences among treatments observed for body weight or pre-weaning ADG ($P < 0.40$) at weaning. Additionally, there were no differences among treatments for scrotal circumference, an indicator of potential sperm production ($P = 0.66$). At the end collection, there were no effects of sire treatment on weight, post-weaning, ADG, or scrotal circumference; however, ram lambs had a greater end weight and post-weaning ADG, as compared to ewe lambs ($P < 0.001$). These findings suggest a potential effect of paternal nutrition on *in utero* development, which resulted in different weights and body measurements at birth. While there is limited information regarding paternal programming in livestock species, these results conflict with those reported in a mouse study, in which nutrient restricted males sired offspring with reduced birth weights (McPherson et al., 2016). Additionally, overfed male mice sired offspring with not only greater birth weights than control males, but also exhibited increased weight gain and fat deposition during their growth (Fullston et al., 2013). In a study with ram lambs supplemented with rumen protected methionine, the offspring sired by treated rams weighed and had numerically smaller scrotal circumference compared to control counterparts, but minimal differences in growth patterns observed (Gross et al., 2020). Although differences in weaning measurements or growth performance were not observed in the current study, there could be influences on other physiological traits, such as nutrient metabolism, fat deposition, or reproduction, that are influenced by paternal diet.

Future studies will focus on evaluating these paternal effects in greater depth, specifically evaluating relevant metabolic indicators, such as glucose metabolism and feed efficiency. Effects of paternal nutrition on offspring reproductive potential will also be evaluated to identify influences on fertility and transfer of gamete genetic material, as transgenerational inheritance has also been reported (Fullston et al., 2013). Together, these findings support the improvement of managerial decisions for sire nutrition, as well as help better understand the long-term implications on offspring performance.

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