# Effect of feeding regimen and selection on sexual behavior, epididymal sperm reserves and gross testicular characteristics in Rambouillet rams

by Kevin Charles Curry

A thesis submitted in partial fulfillment of the requirement for the degree of Master of Science in Animal Science
Montana State University


Abstract:
Objectives of this study were to: 1) determine if selection for a female reproductive trait influenced testicular, epididymal and libido characteristics in male offspring, and 2) evaluate effects of a high protein-energy det, during the growth phase, on the aforementioned traits in rams from lines selected for high and low reproductive rate.

Rambouillet rams (n = 25) were used in each of two trials (Tl,1982; T2,1984). Rams were from lines (LN) selected for either low (L) or high (H) prolificacy and a random-bred line (C) . In both trials, rams were fed a pelleted diet of 80% alfalfa and 20% barley ad libitum from weaning (BW1) until 10 mo of age (BW2). At this age, rams from each LN were assigned to one of two feeding regimens (FR): 1) placed on pasture and fed grass hay for duration of experiment (normal plane; NP) or 2) continued on the pelleted diet for 7 mo then combined with NP rams for duration of experiment (high plane; HP). Body weights were obtained at BW1, BW2, BW3 (termination of HP FR) and BW4 (4 mo after BW3) . After BW4, scrotal circumference (SC) was measured, and testicles removed to evaluate testicular and epididymal characteristics: 1) paired testicular weight (wt; PTW), 2) paired testicular volume (PTV), 3) paired epididymal wt and sperm reserve (PEW and TESR, respectively), 4) paired epididymal caput/corpus wt and sperm reserve (PEHW and PHESR, respectively), 5) paired cauda wt and sperm reserve (PETW and PTESR), 6) epididymal sperm reserve per gram epididymal wt (ESRGEW) and 7) epididymal sperm reserve per gram testicular wt (ESRGTW) . Rams were libido tested in 15 min tests 1 wk before (L1) and 1 (L2) and 2 (L3) wk after castration. Numbers of mount (M) and services (S) and reaction time to first mount (RTM) and services (RTS) were recorded. Line or FR did not affect ($P>.05$) growth rate of rams but rams in Tl grew more rapidly ($P<.05$) than in T2. Trial, LN, FR or their interactions did not affect ($P>.05$) any of the testicular and epididymal characteristics, except there was a LN by FR interaction ($P<.05$) for PEHW. Low LN rams had high correlations for all characteristics, while H and C LN rams had low to high correlations among the aforementioned traits. Rams in Tl had more M and S and shorter RTM and RTS than rams in T2. Low line rams had less M in L2 than H line rams. Rams on the HP FR had more M in L2 than NP rams. Libido decreased ($P<.05$) after castration and more ($P<.05$) rams mounted and serviced ewes in libido tests in Tl than in T2. In conclusion, selecting for a female reproductive trait or feeding a high protein-energy diet did not alter testicular, epididymal and libido characteristics of rams in this study.

# EFFECT OF FEEDING REGIMEN AND SELECTION ON SEXUAL BEHAVIOR, EPIDIDYMAL SPERM RESERVES AND GROSS TESTICULAR CHARACTERISTICS IN RAMBOUILLET RAMS

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Kevin Charles Curry

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of a thesis submitted by

Kevin Charles Curry

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Feb. 28, 1990
Date

James G. Brandenlli
Chairperson, Graduate Committee

Approved for the Major Department

F. 28, 1990
Date

Arthur C. Linton
Head, Major Department

Approved for the College of Graduate Studies

March 16, 1990
Date

Harry L. Parsons
Graduate Dean

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Signature Kevin Curry

Date 2/28/90

# VITA

Name . . . . . Kevin Charles Curry

Parent . . . . . .Cathleen Linahan Curry

Date of Birth . . . . . February 13, 1959

Schools Attended:

Elk Point Public High School . . . . . 1973 to 1977
Elk Point, South Dakota

South Dakota State University . . . . . 1977 to 1978
Brookings, South Dakota

Montana State University . . . . . 1978 to 1981
Bozeman, Montana

Degrees Received:

Baccalaureate of Science in Animal Science . . . . 1982

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## ABSTRACT

Objectives of this study were to: 1) determine if selection for a female reproductive trait influenced testicular, epididymal and libido characteristics in male offspring, and 2) evaluate effects of a high protein-energy det, during the growth phase, on the aforementioned traits in rams from lines selected for high and low reproductive rate.

Rambouillet rams (n = 25) were used in each of two trials (T1,1982; T2,1984). Rams were from lines (LN) selected for either low (L) or high (H) prolificacy and a random-bred line (C). In both trials, rams were fed a pelleted diet of 80% alfalfa and 20% barley ad libitum from weaning (BW1) until 10 mo of age (BW2). At this age, rams from each LN were assigned to one of two feeding regimens (FR): 1) placed on pasture and fed grass hay for duration of experiment (normal plane; NP) or 2) continued on the pelleted diet for 7 mo then combined with NP rams for duration of experiment (high plane; HP). Body weights were obtained at BW1, BW2, BW3 (termination of HP FR) and BW4 (4 mo after BW3). After BW4, scrotal circumference (SC) was measured, and testicles removed to evaluate testicular and epididymal characteristics: 1) paired testicular weight (wt; PTW), 2) paired testicular volume (PTV), 3) paired epididymal wt and sperm reserve (PEW and TESR, respectively), 4) paired epididymal caput/corpus wt and sperm reserve (PEHW and PHESR, respectively), 5) paired cauda wt and sperm reserve (PETW and PTESR), 6) epididymal sperm reserve per gram epididymal wt (ESRGEW) and 7) epididymal sperm reserve per gram testicular wt (ESRGTW). Rams were libido tested in 15 min tests 1 wk before (L1) and 1 (L2) and 2 (L3) wk after castration. Numbers of mount (M) and services (S) and reaction time to first mount (RTM) and services (RTS) were recorded. Line or FR did not affect ($P>.05$) growth rate of rams but rams in T1 grew more rapidly ($P<.05$) than in T2. Trial, LN, FR or their interactions did not affect ($P>.05$) any of the testicular and epididymal characteristics, except there was a LN by FR interaction ($P<.05$) for PEHW. Low LN rams had high correlations for all characteristics, while H and C LN rams had low to high correlations among the aforementioned traits. Rams in T1 had more M and S and shorter RTM and RTS than rams in T2. Low line rams had less M in L2 than H line rams. Rams on the HP FR had more M in L2 than NP rams. Libido decreased ($P<.05$) after castration and more ($P<.05$) rams mounted and serviced ewes in libido tests in T1 than in T2. In conclusion, selecting for a female reproductive trait or feeding a high protein-energy diet did not alter testicular, epididymal and libido characteristics of rams in this study.

# INTRODUCTION

A major goal in the livestock industry is to increase the numbers of offspring produced each year. To accomplish this objective and maximize profit, it is necessary to have a complete understanding of reproductive processes.

Reproductive performance of the male is an important and integral component involved with livestock breeding. Males must have the sexual drive and capabilities to service many females along with an adequate supply of sperm to achieve successful insemination and impregnation so his genetic characteristics can be disseminated upon the population. This is of great importance to the sheep producer, since income to producers is largely dependent upon lamb production.

Reproductive performance and traits related to performance in sheep are known to vary among breeds, but little information is available on how selecting for increased reproductive rate within a breed affects individual reproductive characteristics, i.e., libido and sperm supply. The genetic and physiological mechanisms whereby selection of specific reproductive traits of one sex influences the reproductive phenomena associated with the other sex are not well documented. Furthermore, many studies indicate that proper nutrition is necessary for appropriate development and maintenance of reproductive organs and behavior, and subsequent reproductive performance in domestic ruminants.

This review summarizes how selection for reproductive rates alters reproductive characteristics of female and male sheep and how selection pressure placed upon females influences the reproductive activity of the male. Additionally, it focuses upon the question of how reproductive activities of males respond to changes in nutritional regimens.

# REVIEW OF LITERATURE

## Selection for Reproductive Rate in Sheep

Low reproductive rate is a major factor limiting productivity for the American sheep producer. Reproductive rate in sheep is a function of fertility (number of ewes conceiving), fecundity (number of offspring per pregnancy) and lamb survival (number of offspring surviving the birth process). Due to low heritability and low repeatability of fertility (0.03 to 0.10 and 0.08 to 0.09, respectively) and fecundity (0.04 to 0.26, 0.04 to 0.28 respectively), response to selection for reproductive rate is slow (Bindon and Piper, 1976).

Other factors limiting improvement by selection for reproductive rate include: 1) fertility and fecundity are measured only in ewes; causing traits to be sex-limited and both require the male for expression which contributes to low repeatability, 2) environmental factors such as season (photoperiod) and nutrition, and, 3) age and birth-type (single or multiple) of ewes. Low reproductive rate itself limits the degree of selection pressure which can be applied to a population of sheep, but, selecting for fecundity has resulted in a gain of 0.023 lambs per ewe per year (Bindon and Piper,1976; Land, 1974).

## Female Components of Reproductive Rate

Litter Size. Litter size, or number of offspring per pregnancy, is an important component of reproductive rate. Heritability of litter size in sheep was reported to be 0.15 by Bradford (1972). Several studies have been conducted with different breeds using litter size as the main selection criterion. Merinos selected for or against production of multiple births achieved litter sizes of 1.70 and 1.18 lambs per ewe bred respectively, with an estimated response to selection for litter size of 0.52 (Bradford, 1985). On the other hand, Galways selected for litter size of dam and sire's dam achieved litter size of 1.67 and 1.44 for high and control lines, respectively, with an estimated response of 1.5% increase per year (Hanrahan, 1982). Litter sizes in Romney ewes selected for incidence of multiple births were 1.62, 1.22 and 1.13 lambs born per ewe bred for high, control and low lines, respectively, with an annual rate of improvement of 0.018 lambs per ewe per year for the high line over the control line (Clarke, 1972). Burfening et. al. (1977) reported a difference of 13 in the number of lambs born per 100 ewes lambing between low and high line Rambouillet rams selected on the basis of their dams' lambing record when mated to a randomly bred population of ewes.

The evidence seems clear that selection for litter size in ewes within a breed can increase ovulation rate even in

breeds with comparatively low reproductive rate. Furthermore, males from lines selected for increased reproductive rate appear to have an immediate affect on litter size. The mechanism in not clear, but may be related to embryonic vigor during development.

Ovulation Rate. It has been postulated that ovulation rate is the principal factor which limits litter size in sheep (Bradford, 1972; Hanrahan, 1982). A curvilinear relationship between litter size and ovulation rate was observed by Hanrahan (1982). The data indicated that as ovulation rate increased litter size increased to a point then remained stable, with no further increase. Also, Hanrahan (1982) reported repeatability and heritability of ovulation rate to be 0.67 and 0.45, respectively, which were higher than those for litter size (0.10 and 0.10, respectively). The results of Hanrahan (1982) should be interpreted with some caution since repeatabilities in ovulation rate of 0.69 and 0.24 for within and between years respectively, was reported for Merino ewes by Bindon and Piper (1976). With a high heritability and repeatability, one would expect selecting for ovulation rate would increase litter size. However, in experiments using ovulation rate as the main selection criterion in mice (Bradford, 1969), swine (Cunningham et al., 1979) and sheep (Hanrahan, 1982), ovulation rate did increase, but was not accompanied by an increase in litter size. Thus, factors

other than ovulation rate, such as embryonic mortality or uterine capacity, may come into play to limit reproductive rate in these species.

Embryonic Survival and Uterine Efficiency. The relationship between embryonic survival and litter size is also one of uncertainty. Hanrahan (1982) found that there was no difference in ovulation rate and subsequent litter size between lines of Finn ewes selected for low and high fertility, with no apparent affect on embryonic survival and litter size. In Rambouillet ewes selected for either high or low reproductive rate, embryonic survival was lowest in the high line, but when site of ovulation was taken into account, there was no difference in embryonic survival between the lines (Schoenian, 1988). These data indicate that embryonic survival contributes little to differences in litter size and that there is little genetic difference in embryonic survival in sheep.

Uterine efficiency is conceptualized as the capacity of the uterus to accommodate increasing numbers of embryos without altering the survival of those embryos. It is another factor that may have an impact on reproductive rate. Uterine efficiency probably sets an upper limit within species or breeds for reproductive rate. In reviews by Bindon and Piper (1976) and Meyer (1985), it was concluded that selecting for litter size has resulted in correlated changes in ovulation

rate but, without any substantial improvement in uterine efficiency. Thus, if uterine efficiency does not change as ovulation rate increases, then litter size is not altered and consequently one could only expect small increase in reproductive rate in species which normally bear two or three offspring per pregnancy.

Estrous Cycles and Ovarian Function: The number of estrous cycles a ewe exhibits is a function of ovarian activity. In a review by Land (1974), the frequency of estrus was genetically correlated (0.5 to 0.9) with fertility in the Romney breed and phenotypically correlated (0.8) with ovulation rate in the Romanov breed. Bindon and Piper (1976) reported that high fecundity was found to be correlated with the frequency of estrus and ovulation in Merino ewes. Ewes with high fecundity showed estrous 40% more and had 200% more mean ovulation rated than ewes with low fecundity.

Ovarian function is regulated by gonadotropins released from the anterior pituitary gland under the control of hypothalamic secretion of gonadotropin releasing hormone (GnRH) and modified by ovarian steroids (Reeves, 1987). A positive relationship was found between luteinizing hormone (LH) secretion and ovarian activity in Romanov, Prealpes and the cross between these two breeds (Thimonier and Pelletier, 1972). However, Bindon et al. (1985), found no relationship between LH secretion and prolificacy of the breed between

Booroola (high prolific breed) and control Merino ewes.

Breed differences in follicle stimulating hormone (FSH) concentrations in lambs and mature ewes during the estrous cycle have been reported to be related to prolificacy of the breed (D'man and Merino; Bindon and Piper, 1976; Bindon et al., 1985). Booroola ewes were classified by ovulation rate for repeated records as; FF (greater than 5; putative homozygous for the fecundity gene), F+ (3 to 5; heterozygous carriers), and ++ (less than 3; putative homozygous normal). Differences in ovulation rates among these putative genotypes were not correlated with mean FSH concentrations (Bindon et al., 1985).

In a recent study by Adams et al. (1988), periovulatory changes in LH, FSH, duration of estrus and interval from estrus to LH peak differed among low and high prolific breeds. However, these changes were inconsistent with ovulation rate for each of the breeds. Therefore, quantitative changes in hormone concentrations during the periovulatory period are correlated with ovulation rate.

## Overview of Male Reproductive Physiology

The primary reproductive organ of the ram is the testis. Two major functions of the testis include androgen biosynthesis and secretion by the Leydig (interstitial) cells and sperm production within the seminiferous tubules. The

role of the hypothalamus and anterior pituitary and their relationship in regulation of endocrine and exocrine functions of the testis will be reviewed.

Hypothalamic-Pituitary-Testicular Axis. The hypothalamus integrates inputs from the central nervous system, which controls the stimulation or inhibition of GnRH synthesis and secretion. Gonadotropin-releasing hormone is released in discrete impulses from the hypothalamus to the adenohypophysis (anterior pituitary) via the hypophyseal portal vascular system to stimulate the pulsatile release of LH and the gradual discharge of FSH into the general circulation (Amann and Schanbacher, 1983; Lincoln, 1978).

Luteinizing hormone and FSH bind to specific membrane receptors of the Leydig (LH) and Sertoli cells (FSH) in the testes. Leydig cells synthesize and secrete testosterone (T) which is essential for spermatogenesis, growth and function of epididymis, secondary accessory sex glands and Sertoli cells. Testosterone is also necessary for maintaining male sexual behavior and drive (libido). Sertoli cells synthesize and secrete androgen binding protein which may act to maintain high androgen levels in the seminiferous tubules and epididymis (Amann and Schanbacher, 1983; Bardin et al., 1988).

The hypothalamic-pituitary-testicular axis is a self-regulating system (Amann and Schanbacher, 1983). Release of LH from the anterior pituitary is usually followed by a rise

in circulating T (Sanford et al., 1974; Schanbacher and Ford, 1976). Castrate rams exhibit frequent rhythmic pulses of LH, whereas intact rams exhibit infrequent episodic pulses of LH (Sanford et al., 1974; Schanbacher and Ford, 1976; D'Occhio et al., 1982). Implantation of varying doses of T in wethers suppress LH concentrations, providing evidence that T has a negative feedback action on LH secretion. Estrogens and other androgens produced in the testes can also induce negative feedback inhibition on LH regulation (Schanbacher and Ford, 1977; D'Occhio et al., 1982, 1983; D'Occhio et al., 1985).

Castration of rams causes concentrations of FSH to increase compared to intact rams. Implantation of exogenous androgens, including T, and estrogens in castrate animals suppress FSH concentrations. This indicates that these testicular steroids have a negative feedback effect on FSH secretion (Schanbacher and Ford, 1977; D'Occhio et al., 1985). It has been postulated that the negative feedback effect of androgens acts on the hypothalamus to reduce GnRH release which reduces the synthesis and secretion of FSH from the anterior pituitary (Schanbacher and D'Occhio, 1984).

Although testicular steroids tend to inhibit the secretion of FSH, they do not have the same suppressive effect as they do on LH (Swerdloff and Walsh, 1973). This finding, coupled with the fact that steroid-free testicular extracts added to pituitary cell cultures in vitro effectively suppress FSH secretion, indicate that a protein secreted by the testis

is involved in the in vivo regulation of FSH secretion (Baker et al., 1976). This protein, now known as inhibin, has been isolated, purified and characterized and is synthesized and secreted by the Sertoli cells of the seminiferous tubules.

Seasonality. It is well known that ewes exhibit a definite annual pattern in estrous activity related to season of the year. Increasing the daily light/dark photoperiod ratio causes a cessation in estrous activity while decreasing the ratio stimulates estrous activity (Ortavant, 1977). On the other hand, rams do not exhibit such definite active and inactive periods of sexual activity and are able to produce spermatozoa and ejaculate throughout the year (Pepelko and Clegg, 1965; Ortavant, 1977).

Alternations in photoperiod affect reproductive activities of rams by influencing the rate of synthesis and secretion patterns of gonadotropins from the anterior pituitary, which in turn affects endocrine and exocrine output from the testes along with libido. Gonadotropin and T concentrations are higher during the breeding season than during the non-breeding season. These elevated T concentrations are due to an increase in pulsatile frequency of LH release (Schanbacher and Ford, 1976; Schanbacher and Lunstra, 1976; Sanford et al., 1977). Follicle stimulating hormone concentrations increase as the breeding season approaches and then declines during the winter (Sanford et

al., 1977).

The role of photoperiodicity in the regulation of the aforementioned hormones is illustrated by the following data. Rams maintained under artificial photoperiod of 16 h light (L): 8 h dark(D) had low LH and FSH concentrations and upon an abrupt change to 8L:16D, LH and FSH increased after 2 wk (Lincoln and Davidson, 1977; Lincoln et al., 1977).

Seasonal fluctuations in LH and T are associated with changes in libido (Schanbacher and Lunstra, 1976; Sanford et al., 1977). They reported that LH and T concentrations and mating activity increased as the breeding season progressed, with maximum hormone concentration and libido occurring in October and November, respectively. A positive correlation was observed between changes in mean T and mating activity under seasonal conditions. An increase in scrotal circumference (SC) and libido was observed by Tulley and Burfening (1983) and Mickelsen et al. (1981) as photoperiod decreased; and an increase in libido during short-length photoperiods (8L:16D) was reported by Lincoln and Davidson (1977).

Sanford et al. (1977) reported that ejaculate volume was highest in November, when T concentrations were maximal; and Boland et al. (1985) and Barrell and Lapwood (1978) reported that semen volume increased as the breeding season approached.

Mickelsen et al. (1981) reported that percentage of normal and motility of sperm decreased as photoperiod

increased. Seasonal changes in sexual aggressiveness, testicular diameter, sperm concentration, progressive motility and percentage normal acrosomes were reported by Lunstra and Schanbacher (1976), with values for these variables being lowest during the summer months.

## Male Components of Reproductive Rate

Hormone Concentrations. Since fertility and testicular function are controlled by interactions among gonadotropic and steroid hormones, many studies have focused on the relationship of hormones with these characteristics. Bindon and Turner (1974), Thimonier and Pelletier (1972), and Carr and Land (1975) reported a positive correlation between LH concentrations in ram lambs and breed differences in prolificacy of female relatives. Lucas et al. (1983) reported that Finn (high prolific breed) crossbred ram lambs had higher LH concentrations at 20 and 44 d of age and higher FSH concentrations at 20 d of age than Rambouillet (low prolific breed) crossbred rams. However, differences in LH and FSH were not observed between Finn crossbred and Dorset crossbred ram lambs at 21 and 49 d of age. Breed differences in LH and FSH in prepubertal rams have been reported by Sanford et al. (1982).

Breed differences in LH concentrations have been reported in adult rams. D'Occhio et al. (1982) reported that Finn rams

showed a greater number of LH peaks and higher mean concentrations of LH than Dorset, Rambouillet and Suffolk rams when exposed to a 8L:16D regimen. Prealpes-du-Sud rams (high prolific breed) exhibited similar frequency of LH peaks in December compared to Ile-de-France rams, but twice as many peaks were observed in the Prealpes-du-Sud rams during June compared to the Ile-de-France rams (Pelletier et al., 1982).

Follicle stimulating hormone concentrations did not differ between adult Finn, Suffolk and a synthetic breed in the spring (Sanford et al., 1982). Collectively, patterns of gonadotropins, although important in male functions, do not permit sufficient information to yield an adequate hypothesis concerning the nature of differences in fertility related to breed.

Data for LH and FSH concentrations and their relationship to fertility among genetically alike (within breeds and lines) individuals is scarce and equivocal. Luteinizing hormone concentrations measured in 30-d-old Merino ram lambs did differ between lines selected for or against multiple births (Bindon and Turner, 1974). However, LH and FSH concentrations in ram lambs sired by rams selected for the prolificacy of their daughters, did not differ from ram lambs of the low prolific line between 3 and 11 wk of age (Hochereau-de Riviers, 1985). Furthermore, Moore et al. (1978) reported no differences in LH concentrations between adult Romney rams from a line selected for number of lambs weaned (high

fertility) and rams from a randomly-bred flock (low fertility) before or after exposure to estrous ewes. Luteinizing hormone and FSH concentrations did not differ between adult Booroola rams and control Merino rams (Bindon, 1985).

Testosterone concentrations in the systemic circulation have been reported to vary among breeds. Prepuberal spring-born Ile-de-France ram lambs had lower T concentrations from birth to 10 wk of age compared to highly prolific Romanov and Prealpes-de-Sud ram lambs. Also, rate of increase in T concentrations during this time was greater in Prealpes-de-Sud lambs than those in Ile-de- France lambs (Hochereau-de Riviers, 1985). Consistent with data for immature rams, mature Preaples-du-Sud rams exhibited higher frequency of T peaks during the summer months than did Ile-de- France rams, but both breeds had similar frequencies of T peaks in the winter months (Pelletier et al., 1982). Schanbacher and Lunstra (1976) found that mature Finn rams consistently had higher T concentrations than Suffolk rams throughout the year, except during two summer months. Moore et al. (1978) reported that mature Romney rams from a flock selected for high number of lambs weaned did not differ in T concentrations from rams of the control flock.

Based upon these studies, it would appear that differences in T concentrations, at least during certain periods of ontogeny, are responsible for breed differences in functionality of rams. However, this is only apparent in

breeds that are quite divergent in their prolificacy and T may not be a good indicator of reproductive ability of rams within a line or breed of sheep.

Estrogen and its relationship to fertility reproductive rate in sheep has not been documented. However, during a fall breeding season, there were no differences in mean estrogen concentrations between Finnish-Landrace and Managre Synthetic mature rams (Sanford et al., 1982).

Testicular Size and Scrotal Circumference. Measurement of testicular size or SC have become important techniques for evaluating fertility of males. Cameron et al. (1984) reported that sperm production and daily sperm output in rams were highly correlated with testicular weight. Knight (1977) reported a correlation of 0.85 between testicular weight and number of sperm in the testes of rams. Furthermore, a high positive correlation between testicular weight and diameter has been reported for rams by Land and Carr (1975) and Knight (1977).

Coulter and Foote (1979) reported that testicular weight is an accurate estimate of sperm-producing parenchyma in the testis of the bull. Also, they found a high correlation between testicular weight and SC (0.89) and between SC and sperm output (0.81) in bulls.

Scrotal circumference has been reported to vary among breeds in rams. Braun et al. (1980) evaluated 9 different

breeds of sheep and found that larger maturing breeds had larger SC than smaller maturing breeds and within breeds SC was correlated with body weight (range of r, 0.65 to 0.83). Scrotal circumference in Rambouillet crossed Finn rams increased more rapidly from birth to 150 d in rams that had a greater percentage of Finn genes, however, SC did not differ at 160 d of age between crossbred groups (Notter et al., 1985).

Although testicular weight and SC yield an indication of sperm production by the testis, they do not or have not been experimentally tested with respect to their ability to directly influence reproductive rate in the male.

Libido. Not only must a male be capable of producing gametes, he must have the desire or drive to seek out and impregnate females. This sexual desire or behavior is called libido.

Evaluation of libido was initially done subjectively, however, standard tests with specific criteria for behavior have been developed to quantify this reproductive behavior. It is important to note that results of such tests depend upon the context of the tests. In this respect, relationships among tests conducted in pens to those performed in the pasture has been the subject of many studies.

Wiggens et al. (1953) reported that libido, measured by number of ejaculations in a 30-min period, was positively

correlated with the percentage of ewes lambing. Libido in three 20-min pen tests was highly and positively correlated to subsequent service activity during flock mating (Mattner et al., 1971). Similarly, Kilgour and Whale (1980) found a positive relationship between pen libido tests and flock fertility. Rams exhibiting high serving capacity in 1 and 2 h pen libido tests, raddled and inseminated more ewes during the first 16 d of flock mating than rams exhibiting low serving capacity, but the proportion of ewes lambing after 6 wk of mating was similar in both groups. Data from studies using 20 min or less test periods reflected no relationship between pen libido tests and flock fertility (Cahill et al., 1975; Fletcher, 1976; Walkey and Barber, 1976; Mickelsen et al., 1982). Kilgour and Whale (1980) reported the correlation between mean number of services in two 1-h pen tests and one 20-min test to number of ewes inseminated in the flock to be 0.88 and 0.33, respectively. Repeatability of number of services in a single 3 h libido test was high but low for a single 20-min test (Kilgour, 1985). However, a high positive correlation was found between numbers of mounts and services during the first 15-min interval of 30 or 60-min tests and total number of mounts and services during the entire 30 or 60-minute test (Tulley, 1983).

Libido of rams has been shown to be correlated with prolificacy of related females (Land, 1970; Land and Sales, 1977). The former authors reported that Finnish Landrace rams

mounted more ewes than did the Scottish Blackface rams, while the latter reported that Finnish Landrace and Finn-Merino crossbred lamb rams had a higher number of mounts than did straight-bred Merino rams. Barwick et al. (1985) reported breed differences (Border Leicester, BLI- high fertility sheep related to Border Leicester and BLI X Border Leicester cross) in sexual activity and service capacity in 1.5-yr-old rams, but no differences were observed for older rams.

Winfield et al. (1978) reported that mature Merino rams achieved more services per test and had shorter reaction time to first service than did Romney rams. Boland et al. (1985) found that adult Suffolk rams achieved more mounts in a pen libido test, but had similar number of pasture matings as Texel and Dorset Horn rams. No differences in mating behavior between mature Romney, Border Leicester, Cheviot and Dorset Down rams were found in a study by Winfield and Kilgour (1977).

It appears that there is a considerable difference between breeds in libido that differ in reproductive rate. These differences manifest themselves to a greater degree in growing immature rams than in mature adult rams.

Few studies have been conducted where selection for fecundity and its relationship to libido within a breed have been evaluated. Rambouillet rams from lines selected for high prolificacy achieved more mounts and services and exhibited a shorter reaction time to first mount and(or) service than

rams from lines selected for low prolificacy (Tulley and Burfening, 1983). This is evidence that within line selection of reproductive rate in females can alter certain sexual behaviors in male offspring.

Epididymis and Epididymal Sperm Reserves. The epididymis is a highly convoluted tubular structure, intimately attached to a testicle, which functions in the transportation, maturation and storage of spermatozoa (Garner and Hafez, 1987).

Transportation of sperm through the epididymis is thought to be due to localized contractions of muscular elements in the walls of the duct (Riley, 1963). In rams, it takes approximately 1 to 2, 2 to 3 and 7 to 9 d for sperm to traverse the caput (head), corpus (body) and cauda (tail) of the epididymis, respectively (Robaire and Hermo, 1988).

Sperm maturation in the epididymis includes: 1) development of progressive motility, 2) changes in metabolic activity such as uptake and utilization of oxygen, and 3) acquisition of their fertilizing potential. Approximately 50 to 80% of all sperm cells in the excurrent ducts are stored in the cauda epididymis. Of these, approximately 50% are available for ejaculation (Robaire and Hermo, 1988). The total number of sperm cells found in the epididymis is known as the epididymal sperm reserve or pool (ESR).

Since these are functions that would directly bear upon

the fertility of a male, it would seem likely that selection pressures could change the functions of this structure thereby altering fertility of males. There is little evidence of this occurring in any species. However, Knight (1984) found that selection for fecundity in Romney ewes increased epididymal weight and number of sperm in rams by 11 to 19% and 18 to 60%, respectively, compared to rams from a line of ewes selected against fecundity. He made no attempt to relate these to the fertility of these rams or their offspring.

## Relationships Between Male and Female Reproductive Traits

In sheep and mice, testicular weight or diameter was greater in lines or breeds with the higher ovulation rates, indicating that the quantitative expression of reproductive characteristics in males and females is genetically correlated (Land, 1978). Land and Carr (1975) reported that the testicular diameter of Finnish Landrace, Scottish Blackface and Tasmanian Merinos ram lambs were positively related to ovulation rates of females of these breed types. A similar relationship was found in Finnish Landrace, Border Leiscester and Cheviot breeds (Carr and Land, 1975). In mice, selecting for heavier testicular weight increased ovulation rate in the females (Land, 1978). Direct selection for heavier testicular weight in Merino rams was reported to hasten the onset of the breeding season and increase ovulation rate by 15% in Merino

ewes (Bindon and Piper, 1976). These results indicate a positive relationship between testicular diameter of ram lambs and prolificacy of ewes and testicular diameter may be a suitable selection criterion for increasing prolificacy in sheep.

A similar relationship has been found in beef bulls. Female progeny from bulls with large SC reach puberty at an earlier age. The genetic correlation between SC and age of puberty was reported to be -0.71 (Coulter and Foote, 1979). Blockey (1980) reported that bulls with larger SC achieved higher first service conception rates in heifers than bulls with smaller SC.

Heritability of testicular size was reported to be 0.40 in rams (Kilgour and Blockey, 1980), therefore, it would seem possible that selecting for fecundity in females should increase testicular size and production of sperm in males. Rams from ewes with a high incidence of multiple births for 28 yr had increased testicular diameter, testicular and epididymal weight and number of sperm in the testes compared to rams from ewes with a history of low incidence of multiple births. Rams from ewes selected for prolificacy for 8 yr showed similar trends except for testicular diameter (Knight, 1984). However, in a study with a small number of mature rams, Tulley and Burfening (1983) reported that rams from ewes selected for high prolificacy had smaller SC than did rams from ewes selected for low prolificacy.

However, several studies have indicated a positive correlation between regulation of LH secretion in ram lambs and breed differences in prolificacy of female relatives (Bindon and Turner, 1974; Thimonier and Pelletier, 1972; Carr and Land, 1975).

## Nutritional Factors Affecting Reproductive Performance

Reproduction in mammals is a product of physiological events that occur throughout the year. For optimum reproduction, feed quality and quantity must not be limiting to affect reproductive performance of males and females.

Females. A review by Lindsay (1976) indicated that feeding ewes a submaintenance diet resulted in failure to display estrus. Furthermore, the level of nutrition received in the winter and spring months influenced the number of ewes exhibiting estrus the following autumn. Feeding a high energy diet 6 wk before mating resulted in increased number of twin lambs. Other studies reviewed by Lindsay (1976) indicated that ewes fed a high protein diet had heavier body weights and higher ovulation rates. Lindsay (1976) concluded that: 1) body weight may be the determining factor controlling ovulation rate, 2) supplemental feeding of high protein feeds increases ovulation rates, and 3) when supplement is no longer fed, ovulation rates decrease.

Males. Undernutrition has been reported to affect testicular functions in rams. Parker and Thwaites (1972) reported that semen volume and density, and sperm motility in rams was not reduced by feeding a submaintenance diet during the first 10 wk of an experiment, but values for these variables were reduced during the next 5 wk in rams on the submaintenance diet relative to rams fed the maintenance diet. Lindsay et al. (1984) reported that feeding rams a submaintenance protein level did not influence testicular diameter or volume, but Lindsay et al. (1979) and Martin et al. (1987) found that feeding a high protein supplement for 8 and 15 wk increased testicular volume in mature rams. However, Lindsay et al. (1979) found that the increase in volume had no affect on return rates of ewes bred by rams on both types of diets.

Braden et al. (1974) reported that level of dietary energy greatly affected numbers of sperm in the ejaculate and testicular weight, while level of protein affected only testicular weight. Oldham et al. (1978) found that rams fed lupin (28% protein) had increased testicular weights and sperm production. Salamon (1964) reported that rams fed a high level of supplementary feed had greater semen volume and daily sperm output than rams fed a low level of supplementary feed.

Coulter and Kozub (1984) reported that Hereford bulls fed a high energy diet had 75% fewer epididymal sperm reserves then Hereford bulls fed a medium diet. Angus bulls did not

show such marked differences in epididymal sperm reserves when fed these same two diets. These same authors in another trial, reported that Hereford bulls fed a high energy diet had 35% fewer epididymal sperm reserves than Hereford bulls fed a medium diet. Angus bulls fed a high energy diet had 14% fewer epididymal sperm reserves than Angus bulls fed a medium diet.

The physiological mechanisms through which nutrition affects testicular functions, is not understood. Rams fed a high protein diet had greater number of LH pulses when measured monthly than rams fed a low protein diet (Lindsay et al., 1984). However, Martin et al. (1987) reported that diet had no effect on either LH or T secretion in rams.

Mattner and Braden (1975) reported that rams fed a high protein diet for 5.5 wk did not exhibit increased libido over rams fed a low protein diet. Also, they reported that undernourished rams had similar libido scores compared to control rams for the first 4 wk of the experiment, but for wk 5 to 8, libido scores were lower in undernourished rams. Similarly, Parker and Thwaites (1972) showed no effects of undernourishment on libido during the first 8 wk of an experiment, but during the second 8 wk, rams fed 50 and 75% of maintenance diet exhibited depressed libido compared to rams fed 100% maintenance diet.

Filpse and Almquist (1961) reported that bulls fed a high energy ration from birth to 4 yr of age became slower in

sexual reactions. Wierzbowski (1978) compared bulls at 5 yr of age which weighed 235 kg less than brothers. Bulls of lighter weight showed enhanced reaction time to first mount, time between copulations, total semen collection time, total mounts per copulation and total sexual efficiency. These data indicate that accelerated growth rate induced by overfeeding may be detrimental to appropriate development of libido and sexual ability.

There have been no reports on the influence of any carry-over effects of changing nutritional regimens after weaning and before the breeding season in rams. This would seem an appropriate research endeavor, since alternations in environment during puberty could impact reproductive activity of mature males.

## STATEMENT OF THE PROBLEM

Fertility (number of females conceiving) and fecundity (number of offspring per pregnancy) are female components of reproductive rate. The repeatability and heritability of these components are small, but in experiments where continual direct selection was applied on either of these components, small genetic gains (lambs per year per ewe) have been achieved.

Fertility in the male is defined as the ability to produce offspring by exhibiting the necessary sexual drive (libido) to fertilize females with sufficient quantity and quality of sperm. Selecting males on the basis of large scrotal circumference, has increased overall testicular size in some species, which indirectly has increased sperm production and quantity.

Testicular characteristics and hormone concentrations in several species, such as the ram, have been reported to be genetically correlated with ovulation rate, onset of puberty and prolificacy of the breed, indicating selection for a female reproductive characteristic can alter a male reproductive characteristic and vice versa. Selection experiments for increased fertility within a breed have shown increased libido and larger testicular characteristics when compared to males selected against fertility.

Environmental factors such as nutrition can also affect reproductive rate in several species, especially in young growing individuals. Undernourished females are less likely to exhibit estrus, conceive and give multiple births than those females given proper nutrition. Undernourished males have exhibited smaller scrotal circumference, less numbers of sperm and lower libido and service capacity scores than males fed a proper ration.

The purpose of this study was to determine: 1) if selection applied to a female reproductive trait influences testicular, epididymal and libido characteristics in the male offspring, and 2) to evaluate the effect of a high protein diet, during the growth phase, on the aforementioned characteristics in rams from lines selected for high and low reproductive rate .

# MATERIALS AND METHODS

This study was conducted at the Montana State University, Fort Ellis Sheep Experiment Station, Bozeman. Rambouillet rams were from lines selected for high (H) and low (L) reproductive rate, and a randomly bred control line (C). High and L reproductive rate lines were derived via a selection index based on the lambing records of ewes using the following equation:

$$\text{Index} = \frac{\text{number of lambs born in lifetime}}{\text{age of ewe in years} - 1}$$

Only rams from ewes with the highest and lowest indexes from each selection line were used in this study. A complete description of the establishment, breeding management and response to selection for reproductive rate of these lines was given by Burfening and Hanford (1986).

Two trials were conducted, one in 1982 (T1) and another in 1984 (T2) utilizing rams born in April of 1981 and 1983 for T1 and T2, respectively. In both trials rams were fed a pelleted diet of 80% alfalfa and 20% barley ad libitum from weaning (August) until 10 mo of age (180 d; February the next year). Within each trial, rams from H, L and C lines were assigned randomly to one of two feeding regimens beginning in February: 1) placed on pasture and fed grass-hay for 7 mo (normal plane; NP) or 2) continued on the pelleted diet for 7 mo (high plane; HP), which is similar to how rams are fed

when being prepared for fall ram sales.

After the 7-mo feeding period, HP rams were combined with NP rams and placed on pasture and fed grass-hay for the remainder of the experiment. The design of the experiment and number of rams in each treatment are summarized in Table 1.

TABLE 1. Number of rams in each treatment group

| Trial | Feeding Regimen | Lines | | | Total |
|---|---|---|---|---|---|
| | | L | H | C | |
| 1 | NP | 4 | 5 | 4 | 13 |
| | HP | 4 | 6 | 2 | 12 |
| 2 | NP | 5 | 5 | 5 | 15 |
| | HP | 4 | 2 | 4 | 10 |
| Total | | 17 | 18 | 15 | 50 |

Body weights (BW) of rams were taken at: weaning (4 mo of age; BW1), initiation of feeding regimen (10 mo of age; BW2), termination of feeding regimen (17 mo of age; BW3) and in December (20 mo of age; BW4) just before commencement of libido tests.

Standardized libido tests (Tulley and Burfening, 1983) were conducted on each ram 1 wk before and 1 and 2 wk after orchidectomy (L1, L2 and L3, respectively). Each ram was placed into a 4.9 by 6.1 m pen with three immobilized non-estrous ewes for 15 min. Ewes were tethered and constrained laterally to prevent them from moving sideways. Number of

mounts (M), services (S) and reaction time to first mount (RTM) and first service (RTS) for each ram were recorded for each libido test. A mount was recorded when the rams' front feet left the ground and straddled the rear quarters of a ewe without intromission and ejaculation. A service was recorded if mounting was followed by exhibition of: 1) intromission, 2) a distinct pelvic thrust with head thrown back, 3) ejaculation, 4) dismounting and 5) lack of interest in the ewe. If no mount or service occurred for any ram during a test, then a time of 15 min was assigned for the purpose of statistical analyses of RTM and RTS. Two observers recorded behavioral data for rams in two different pens simultaneously.

In December of both trials, each ram was placed into a holding crate, sedated with thiamylyl sodium (4% solution in 0.9% sterile saline) and scrotal wool was removed by electric clippers. Both testes were pulled down firmly into the scrotum and scrotal circumference (SC) was measured to the nearest .5 cm using a steel scrotal tape at the point of greatest circumference.

After measuring SC, each ram was orchidectomized bilaterally via 8 cm incision along the anterio-medial plane of each scrotal lobe. Each testis was removed from the tunica coverings and scrotum after double ligature of the spermatic cord approximately 5 cm from the inguinal canal. Incisions were closed with medical grade non-absorbable suture and the ram allowed to recover.

The epididymis from each testis was dissected from the testis, cleared of extraneous connective tissue, weighed and frozen for later assay of epididymal sperm reserve (ESR). Each testis was weighed and volume determined by hydrometrical methods.

Processing and counting epididymal sperm reserves was based upon the procedure of Swierstra (1970). Epididymides were thawed at room temperature, then bisected at the first enlargement between the corpus and cauda. This procedure yielded two portions: 1) caput and corpus and 2) cauda. Each portion was weighed and then macerated with scissors and forceps in a petri dish containing a solution composed of 0.05% Triton X-100 in 0.85% NaCl (counting solution). Minced tissue was transferred into a Waring blender: scissors, forceps and petri dish were rinsed with counting solution and poured into a blender vessel. Tissue was homogenized at high speed for 1 min and decanted into a 1 L beaker. The blender vessel was rinsed thoroughly with counting solution and the rinse transferred to the 1 L beaker. A total of 500 ml of counting solution was used during this procedure for each portion of the epididymis.

A 10 ml sample was withdrawn from the homogenate after mixing on a magnetic stir plate for 2 min. A preliminary sperm cell count of the sample was obtained with an improved Neubauer-Ultraplane hemocytometer using the following procedure. A small drop of homogenate was placed onto the

central square (1 mm X 1 mm) of one of two chambers on the hemocytometer, a slide cover was placed over the chambers and the number of sperm cells were counted in approximately three of the 25 "smaller squares" of the central square. If the mean number of sperm cells per small square was greater than 25, then the 10 ml sample was diluted with counting solution to achieve approximately 20 sperm cells per smaller square.

Actual sperm cell counts were obtained by counting all sperm cells that were within and any sperm head that touched the top and right side-lines in the nine smaller squares that fall along both diagonals. Samples from each homogenate were placed onto both chambers of three different hemocytometers. Mean number of sperm per sample was obtained by summing counts from each chamber and dividing by six. Sperm reserve in each portion of the epididymis was calculated by the following equation:

Mean no. sperm per sample X 25/9 X 10 X 1000 X dilution rate

= sperm reserves in portion of epididymis

where: 25/9 = correction for all 25 squares,

10 = corrects volume to 1 mm3,

1000 = corrects volume to 1 ml,

dilution rate = correction for counting volume.

## Statistical Analyses

Data were analyzed by an analysis of variance for a 2 X 3 X 2 factorial arrangement of treatments in a completely random design using the General Linear Model procedure of SAS (SAS, 1987). In a preliminary analysis, side was used as an independent variable for testicular and epididymal characteristics, except for scrotal circumference. Side was found not to be significant source of variability and therefore testicular and epididymal data from left and right sides were pooled for further analyses.

Body weight (BW), scrotal circumference (SC), paired testicular weight (PTW) and volume (PTV), paired epididymal weight (PEW), paired caput and corpus, and cauda epididymal weights (PEHW and PETW, respectively), paired caput and corpus, and cauda epididymal sperm reserve (PHESR and PTESR, respectively), paired epididymal sperm reserve per gram of epididymal tissue (PESRGEW), paired epididymal sperm reserve per gram of testicular tissue (PESRGTW), number of mounts (M) and services (S), and reaction time to first mount and service (RTM and RTS, respectively) were dependent variables. Independent variables (factors) were trial (T1 and T2), line (H, L and C) and feeding regimen (NP and HP) and two- and three-way interactions. The error term used to test the effects of trial, line and feeding regimen on body weights and libido characteristics was animal within trial by line by

feeding regimen. Body weight (BW4) was used as a covariate in analyses of paired testicular and epididymal characteristics. Means were compared using Duncan's Range Test in SAS (SAS, 1987).

Correlation coefficients were derived for testicular and epididymal characteristics within line and over all treatments by using the Correlation procedure (SAS, 1987).

Proportions of rams that mounted and serviced ewes in the three libido test were analyzed by the CATMOD procedure of (SAS, 1987).

# RESULTS

## Body Weight

Rams did not differ (P>.05) in bodyweight at weaning time (BW1; Tables 2 and 3). There was a trial by weigh period interaction (P<.05) for body weight (Table 2). Rams in T1 gained more weight between BW1 and BW2 than rams in T2, however, rams in T2 gained more weight between BW2 and BW3 than rams in T1. Rams in T1 lost more weight between BW3 and BW4 than rams in T2. Body weights of rams were not affected (P>.05) by line or the interactions of line with other independent variables.

TABLE 2. Least squares means for body weights (BW;kg) of rams during Trials 1 (T1) and 2 (T2) for the four weigh periods[a]

| | Weigh Period | | | |
|---|---|---|---|---|
| Trial | BW1 | BW2 | BW3 | BW4 |
| T1 | 28.5[b] | 80.3[c] | 91.4[d] | 83.6[e] |
| T2 | 28.7[b] | 67.3[f] | 85.2[e] | 78.6[c] |

[a] Least squares standard deviation = 3.76; df = 180.
[b,c,d,e,f] Means with different superscripts within a column or row differ at P<.05.

In addition, there was a feeding regimen by weigh period interaction (P<.05) for body weights at BW3 and BW4 (Table 3).

Rams on the HP regimen gained weight more rapidly between BW2 and BW3 compared to rams fed the NP regimen. Rams on the HP regimen lost more weight than NP rams between BW3 and BW4 (Table 3), but the former rams were still heavier than the latter rams at BW4.

TABLE 3. Least squares means for body weights (BW;Kg) of rams fed the normal (NP) or high (HP) feeding regimen for the four weigh periods[a]

| Feeding Regimen | Weigh Period | | | |
|---|---|---|---|---|
| | BW1 | BW2 | BW3 | BW4 |
| NP | 28.2[b] | 73.5[c] | 78.2[c] | 76.5[c] |
| HP | 29.0[b] | 74.0[c] | 98.4[d] | 85.7[e] |

[a]Least squares standard deviation = 3.76; df = 180.
[b,c,d,e]Means with different superscripts within a column or row differ P<.05.

## Testicular Characteristics

Trial, line and feeding regimen or their interactions did not affect (P>.05) scrotal circumference (SC), paired testicular weight (PTW), paired testicular volume (PTV), paired epididymal cauda weight (PETW) and paired epididymal weight (PEW; Table 4). Paired epididymal caput and corpus weight (PEHW) did not differ (P>.05) between trials, lines or feeding regimens (Table 4). There was a line by feeding

TABLE 4. Least squares means for testicular and epididymal characteristics as affected by trial (1 and 2), line (L, H and C) and feeding regimen (NP and HP)

| | SC[ab] | PTW[c] | PTV[d] | PEHW[c] | PETW[c] | PEW[c] |
|---|---|---|---|---|---|---|
| Trial | | | | | | |
| 1 | 28.5 | 243.8 | 253.0 | 29.7 | 24.2 | 59.1 |
| 2 | 29.0 | 265.3 | 255.1 | 31.7 | 25.9 | 61.1 |
| Line | | | | | | |
| L | 27.8 | 239.3 | 238.3 | 29.9 | 25.7 | 60.4 |
| H | 29.4 | 264.4 | 261.0 | 32.0 | 25.6 | 61.5 |
| C | 29.1 | 259.1 | 262.9 | 30.2 | 23.8 | 58.4 |
| Feeding Regimen | | | | | | |
| NP | 28.2 | 246.9 | 253.2 | 29.8 | 24.5 | 58.6 |
| HP | 29.4 | 261.5 | 254.9 | 31.6 | 25.6 | 61.6 |
| Mean | 28.6 | 250.4 | 251.0 | 30.5 | 25.0 | 59.8 |
| SD | 2.8 | 77.3 | 73.9 | 5.9 | 6.0 | 12.3 |

[a,b] centimeters; (SC) scrotal circumference, (PTW) paired testicular weight, (PTV) paired testicular volume, (PEHW) paired epididymal caput/corpus weight, (PETW) paired epididymal cauda weight and (PEW) paired epididymal weight.
[c] grams.
[d] cubic centimeters.

TABLE 5. Least squares means for paired epididymal head (caput/corpus) weight (g) as affected by line (L, H and C) and feeding regimen (NP: normal plane, HP: high plane)

| Feeding Regimen | Line | | |
|---|---|---|---|
| | L | H | C |
| NP | 25.9[a] | 31.2[b] | 32.4[b] |
| HP | 34.0[b] | 32.8[b] | 28.1[a] |
| SE = 5.9 | | | |

[a,b,c] Means with different superscripts within a column or row differ at P<.05.

regimen interaction for PEHW (P<.05; Table 5). Low line rams had lighter PEHW than H and C line rams on the NP feeding regimen, whereas, C line rams had lighter PEHW than H and L line rams on the HP feeding regimen.

Paired caput and corpus epididymal sperm reserve (PHESR), paired cauda epididymal sperm reserve (PTESR), total epididymal sperm reserve (TESR), epididymal sperm reserve per gram of epididymal tissue (ESRGEW) and epididymal sperm reserve per gram of testicular tissue (ESRGTW) were not influenced by trial, line, feeding regimen or their interactions (P>.05; Table 6).

Correlation coefficients were used to evaluate the relationships among SC, PTW, PTV, PEW, PEHW, PETW, PHESR and PTESR for all rams. High positive correlations were obtained

TABLE 6. Least squares means for epididymal sperm reserve and its components[ab]

| | PHESR | PTESR | TESR | ESRGEW | ESRGTW |
|---|---|---|---|---|---|
| Trial | | | | | |
| 1 | 13.3 | 47.7 | 61.0 | 1.02 | 0.26 |
| 2 | 12.4 | 44.3 | 56.8 | 0.90 | 0.22 |
| Line | | | | | |
| L | 12.0 | 52.6 | 64.7 | 1.03 | 0.27 |
| H | 14.1 | 44.0 | 58.1 | 0.95 | 0.23 |
| C | 12.6 | 41.3 | 53.8 | 0.91 | 0.22 |
| Feeding regimen | | | | | |
| NP | 13.3 | 47.6 | 60.9 | 1.04 | 0.26 |
| HP | 12.5 | 44.3 | 56.8 | 0.89 | 0.21 |
| Mean | 12.7 | 45.4 | 58.1 | 0.96 | 0.24 |
| SD | 7.5 | 22.8 | 28.8 | 0.41 | 0.22 |

[a] $10^9$ sperm

[b] (PHESR) paired epididymal caput/corpus sperm reserve, (PTESR) paired epididymal cauda sperm reserve, (TESR) total epididymal sperm reserve, (ESRGEW) epididymal sperm reserve per gram epididymal weight, (ESRGTW) epididymal sperm reserve per gram testicular weight.

for testicular and epididymal measurements, with moderate correlations for PHESR and PTESR ($P<.05$; Table 7).

Within selection line correlation coefficients were also obtained for SC, PTW, PTV, PEW, PEHW, PETW, PHESR and PTESR. Low line rams had high positive correlations (0.56 to 0.98; $P<.05$) among these characteristics (Table 8). Whereas, in H line rams, moderate to high correlations (0.52 to 0.89; $P<.05$) were found between SC, PTW, PTV, PEW, PEHW and PETW (Table 9), while SC was not correlated ($P>.05$) with PHESR or PTESR. Furthermore, there was no correlation ($P>.05$) between PTESR and PTW, PTV, PEW, PEHW, PETW and PHESR. In C line rams, SC was moderately correlated (0.56 to 0.78; $P<.05$) with all other characteristics (Table 10). Paired testicular weight was correlated (0.85; $P<.05$) with PTV, but not correlated ($P>.05$) with any other epididymal characteristic. Paired testicular volume was correlated (0.61; $P<.05$) with PTESR, but not correlated with any other epididymal characteristic. Paired epididymal weight was correlated ($P<.05$) with PEHW (0.95) and PETW (0.86), but not correlated ($P>.05$) with PHESR and PTESR. Paired epididymal caput and corpus weight was correlated (0.74; $P<.05$) with PETW, but not with PHESR and PTESR. Paired epididymal caput and corpus epididymal sperm reserve was correlated (0.81; $P<.05$) with PTESR.

TABLE 7. Correlation coefficients for all rams for relationships in testicular and epididymal characteristics[ab]

| | SC | PTW | PTV | PEW | PEHW | PETW | PHESR | PTESR |
|---|---|---|---|---|---|---|---|---|
| SC | | .70 | .80 | .74 | .72 | .67 | .54 | .40 |
| PTW | | | .82 | .63 | .66 | .49 | .62 | .34 |
| PTV | | | | .69 | .66 | .59 | .62 | .47 |
| PEW | | | | | .93 | .93 | .66 | .49 |
| PEHW | | | | | | .81 | .63 | .40 |
| PETW | | | | | | | .58 | .47 |
| PHESR | | | | | | | | .63 |

[a] (SC) scrotal circumference, (PTW) paired testicular weight, (PTV) paired testicular volume, (PEW) paired epididymal weight, (PEHW) paired epididymal caput weight, (PETW) paired epididymal cauda weight, (PHESR) paired epididymal caput/corpus sperm reserve, (PTESR) paired epididymal cauda sperm reserve.

[b] $P<.05$.

TABLE 8. Correlation coefficients for relationships in testicular and epididymal characteristics in low line rams[ab]

| | SC | PTW | PTV | PEW | PEHW | PETW | PHESR | PTESR |
|---|---|---|---|---|---|---|---|---|
| SC | | .86 | .80 | .90 | .95 | .88 | .78 | .68 |
| PTW | | | .90 | .84 | .84 | .77 | .86 | .61 |
| PTV | | | | .80 | .79 | .73 | .85 | .57 |
| PEW | | | | | .98 | .96 | .84 | .61 |
| PEHW | | | | | | .94 | .81 | .60 |
| PETW | | | | | | | .78 | .56 |
| PHESR | | | | | | | | .75 |

[a] (SC) scrotal circumference, (PTW) paired testicular weight, (PTV) paired testicular volume, (PEW) paired epididymal weight, (PEHW) paired epididymal caput weight, (PETW) paired epididymal cauda weight, (PHESR) paired epididymal caput/corpus sperm reserve, (PTESR) paired epididymal cauda sperm reserve.

[b] $P<.05$.

TABLE 9. Correlation coefficients for relationships in testicular and epididymal characteristics in high line rams[a]

| | SC | PTW | PTV | PEW | PEHW | PETW | PHESR | PTESR |
|---|---|---|---|---|---|---|---|---|
| SC | | .61[b] | .82[b] | .66[b] | .53[b] | .61[b] | .25[c] | .04[c] |
| PTW | | | .72[b] | .65[b] | .68[b] | .53[b] | .58[b] | .14[c] |
| PTV | | | | .78[b] | .68[b] | .70[b] | .53[b] | .36[c] |
| PEW | | | | | .89[b] | .95[b] | .59[b] | .41[c] |
| PEHW | | | | | | .78[b] | .52[b] | .23[c] |
| PETW | | | | | | | .56[b] | .47[c] |
| PHESR | | | | | | | | .59[c] |

[a] (SC) scrotal circumference, (PTW) paired testicular weight, (PTV) paired testicular volume, (PEW) paired epididymal weight, (PEHW) paired epididymal caput weight, (PETW) paired epididymal cauda weight, (PHESR) paired epididymal caput/corpus sperm reserve, (PTESR) paired epididymal cauda sperm reserve.

[b] $P<.05$.

[c] $P>.05$.

TABLE 10. Correlation coefficients for relationships in testicular and epididymal characteristics in control line rams[a]

| | SC | PTW | PTV | PEW | PEHW | PETW | PHESR | PTESR |
|---|---|---|---|---|---|---|---|---|
| SC | | .62[b] | .78[b] | .63[b] | .56[b] | .60[b] | .65[b] | .64[b] |
| PTW | | | .85[b] | .37[c] | .40[c] | .16[c] | .43[c] | .37[c] |
| PTV | | | | .49[c] | .46[c] | .37[c] | .50[c] | .61[b] |
| PEW | | | | | .95[b] | .86[b] | .47[c] | .46[c] |
| PEHW | | | | | | .74[b] | .44[c] | .40[c] |
| PETW | | | | | | | .32[c] | .34[c] |
| PHESR | | | | | | | | .81[b] |

[a] (SC) scrotal circumference, (PTW) paired testicular weight, (PTV) paired testicular volume, (PEW) paired epididymal weight, (PEHW) paired epididymal caput weight, (PETW) paired epididymal cauda weight, (PHESR) paired epididymal caput/corpus sperm reserve, (PTESR) paired epididymal cauda sperm reserve.
[b] $P<.05$.
[c] $P>.05$.

## Libido Characteristics

Rams in T1 had greater ($P<.05$) numbers of mounts (M) in L1 and L2 than rams in T2 (Table 11). There was a trial by line interaction in L3, with C rams in T1 having 14.6 M, whereas in T2, they had 0.3 M (Table 12). There was also a trial by line by feeding regimen interaction ($P<.05$) for M in L3 (Table 13). This was caused by C rams fed the HP regimen in T1 displaying 20.5 M, while in T2, these same rams had 0.5 M. In L2, H line rams had more ($P<.05$) M than L line rams and C line rams were intermediate, but there was no differences ($P>.05$; Table 11) among the lines in L1 and L3. Feeding regimen had no affect ($P>.05$) on M in any of libido test.

Rams in T1 had greater ($P<.05$) numbers of services (S) for each of the three libido tests compared to rams in T2 (Table 11). Line, feeding regimen, or the interactions among the main effects did not affect ($P>.05$) numbers of S in any libido test.

Rams in T1 had shorter ($P<.05$) RTM in L1 and L3 than rams in T2 (Table 14). There were no affect of line, feeding regimen or their interactions on RTM for L1 and L3. However, there was a trial by line interaction ($P<.05$) for RTM in L2 (Table 15). During L2 rams fed the HP regimen had shorter ($P<.05$) RTM compared to rams fed the NP regimen.

TABLE 11. Least squares means for numbers of mounts (M) and services (S) in rams as affected by trial (T1 and T2), line (L, H and C) and feeding regimen (NP and HP) during three libido tests (L1, L2 and L3)

| | Libido test | | | | | |
|---|---|---|---|---|---|---|
| | M | | | S | | |
| Effect | L1 | L2 | L3 | L1 | L2 | L3 |
| T[a] | | | | | | |
| 1 | 9.9 | 8.0 | 7.8 | 1.8 | 1.2 | 0.8 |
| 2 | 1.6 | 3.1 | 1.8 | 0.4 | 0.4 | 0.2 |
| LN | | | | | | |
| L | 4.9 | 2.6[b] | 4.3 | 0.8 | 0.5 | 0.4 |
| H | 5.6 | 7.3[c] | 2.6 | 1.4 | 0.9 | 0.6 |
| C | 6.7 | 6.8[c] | 7.4 | 1.0 | 0.9 | 0.4 |
| FR | | | | | | |
| NP | 5.3 | 4.1 | 3.5 | 1.1 | 0.7 | 0.4 |
| HP | 6.2 | 7.1 | 6.1 | 1.1 | 0.9 | 0.5 |
| Mean | 5.4 | 4.9 | 4.0 | 1.0 | 0.7 | 0.4 |
| SD | 4.8 | 5.1 | 4.9 | 0.9 | 0.9 | 0.7 |

[a] Means between trials did differ $P<.05$.
[b,c] Means in same column with different superscripts are different ($P<.05$) within line and feeding regimen.

TABLE 12. Least squares means for number of mounts during libido test three for trials 1 (T1) and 2 (T2) for low, high and control lines (L, H and C, respectively)[a]

| | Line | | |
|---|---|---|---|
| Trial | L | H | C |
| 1 | 4.6 | 4.25 | 14.6 |
| 2 | 4.0 | 1.00 | 0.3 |

SD = 4.9

[a] Trial by line interaction ($P<.05$).

TABLE 13. Least squares means for number of mounts during libido test three for trials 1 (T1) and 2 (T2) for each low, high and control lines (L, H and C, respectively) as affected by feeding regimen (NP: normal plane, HP: high plane)[a]

| | | Line | | |
|---|---|---|---|---|
| Trial | Feeding Regimen | L | H | C |
| 1 | NP | 6.3 | 5.0 | 8.8 |
| | HP | 3.0 | 3.5 | 20.5 |
| 2 | NP | 0.0 | 1.0 | 0.0 |
| | HP | 8.0 | 1.0 | 0.5 |

SD = 4.9

a Trial by line by feeding regimen interaction ($P<.05$).

TABLE 14. Least squares means for reaction time to first mount (RTM) and service (RTS) in rams as affected by trial (T1 and T2), line (L, H and C) and feeding regimen (NP and HP) during three libido tests (L1, L2 and L3)

| | Libido test | | | | | |
|---|---|---|---|---|---|---|
| | RTM | | | RTS | | |
| Effect | L1 | L2 | L3 | L1 | L2 | L3 |
| T[a] | | | | | | |
| 1 | 3.6 | 4.2 | 4.6 | 6.7 | 7.5 | 8.6 |
| 2 | 9.8 | 10.8 | 12.1 | 12.0 | 12.9 | 13.5 |
| LN | | | | | | |
| L | 8.5 | 10.8[b] | 10.4 | 10.7 | 11.3 | 12.6 |
| H | 5.5 | 4.9[c] | 7.4 | 7.4 | 9.7 | 10.1 |
| C | 6.5 | 6.9[c] | 7.2 | 9.9 | 9.6 | 10.4 |
| FR | | | | | | |
| NP | 7.2 | 9.3[b] | 8.9 | 9.7 | 11.3 | 11.6 |
| HP | 6.1 | 5.7[c] | 7.7 | 9.0 | 9.1 | 10.5 |
| Mean | 7.0 | 8.3 | 8.9 | 9.6 | 10.5 | 11.4 |
| SD | 5.4 | 4.9 | 5.4 | 4.2 | 5.5 | 4.7 |

[a] Means between trials did differ $P<.05$.
[b,c] Means in same column with different superscripts are different ($P<.05$) within line and feeding regimen.

TABLE 15. Least squares means for reaction time to first mount during libido test two for trials 1 (T1) and 2 (T2) for each low, high and control lines (L, H and C, respectively)[a].

| | Line | | |
|---|---|---|---|
| Trial | L | H | C |
| 1 | 9.7 | 2.5 | 0.5 |
| 2 | 11.9 | 7.3 | 13.2 |
| SD = 4.9 | | | |

[a]Trial x line interaction (P<.05).

Reaction time to first service (RTS) in each libido test was shorter (P<.05) for rams in T1 than for rams T2. Line, feeding regimen or their interactions, or their interactions with trial did not affect (P>.05) RTS in any of the libido tests.

Percentages of rams that mounted ewes decreased (P<.05) from 65% in L1 55% in L2 and decreased (P<.05) to 48% for rams in L3. Further analyses of percentages of rams that mounted ewes indicated a trial by line by feeding regimen interaction (P<.05). This was due to: 1) greater percentages of rams in T1 compared to T2 exhibiting mounts in all three libido tests, 2) greater percentages of H and C line rams in T1 exhibiting mounts stayed at the same level overall tests compared to low declining percentages of rams in these lines that mounted in T2, 3) a greater percentage of H line rams

TABLE 16. Percentages of rams exhibiting mounts during the libido tests (L1, L2 and L3) as affected by trial (T1 and T2), line (L, H and C) and feeding regimen (NP and HP)

| T | Line | Feeding Regimen | L1 | L2 | L3 |
|---|---|---|---|---|---|
| 1 | L | NP(4)[a] | 100 | 50 | 50 |
| | | HP(4) | 75 | 50 | 50 |
| | | Total(8) | 88 | 50 | 50 |
| | H | NP(5) | 100 | 100 | 100 |
| | | HP(4) | 100 | 100 | 75 |
| | | Total(9) | 100 | 100 | 89 |
| | C | NP(4) | 100 | 100 | 100 |
| | | HP(2) | 100 | 100 | 100 |
| | | Total(6) | 100 | 100 | 100 |
| | | Total(23) | 96 | 83 | 78 |
| 2 | L | NP(5) | 40 | 20 | 0 |
| | | HP(4) | 75 | 75 | 22 |
| | | Total(9) | 56 | 44 | 22 |
| | H | NP(5) | 60 | 20 | 20 |
| | | HP(2) | 50 | 100 | 50 |
| | | Total(7) | 58 | 43 | 29 |
| | C | NP(5) | 40 | 0 | 0 |
| | | HP(4) | 25 | 25 | 25 |
| | | Total(9) | 33 | 11 | 11 |
| | | Total(25) | 48 | 32 | 20 |

[a] Number of rams in each group.

exhibited mounts in T1 compared to L line rams in T1, and, 4) percentages of H and L line rams that mounted in T2 did not differ over the three libido tests.

Percentage of rams that serviced ewes was greater ($P<.05$) in L1 (60%) than in L2 and L3 (39% and 31%, respectively; Table 17). Percentages of rams in T1 that exhibited a S were 91, 61 and 61% for L1, L2 and L3, respectively, while in T2, percentages were 32, 24 and 8% for L1, L2 and L3, respectively. There was a trial by line interaction ($P<.05$) for percentages of rams that serviced ewes caused by a greater percentage of C line rams in T1 exhibiting a S compared to C line rams in T2 (100, 67 and 100% in T1 vs 11, 11 and 0 in T2 for L1, L2 and L3, respectively). Furthermore, greater percentages ($P<.05$) of H line rams in T1 at each libido test (100, 67 and 56%) exhibited more services than H line rams in T2 (57, 29 and 29%) for each test, however, percentages of L line rams that serviced ewes at each test did not differ ($P>.05$) between trials in L line rams.

TABLE 17. Percentages of rams exhibiting services during the libido tests (L1, L2 and L3) as by affected trial (T1 and T2), line (L, H and C) and feeding regimen (NP and HP)

| T | Line | Feeding Regimen | L1 | L2 | L3 |
|---|---|---|---|---|---|
| 1 | L | NP(4)[a] | 75 | 50 | 25 |
| | | HP(4) | 75 | 50 | 50 |
| | | Total(8) | 75 | 50 | 38 |
| | H | NP(5) | 100 | 60 | 40 |
| | | HP(4) | 100 | 75 | 75 |
| | | Total(9) | 100 | 67 | 56 |
| | C | NP(4) | 100 | 50 | 100 |
| | | HP(2) | 100 | 100 | 100 |
| | | Total(6) | 100 | 67 | 100 |
| | | Total(23) | 91 | 61 | 61 |
| 2 | L | NP(5) | 20 | 20 | 0 |
| | | HP(4) | 50 | 50 | 0 |
| | | Total(9) | 33 | 33 | 0 |
| | H | NP(5) | 60 | 20 | 20 |
| | | HP(2) | 50 | 50 | 50 |
| | | Total(7) | 57 | 29 | 29 |
| | C | NP(5) | 0 | 0 | 0 |
| | | HP(4) | 25 | 25 | 0 |
| | | Total(9) | 11 | 11 | 0 |
| | | Total(25) | 32 | 24 | 8 |

[a] Number of rams in each group.

# DISCUSSION

Feeding rams a pelleted diet, high in both energy and protein, for 180 d increased growth rate of rams in both trials of this study. This result is consistent with reports in the literature indicating that higher planes of nutrition increase growth rates of rams after weaning and during the growth phase of development (Parker and Thwaites, 1972; Lindsay et al., 1984; Martin et al., 1987). However, the pattern of growth differed between trails (years): growth rate increased more rapidly in rams in T1 initially, while growth rate of rams in T2 increased more rapidly later during the 180 d period from February to August. Furthermore, rams in T1 lost more weight after this period than rams in T2.

The cause of this interaction is not clear considering the facts that rams of both years were born during the same month, weaned at the same time, handled and managed in the same manner, fed the same diet before the 180 d period, and had similar weights at the beginning period. There is the possibility that this interaction was caused by weather and its influence on forage. In T1 (1982), temperatures were warmer during February and March than in 1984 and there was much less snow cover. This type of condition is thought to promote rapid development of the vegetative range community and stimulate plant growth. Spring vegetation is rich in nutrients that can be utilized by ruminants (J. Lacey,

personal communication). Thus, rams in T1 could have had access to a higher quality forage than rams in T2 thereby accounting for the more rapid growth in T1.

Conversely, the rapid loss of weight found for rams in T1 between August and December relative to rams in T2 could have been associated with forage availability and(or) quality of forage in their diet, i. e., a hot dry summer.

Changes in body weights of rams were not affected by line or interactions of line with other effects. It is well known that breeds differ in their growth rates and growth rate changes induced by nutritional alterations (Lindsay, 1976). However, there is little evidence in the literature that selection for reproductive rate within a breed alters patterns of growth or interacts with plane of nutrition. Knight (1984) did not detect a difference in growth rate of Romney rams from weaning to 77 wk of age in lines selected for and against prolificacy for 28 yr. Burfening et al, (1989) reported no differences in body weight in ewes between lines selected for low and high prolificacy.

The main effects of trial, line and feeding regimen did not affect SC, PTW, PTV, PETW, PEW, PHESR, PTESR, TESR, ESRGTW or ESRGTW when measured four months after termination of feeding regimen. We did not expect a trail effect because we attempted to have the same protocol for managing sheep and conducting the experiment. The most important question of our study was, is there a difference among rams from lines

selected for reproductive rate? Various testicular characteristics have been reported to vary between breed (Braun et., 1980; Notter et al., 1985). Additionally, there is evidence that selection for or against prolificacy induces changes in testicular traits. Knight (1984) reported that SC, testicular weight, epididymal weight, and numbers of testicular and epididymal sperm were higher for adult Romney rams from line selected for high prolificacy compare to those from rams of the low prolific selection line. Also, Tulley and Burfening (1983) found that SC was larger in H line rams compared to low line rams from the lines employed in the present study. The reason for our inability to confirm these results is not known.

The TESR values obtained in this study are similar to values obtained by Knight (1977) in Romney rams, but higher 58 vs 44 (x $10^9$) than values obtained by the same author in Merino rams. However, Knight (1984) reported TESR values of 88 to 102 (x $10^9$) in Romney rams.

There was a line by feeding regimen interaction for PEHW caused by a change in rank between low line rams (lightest PEHW) on the NP and C line rams on the HP (lightest PEHW). One could interpret this result to mean that selection has influenced the manner in which this epididymal trait responds to changes in nutrition during the growth phase. If nutrients are limiting then low line rams will be impacted to a greater degree than the other lines. Whereas, if nutrients are in

oversupply then non-selected rams are affected more. The physiological consequences of reduced PEHW are not apparent, especially in light of the fact that this interaction was not found for PHESR. There are no reports in the literature concerning this trait and the significance of this finding is not clear.

Within line correlation coefficients among testicular and epididymal traits are quite interesting. Low line rams had high positive correlations among all traits; this is consistent with correlations reported in the literature for some of these traits (Knight, 1977; Knight, 1984), however, there has been no report in the literature where this large a group of traits have been evaluated. Control line rams had moderate to high correlations for most traits but some correlations were low, i. e., PEW was not correlated with PHESR. Furthermore, and most surprisingly, was the finding that PTESR was not correlated with any other trait, not even SC!

This finding is unusual since the literature indicates that the number of sperm in the epididymis is highly and positively correlated with SC in sheep (Knight, 1977) and bovine (Coulter and Foote, 1978). Furthermore, SC is also related to fertility in these species (Knight, 1984; Coulter and Foote, 1978).

Rams in T1 exhibited substantially more M and S and shorter RTM and RTS than rams in T2 and the proportion of rams

exhibiting libido was 2 to 3 times greater in T1 than T2.

Mounts and S did not differ between the three lines ($P>.05$) during L1 and L3. However in L2, H line rams had greater numbers ($P<.05$) of M than L line rams. This was caused by 6 rams having more than 10 M during this test period. Low line rams exhibited more M ($P>.05$) than H line rams during L3. This was caused by 3 L line rams having greater than 14 M. The high value for M during L3 for C rams is attributed to two rams having 15 and 29 M respectively. Services among the lines during L2 did not differ ($P>.05$)

Tulley and Burfening (1983) reported H rams having more M and S and shorter reaction time to first M and(or) S than L line rams during a 30 min libido test. In this study, reaction time to first M did not differ between lines in L1 and L3, but in L2, L rams had longer RTM than H rams ($P<.05$; 10.8+1.2 and 4.9+1.3, respectively). Reaction time to first service was similar between the lines, with H rams having a shorter RTS ($P>.05$) in each of the three libido tests.

The reason for discrepancy between the findings of Tulley and Burfening (1983) and the present study is probably due to the fact that the former researchers used 30 min libido tests with estrous ewes over a 13-mon period, while a 15-min libido with anestrous ewes was used in this study. Rams in the former study had time to acclimate to the facilities and ewes, while in our study there was no acclimation period. Kilgour and Wilkens (1980) and Kilgour (1985) reported that rams need

one or two introductory periods of 20-min to one h to allow rams to overcome shyness and exhibit true serving capacity. In this study, first exposure of rams to ewes was during L1, and this could explain why only 1 (M in L2) difference between lines was observed.

The length of the libido test (15 min) in this study may have been too short to properly evaluate libido. Mattner et al. (1971) reported flock fertility was highly correlated with number of services in three 20 min libido tests, but Fletcher (1976) reported no relationship between 20 min libido tests and number of ewes lambing. Kilgour and Wilkens (1980) and Kilgour (1985) indicated that 20 min libido tests give a poor prediction of subsequent flock mating, while 1 and 2 h libido tests were found to be highly correlated to subsequent flock mating activity and fertility. This may also explain why minimal differences between lines and(or) feeding regimens were observed in this study.

Literature has shown that rams fed a low protein or sub-maintenance diet exhibited less libido than rams fed a high protein or maintenance diet (Parker and Thwaites, 1972; Mattner and Braden, 1975; Lindsay et al., 1979). The reason for the difference between results of this study and the aforementioned studies is probably due to libido tests in this study being conducted 4 mo after the termination of the HP regimen. Bodyweights of rams were similar at BW4, therefore any affects nutrition would have had on libido would have

manifested during BW3.

Finally, percentages of rams that showed both mounting and servicing activity in both trials decreased after castration. This is in agreement with Clegg et al (1969) who reported services declined by 50% three wk after castration of rams. Thus absence of the testes for just 7 d in this study has a profound effect on sexual behavior in these rams and points to the fact that maintenance of libido and serving capacity requires the continued presence of testicular steroids.

In conclusion, it appears that selecting for reproductive rate may minimally influence testicular and epididymal characteristics in Rambouillet rams, but, it may take many generations of selection before any differences can be detected. Selecting for reproductive rate in ewes may affect libido in rams, but, 1 to 2 hr libido tests should be conducted over a period of time to properly evaluate any differences that may occur. Nutrition does affect testicular, epididymal and libido characteristics in males, but to properly evaluate any differences that may occur between diets, measurements should be taken when differences in weight between individuals is greatest.

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