ASSOCIATION OF NATURAL PHOTOPERIOD WITH SCROTAL CIRCUMFERENCE, INGUINAL CUTANEOUS HYPEREMIA, ENDOCRINE FUNCTION AND MAY-JUNE FERTILITY IN MATURE F_2 FINNISH LANDRACE X DORSET RAMS

By

KRIS ALAN RINGWALL

Bachelor of Science in Agriculture
North Dakota State University
Fargo, North Dakota
1975

Master of Science
Oklahoma State University
Stillwater, Oklahoma
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Thesis Approved:

Thesis Adviser

Richard R Frahm

Robert P. Wettemann

Duane T. Gaunt

Rodney D. Geisert

Dean of the Graduate College

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CHAPTER I

INTRODUCTION

The livestock industry is under continual pressure to increase efficiency, and inefficient segments of the industry are slowly replaced. The sheep producer has little influence on the price that he receives for his product. So, increased efficiency is his main alternative for survival. "How does the producer increase efficiency?" There are several approaches to the answer.

The topic of this thesis approaches the question of increased efficiency from the field of biology. Man cannot take much credit for the biochemical, physiological and genetic make-up of domestic sheep. The researcher must recognize that organisms are products of natural selection and not easily altered. Forces of natural selection that were present when sheep were first domesticated 10,000 years ago are still present today (Zeuner, 1963). Many early attempts at modifying the biology of sheep failed because researchers did not fully understand the complex mechanisms that regulate physiological processes. By increasing the understanding of biological processes, perhaps successful attempts can be made to improve sheep production.

The most limiting factor to increased efficiency of sheep production is seasonal infertility. The term seasonal is used throughout this thesis to mean the lack of a constant level of fertility during the year. Seasonal reproduction is partially dependent on photoperiod

(duration of light in a day). Long and short photoperiods infer more than 12 h or less than 12 h of light, respectively, while equitorial photoperiods have equal hours of light and dark. Seasonal infertility may be reduced by research directed toward ewes or rams. I will address the question of how to increase efficiency in sheep production by investigating the seasonal reproductive characteristics of the ram and attempt to identify traits that could be used for selection against seasonal infertility.

The mature ram is well-suited for studying methods to improve fertility because the primary reproductive organ, the testis, can be readily observed and measured. The initial phase of this study determined if scrotal circumference and inguinal cutaneous hyperemia (ICH) changed throughout the year. The monthly changes in scrotal circumference were obvious early in the study and prompted the following three questions:

1) Do rams that have greater decreases in scrotal circumference from October to April also have decreased fertility during the spring period when more ewes are anestrus?

2) Are plasma concentrations of testosterone and luteinizing hormone related to seasonal changes in scrotal circumference?

3) Are there seasonal changes in the response of the pituitary to GnRH (gonadotropin releasing hormone), and do seasonal rams respond differently than nonseasonal rams?

CHAPTER II

REVIEW OF LITERATURE

Introduction and Scope of Review

This review concentrates on the effect of natural changes in photoperiod on fertility in the ewe, ram, stag deer, male hamster, and stallion. Seasonal fertility is represented by two broad classifications; short daylength and long daylength breeders (i.e., those that are fertile under periods of short or long daylengths, respectively). Many species of ungulates are short daylength breeders. Sufficient information is primarily available on sheep and deer that will add to our understanding of this event. The hamster and stallion are examples of long daylength breeders. Seasonal reproductive changes are discussed in males of these species.

Domestic ungulates, cattle and swine, are not included since the role of photoperiod is minor in comparison to the effects of nutrition and temperature (Minton, 1983; Mauget, 1982; Tucker, 1982; Gangwar, 1980). In contrast, most wild African ungulates have very marked seasonal reproductive cycles. Field studies suggest that photoperiod is the primary factor governing reproduction (Skinner et al., 1973). Unfortunately, data are lacking as to the mechanisms involved in modulating seasonal reproduction in African ungulates.

Seasonal Reproduction in the Ewe

Photoperiod effects. Infertility has been examined in ewes for almost a century. Heape (1899) listed causes for infertility as the age of ewes and rams, proportion of ewes per ram, changing of rams, district and subsoil, rainfall, food and body condition. With these field observations, Heape concluded that the principal cause of ewe infertility was body condition. Not until several decades later did researchers determine that the major cause of seasonal infertility was daylength.

Duration of photoperiod is the event that regulates reproduction in the ewe. During the 1930s, Marshall (1937) speculated that light was the main cue for the onset of estrus in the ewe. The annual reproductive cycle of Marshall's ewes shifted in accordance with a new photoperiodic environment after transferring the ewes across the equator. The resulting estrous cycles were in accordance with the new photoperiodic environment. The percentage of Cheviot, Dorset, Finnish Landrace, Romney and Suffolk ewes that express estrus is greatest during October and progressively declines to less than 10% during May, June and July (Lamberson and Thomas, 1982). Estrous activity is greatest during short photoperiods and least during long photoperiods.

Upgraded Suffolk ewes at the University of Cambridge, England responded to artificially decreased daylength by initiating estrus within 13-16 weeks (Yeates, 1949). The cessation of the sexual season occured 14-19 weeks after light was increased. After observing three natural breeding seasons, Hafez (1952) noted breed differences in the length of the breeding season, estrous cycle length, incidence of silent

estrus and duration of estrus. The same trends within each breed were repeated from one year to the next.

The value of light regimes for modifing sheep reproduction was demonstrated by Mauleon and Rougeot (1962) in France. They initiated two complete sexual cycles in a period of 12 months by exposing ewes to a biannual light rhythm of two complete photoperiodic cycles within one year. Clun Forest ewes that were exposed to either gradual or abrupt changes in duration of photoperiod at the beginning of the normal breeding season expressed estrus sooner when light was decreased abruptly (Ducker and Bowman, 1970; Ducker et al., 1970).

Southdown ewes, maintained under constant equatorial lighting, became very sporadic breeders with reduced fertility compared to ewes under normal light (Thwaites, 1965). Thwaites suggested an inherent rhythm may maintain some degree of seasonality. Fifteen years later, Legan and Karsch (1980) demonstrated that Suffolk ewes maintained in Michigan under artificial light would initiate reproductive cycles every 90 to 120 days. They concluded that exposure to long days caused a shift to anestrus, and exposure to short days initiated estrous cycles.

Other factors are also involved in seasonal infertility of ewes. Temperature is generally confounded in many of the experiments and certainly a potential regulator. Research during the sixties with the Peppin Merino and Southdown ewes subjected to different thermal seasons and daylengths confirmed that light, not temperature, is the major regulator of seasonal infertility (Wodzicka-Tomaszewska et al., 1967).

Photoperiodic Pathways. The knowledge that light controls reproduction in sheep has not increased reproductive efficiency. Efforts are being made to locate and understand the controlling mechanisms. The

biology of many seasonal species has been studied and provides insight into the pathways leading from external cues to internal regulatory mechanisms. The ewe has the ability to receive the stimuli and differentiate between different daylengths.

The pathway that transmits the light stimuli was described by Karsh et al. (1984). Photoreceptors in the retina of the eye are activated by light and neural impulses are transmitted to the suprachiasmatic nuclei of the hypothalamus. From the hypothalamus, the impulses pass through the paraventricular nuclei, the superior cervical ganglia, and to the pineal gland. The pineal transduces the neural input into a hormonal output to produce modulating hypothalamic-hypophyseal activity and, in turn, the seasonal changes in reproductive function.

Not until the last few years has this intricate pathway been fully appreciated as the link between the external environment and internal regulation of seasonal responses. Most previous models of photoperiodic control approached the subject by centering the model around the gonads. Although such models explain the results of individual experiments, the results do not hold up under broader environments and suggest other regulatory mechanisms. The acceptance of the photoreceptive pathway allows the discussion of internal responses to photoperiod to involve higher centers of the brain, endocrine system and gonads.

The pineal response involves the circadian system of photoperiodic time measurement. This system depends upon the phase relationship between light and circadian oscillators involved in the transmission of information about daylength to the hypothalamus (Turek et al, 1984). Because an extensive review of circadian oscillators is available from

Suda et al.,(1979), Follett and Follett (1980) and Aschoff et al., (1982).

The Ovine Estrous Cycle. The normal estrous cycle must be evaluated before anestrus can be understood. The hypothalamus regulates surge and tonic luteinizing horome (LH) through gonadotropin-releasing hormone (GnRH). Haresign et al. (1983) postulated the median eminence-arcuate nucleus region is concerned with basal or tonic LH secretion in ewes while the preoptic-suprachiasmatic area promotes the preovulatory LH surge. LH stimulates the ovary and in greater concentration (surge LH) induces ovulation (Gordon, 1983). The sustained increase in tonic LH after luteolysis is critical for increased estrogen (Baird and Scaramuzzi, 1976).

Estrogen, secreted by the follicle due to increased LH and FSH, has a positive effect on the hypothalamic neurons which cause the large pre-ovulatory LH surge (Goodman and Karsch, 1981). Maximal estrogen concentrations initiate sexual receptivity and the ovulation-inducing secretion of gonadotropins from the pituitary. However, the hypothalamic-pituitary axis quickly turns refractory to estrogen and reinstates the negative effects of estrogen (Goding et al., 1969; Scaramuzi et al., 1971; Karsch and Foster, 1975). A surge in LH may result due to a positive effect on preoptic-suprachiasmatic hypothalamic neurons responding to increased estrogen. Sufficient stimulation for LH synthesis may not occur or be accessable until maximal concentrations of estrogen are present.

Following ovulation, the corpus luteum forms and starts to produce progesterone about day 4 of the cycle. The corpus luteum terminates about day 14 by the release of prostaglandin from the uterine

endometrium, thus allowing the cycle to be repeated (Goding, 1974). Behavioral estrus precedes ovulation by 24-30 hours. Estrus occurs when maximal concentrations of estrogen are present prior to the preovulatory surge of LH and the hypothalamus has been recently exposed to progesterone (Robertson, 1977). Estrogen alone will not produce behavioral estrus.

The inhibitory feedback action of estradiol at the hypothalamus increases during long photoperiods so slight increases in estradiol concentration have a negative effect on LH secretion. Therefore, basal LH concentrations are not great enough to stimulate estrogen production to the threshold concentration which in turn will stimulate hypothalamic receptors to initiate an LH surge (Goodman and Karsch, 1981). The changes in estradiol feedback, which are the same in blinded and pinealectomized ewes, are a consequence of either unknown environmental cues or of an endogenous circannual rhythm.

Seasonal control of reproduction in the ewe could be based on changes that occur in response to estrogen stimulation during the estrous cycle (Legan et al., 1977). Both amplitude and frequency of tonic LH and FSH in ovariectomized ewes with estradiol implants are reduced during the anestrus season compared to noncastrated ewes. Estradiol suppression of these hormones is minimal during the breeding season. Thus, the sensitivity of the hypothalamus and pituitary to steroids is dependent upon the season of the year.

LH release is dependent upon GnRH release from the hypothalamus. Although LH response may vary, there is a direct link between the release of GnRH and LH. GnRH infusion in ovariectomized ewes will produce increased LH concentrations either during or soon after a GnRH

pulse (Levine et al., 1982). The amplitude of the corresponding GnRH pulse and the following increase in LH concentrations are syncronized (Clarke and Cummins, 1982). GnRH regulation has the potential to control seasonal changes in the estrous cycle since GnRH release influences LH release.

The Pineal Gland. The estrous cycle of pinealectomized ewes over two years became asynchronous and out of phase with control ewes which responded to the natural seasonal transitions (Karsch et al., 1984). The pineal has both inducing and inhibiting effects on reproductive functions (Thorpe and Herbert, 1976; Farrar and Clarke, 1976). Melatonin (the principal pineal indoleamine) is released rhythmically during the night, has maximal concentrations at night, has a circadian rhythm which will persist in constant darkness and is normally entrained by the light/dark cycle (Rollag and Niswender, 1976). The connection between the pineal (or some other component of photoreceptive pathway) and the hypothalamus (for control of the hormonal pathways) involves pineal secretory products such as melatonin.

The secretion of melatonin also changes throughout the year and could be a key to circannual regulation. The duration of elevated night time melatonin concentration are longest during the breeding season (Rollag et al, 1978). In Suffolk ewes under natural and artificial light, the duration of the increase in night time melatonin is proportional to the length of night (Bittman et al., 1983b). Melatonin secretion is modified within two days of a change in light treatment.

Pinealectomized ewes (assuming no internal source of melatonin) infused with concentrations of melatonin that mimic long day concentrations have decreased LH. If the treatment is reversed, short

day melatonin concentrations infused, LH is increased thus mimicking intact ewes. Pinealectomized ewes cannot respond to the shift in daylength without melatonin infusion. Thus, melatonin appeared to be involved in the photoperiodic response in these ewes (Bittman et al., 1983b). Melatonin is also suppressed by gonadal steroids during long photoperiods (Arendt et al., 1981b).

Three mechanisms are postulated as to how changes in daylength effect melatonin secretion. In the Soay sheep, the amplitude of melatonin release was changed by the amount of darkness (Lincoln et al., 1982). Thus, the period of greatest concentration (amplitude) indicated a causal relationship with daylength. In the Suffolk ewe, Bittman and Karsch (1984) considered duration, not amplitude, of melatonin release the main response to changes in light. In addition, melatonin secretion shifts from two periods of maximal concentration within one dark period during long nights of the breeding season to a single period of greater concentration during anestrus (Arendt et al., 1981).

Melatonin concentrations influence the reproductive cycle. Karsch et al. (1984) proposed a link between melatonin and GnRH and no connection between melatonin and modification of the anterior pituitary and(or) a modulation of the anterior pituitary's response to GnRH. Melatonin may interact with a neural oscillator involving GnRH and steroid feedback. Although changes in melatonin occur in sheep, corresponding changes in reproduction are not always noted. Daily administration of melatonin does not induce estrus during anestrus, but tends to increase conception rate in those ewes that do express estrus (Kennaway and Seamark, 1980; Stellflug et al., 1984). Ewes continue to breed despite immunization

against melatonin (Symons, 1973). The mechanism by which melatonin influences reproductive activity has not been clarified.

Summary. Two regulatory steps during the estrous cycle are the ability to produce adequate GnRH to stimulate LH release and the sensitivity change in the hypothalamus to estrogen which influences release of GnRH. If seasonal modification occurs at either step, the ewe will not exhibit estrous cycles. Two basic views are held concerning seasonal anestrus in the ewe.

Legan and Karsch (1979) and Land et al. (1979) suggest that seasonal anestrus is a shift in photoperiodic inducible changes in the sensitivity of the hypothalamic-pituitary axis to the negative feedback action of ovarian steroids. Therefore, as the inhibitory effects of estradiol increase, LH concentrations in plasma decrease. Serum LH concentrations are not great enough to stimulate estrogen production which, in turn, cannot reach the threshold amount to stimule the hypothalamic surge receptors for LH. The other view is that the frequency of episodic GnRH secretion decreases independent of estrogen therefore plasma LH concentrations are not great enough to stimulate adequate follicular growth during long photoperiods (Brinkley, 1981).

Seasonal Reproduction in the Ram

Photoperiod effects. In contrast to the ewe, seasonal effects on ram reproduction have only been studied extensively during the last decade. Summaries of mating records indicate that rams of several breeds are relatively infertile at certain times of the year. For example, ewes exposed to rams of two breeds produced lambs sired by only one breed (Lees, 1965).

There is marked seasonal variation in testicular weight of rams (Thimonier, 1981). In the Ile-de-France breed, testicular weight averaged about 210 grams in January through May and increased to 285 grams by the end of October. The change in testicular weight started before the longest day and reached a maximum before the shortest day. The variation in testicular weight of Ile-de-France rams is similar to changes in the average number of germ cells in cross sections of seminiferous tubules. Similar results have been found by Land and Sales (1976), Islam and Land (1977), Lincoln (1978), Howles et al. (1980) and Mickelsen et al. (1981).

The natural photoperiodic response in Soay rams (a domesticated but primitive breed from the United Kingdom) occurs gradually. An abrupt change in daylength increased the rate of response and demonstrates endocrine and anatomical changes during the transition period from long to short days. Within 6 days of a switch to short photoperiods, the frequency of episodic LH surges increased followed by an increase in plasma testosterone. By 12 days, concentrations of FSH in plasma increased and by 26 days the testes began to increase in diameter. The testes became fully enlarged within 100 days after the rams were exposed to short photoperiods (Lincoln, 1978).

Several breeds have been evaluated for changes in scrotal circumference throughout the year. In England, Islam and Land (1977) evaluated Finnish Landrace, Tasmanian Merino, Finn-Merino, and Finn-Dorset rams. These breeds differed in the onset of scrotal change, however, October and November were the months when rams exhibited the largest scrotal circumference. The rams in the various breeds had gradual declines in scrotal circumference through June, then scrotal

circumference started to increase, with the exception of Merino rams. The scrotal circumference of Merino rams increased during April.

The period of rapid decrease in scrotal circumference is not constant for all breeds or locations. The smallest scrotal circumference of native Icelandic rams occurred during March and April and the decrease was 15% from scrotal circumference in the fall (Dyrmundsson et al., 1981). Suffolk, Lincoln, Columbia and Polypay rams obtained minimal scrotal circumference in January and February in North America (Mickelsen et al., 1982). These rams had an average scrotal circumference of 37.8 cm in October and 32.6 cm in February.

Suffolk and Managra breeds in Manitoba achieved maximal scrotal circumferences in September through November and minimal circumferences during March to April (Sanford and Yarney, 1983). Rambouillet rams in Montana had maximal scrotal circumference in October to November, with the smallest circumference in February to March (Tulley and Burfering, 1983). Even in Merino rams, in which the ewe is noted for having an extended lambing season, maximal scrotal circumference is greater in the fall than in the spring (Skinner and van Heerden, 1971).

Semen Production. When rams were exposed to short photoperiods, testicular weight increased by 45% compared to rams on long photoperiods, and sperm production was doubled (Schanbacher and Ford, 1979). The changes appear to be regulated by the hypothalamus, since administration of GnRH reduced the seasonal differences in sperm production. The decreases in percentages of live sperm, normal sperm, sperm with normal acrosomes, and sperm motility, which occur due to long photoperiods, were reduced by daily intramuscular injection of 50 ug of GnRH (Schanbacher and Lunstra, 1977).

Average daily sperm output decreased slightly from December to February and then decreased over 50% from February to May in Finnish Landrace, Tasmanian Merino and Finn-Dorset rams (Islam and Land, 1977). The greatest percentage of morphologically normal spermatozoa was 82.3% for Suffolk, Lincoln, Columbia and Polypay rams during September and decreased to 57.8% in February (Mickelsen et al., 1982). Decreased natural photoperiods only slightly modify ejaculate volume and percentage of motile, morphologically normal spermatozoa (Land, 1970; Skinner and van Heerden, 1971; Jackson and Williams, 1973; Barrell and Lapwood, 1978/1979).

An extreme effect of season on sperm production occurs in Soay rams (Lincoln and Short, 1980). Spermatozoa production was completely arrested during sexual quiescence in Soay rams. Testes regressed and the diameter of seminiferous tubule and germ cell numbers were greatly reduced. Sperm production decreased 50% in Ile-de-France, Prealpes du Sud and Romanov rams as determined by monitoring rete testis fluid from fall to spring (Dacheux et al., 1981). Little doubt remains that the season of the year affects spermatozoa production, and changes in morphology also occur.

The Pineal Gland. Response to photoperiod can be modified by removing innervation of the sympathetic nervous system (ganglionectomy) to the head (Lincoln, 1979b; Lincoln et al., 1982). Ganglionectomy will affect many areas of the head, in addition to the pineal, including vasoconstrictive control of blood vessels in the brain, pituitary gland and eye. Scrotal circumference and plasma testosterone concentrations of cranially sympathectomized Soay rams do not change in response to changes in photoperiod. Seasonal effects on the secretion of LH and

testosterone are reduced by pinealectomy and are similar to secretion in ganglionectomized rams (Barrell and Lapwood, 1979b).

Long term ganglionectomized rams maintained in light chambers remain in a stimulated state (large scrotal circumference), similar to the breeding season (Lincoln, 1979b). Long term ganglionectomized rams have seasonal variations in scrotal circumference if exposed to the natural environment, since these rams will obtain cues from nonganglionectomized individuals (Lincoln, 1979b). This explains some of the early contradictions of seasonal responses in ganglionectomized rams (Karsh et. al., 1984). Ganglionectomy did not prevent external cues other than light, from influencing testicular function.

The pineal gland is involved in seasonal regulation of reproduction in the ram, just as it is in the ewe. Melatonin is one of the secretory products of the pineal and attains maximal concentration during dark hours. Ganglionectomized rams have undetectable concentrations of melatonin (Lincoln and Short, 1980), suggesting anti-gonadal effects of melatonin since these rams remain in a sexually active state.

Several conclusions can be made concerning melatonin (Lincoln and Almeida, 1981). Plasma melatonin concentrations are minimal during periods of light and maximum values occur during periods of dark. Under prolonged darkness, melatonin rhythm continues but can be sychronized by light. In the ram, melatonin has a causal relationship with testicular activity and infusion of melatonin will block normal changes in testicular activity if rams are placed under short photoperiods. However, rams immunized against melatonin have seasonal testicular change if kept in natural photoperiods.

Hypothalamic Control of the Pituitary and Testis. Recent investigations have determined the roles of LH and testosterone in the ram and have described how photoperiod influences plasma concentration of these hormones. FSH is related to testicular size (Courot and Ortavant, 1981), but the influence of photoperiod on plasma FSH concentration is not readily apparent (Lincoln and Short, 1980).

Plasma concentration of both LH and testosterone are positively related to testicular size in rams (Courot and Ortavant, 1981). Plasma concentrations of testosterone are greatest during the fall and least during the spring or nonbreeding season (Schanbacher and Ford, 1976; Sanford et al., 1978; Barrell and Lapwood, 1978/1979; Sanford and Yarney, 1983; Barenton and Pelletier, 1983; D'Occhio and Brooks, 1983). The month of maximal concentrations of testosterone is modified by the environment and the breed studied (Gomes and Joyce, 1975; Darbeida and Brudieux, 1980).

The hypothalamic regulatory peptide that controls synthesis and release of LH is GnRH (Galloway and Pelletier, 1975; Bremner et al., 1976; Schanbacher, 1978; Lincoln, 1979; Frazer and Lincoln, 1980; Frazer et al., 1981). Chronic administration of GnRH stimulates testicular growth while acute treatments with GnRH result in increased concentration of LH in plasma (Stelmasiak, 1980). Neutralization of GnRH with antibodies results in a rapid decline in circulating concentrations of LH (Lincoln and Fraser, 1979).

Exogenous GnRH will produce spontaneous episodic surges of LH. Twice daily injections of GnRH (50 ug) during April resulted in testicular growth and an increase in serum concentrations of testosterone (Schanbacher and Lunstra, 1977; Schanbacher, 1978). Plasma LH was

elevated in adult Soay rams exposed to long photoperiods when 100 ug of GnRH was infused into the jugular vein two, four or seven times/d for 10 d (Lincoln, 1979). Larger doses of GnRH (over 100 ug) produced a longer period of elevated LH. Plasma LH increased 25- to 50-fold within 12 min when mature rams were injected intravenously with 100 ug GnRH and remained elevated for more than 3 hours (Galloway et al., 1974; Falvo et al., 1975).

Plasma LH is secreted episodically in response to endogenous GnRH (Sanford et al., 1974; Lincoln 1976; Schanbacher and Ford, 1976; Sanford et al., 1978; and Walton et al., 1980). The frequency of GnRH discharge from the hypothalamus is greater during the breeding season than during the non-breeding season (Lincoln and Short, 1980) and pituitary responsiveness to GnRH is decreased in the non-breeding season. The secretory pattern and mean plasma concentration of LH differ between breeding versus non-breeding seasons (increasing daylength). The frequency of release of LH during the breeding season is increased, but the amplitude of each LH pulse is less when compared to the non-breeding season (Lincoln and Short, 1980). There are two functional pools of pituitary LH in rams (Bremner et al., 1976; Stelmasiak and Galloway, 1977). One pool appears to be available for immediate release by GnRH and the other pool is nonreleasable or stored LH.

Summary. For each episodic discharge of GnRH, there is a corresponding episodic release of LH in the ram. The discharge of GnRH from the hypothalamus controls the secretion of LH. The pituitary response to GnRH will vary depending upon the season. During the testicular regressed phase (Spring), LH is released rapidly after the stimulus of GnRH. LH is released in smaller amounts during the active or

breeding season (fall), but the secretion continues for a longer period of time. The change in the ability to release LH for a longer time would indicate a change in the synthetic capacity of the gonadotrope cell. A long release would be dependent on increased protein synthesis controlled by RNA (Vilchez-Martinez et al., 1976).

The effect of testosterone feedback is unclear. Galloway and Pelletier (1975) indicated that testosterone modifies the pituitary response to GnRH. Bremner et al., (1977) and Lincoln and Short (1980) found no effect of testosterone feedback in seasonal regulation. The testis does change in its ability to respond to LH (Lincoln and Short, 1980). The regressed testis during the nonbreeding season responds less to LH stimulation. Large exogenous doses of LH do not produce additional testosterone secretion during the nonbreeding season.

The pineal gland is involved in control of the hypothalamus. Removal of the pineal destroys the seasonal pattern of reproductive hormones and testicular changes, provided the ram is not exposed to rams undergoing seasonal changes. Melatonin, the principal hormone of the pineal, has anti-gonadotropin effects in rams.

Seasonal Reproduction in the Male Deer

Sheep are the short daylength breeders that have been studied most extensively. The probable reason for this is that undomesticated species are very difficult to maintain in captivity, and the experiments needed to decipher reproductive changes are difficult to conduct under field conditions.

Photoperiod Effects. Seasonal changes in male deer are similar to those for Soay rams, and perhaps are even more distinct. In

the Wapiti (Cervus elaphus), scrotal circumference increases rapidly from less than 20 cm in June and July to a maximum of 26 cm in September (Aughey, 1969; Lincoln, 1971a, 1971b; Haigh et al., 1984). Scrotal circumference remains maximal for September and then declines and stabilizes at approximately 22 cm from November to March. By May, scrotal circumference decreases another 4 cm and is indicative of almost complete testicular involution (Aughey, 1969; Lincoln, 1971a, 1971b; Haigh et al., 1984).

Similar results have been found in fallow (Dama Dana L.), black-tailed (Odocoileus hemionus columbianus) and mule deer (Odocoileus hemionus), except testicular volumes are maximal in November and then decline (Chapman and Chapman, 1970; Markwald et al., 1971; West and Nordan, 1976). In contrast, the roe deer (Capreolus capreolus) has its maximal testicular weight in July and then a rapid decline in weight. By September testicular weight of the roe stag decreases by more than 50% (Bramley, 1970).

White-tailed deer (Odocoileus virginianus) have seasonal changes in testicular weight similar to the Wapiti (Wislock, 1949; Robinson et al., 1965; Mirarchi et al., 1977). Testicular weight increases from less than 12 grams in June to over 44 grams in September. Then testicular weight decreases rapidly from September to less than 12 grams in February.

Semen Production. Spermatozoa production would be expected to vary with the season since large seasonal variations occurs in scrotal circumference. Histological studies of the testis of red, white-tailed, black-tailed and roe deer all indicate a decrease in spermatozoa production during long days. Involution of the seminiferous tubules and azospermia are characteristic of the stag following the fall breeding

season (Robinson et al., 1965; Lincoln, 1971a; West and Nordan, 1976; Mirarchi et al., 1977).

Roe deer initiate spermatogenesis two to three months before other species, but spermatogenesis also is reduced two to three months earlier (Short and Mann, 1966). Roe doe also initiate estrus earlier than other species, but implantation is delayed by five months. Thus, despite an early onset of reproductive activity, kids are not born until May.

Except for roe deer, male deer are capable of siring fawns from September through February, even though scrotal circumference and spermatogenic activity are maximum for only a short time (Chapman and Chapman, 1970; Mirarchi et al, 1977). There is a distinct relationship between age of stags and the time of initiation of the reproductive cycle. As a stag grows older, the reproductive cycle is gradually shifted earlier in the year (Lincoln, 1971b). Mature red deer stags start the rut in mid-September; the 4- and 5-year-olds are most active in late October and November, and the 2- and 3-year-olds show some interest in female deer during December. However, maximal testosterone in plasma occurs in October regardless of age. Seminal fructose concentrations decrease to values typical of the nonbreeding season by January, long before the reduced concentration of testosterone from the testis (Lincoln et al., 1970).

Spermatogenesis and steroidogenesis are closely related in mule deer (Short and Mann, 1966). Serum testosterone increases corresponding to the fall rut and another lesser increase occurs at the beginning of antler production. An increase in normal spermatozoa is associated with each of these time periods (West and Nordan, 1976; Buberik et al., 1982; Haigh et al., 1984).

Hypothalamic Control of the Pituitary and Testes. Concentrations of testosterone and LH in plasma have been estimated in male deer. Both hormones are markedly episodic throughout the year, and the principal change due to season is size and frequency of episodes of LH and testosterone release (Lincoln and Kay, 1979). Distinct annual changes in LH and testosterone occur in blood samples collected at monthly intervals. Concentrations of LH are maximal prior to testosterone and decrease sharply prior to(or) concommitant with the increase in testosterone concentrations. Greatest concentrations of testosterone occur during October to November for the majority of deer species (McMillan et al., 1973; West and Nordan, 1976; Lincoln, 1971a; Mirarchi et al., 1977; Haigh, 1984). Testosterone within the testis has the same seasonal change as plasma testosterone (Lincoln et al., 1970).

Changes in LH secretion precede changes in testosterone secretion during sexual development and fall rut (Lincoln and Kay, 1979). This relationship is not apparent throughout the year because of reduced testosterone response to LH during sexual quiescent periods. There is no clear evidence that concentrations of LH in plasma in the intact stag change with season, independent of testosterone. Castrated male deer in Scotland did not have seasonal fluctuations in plasma LH concentration (Lincoln and Kay, 1979). Therefore, this would suggest steroid feedback in the intact stag occurs throughout the year and hypothalamic sensitivity to negative feedback is modulating reproduction. However, Buberik (1982) found seasonal changes in plasma concentrations of LH in castrated deer which would suggest steriod independent mechanisms are also present.

Summary. All species of deer undergo seasonal changes in testicular activity. The period of maximal activity occurs during the fall rut (breeding season) and is followed by a less active or sexually quiescent period from midwinter to late spring. The reproductive cycle of the male deer can be divided into four seasons: maximal activity (early fall); regression (late fall through early winter); minimal or no activity (late winter through early spring); and redevelopment (late spring to late summer). Scrotal circumference is maximal for only a short time and remains at an involuted stage during the winter months. Spermatozoa production and hormone secretion follow the same profile as scrotal circumference. There are no obvious differences between the seasonal reproductive cycle of the stag and ram.

Long-Day Breeder

The second type of seasonal breeder, the long daylength breeder, is fertile during periods of long daylength. This category of seasonal breeders constitutes the majority of species with known seasonal reproduction. The two species covered in this review will be the male Golden Hamster and the stallion.

Seasonal Reproduction in the Male Hamster

Photoperiod Effects. The male golden (Syrian) hamster (Mesocricetus auratus) is an excellent example of a long daylength breeder. All North American stocks of golden hamsters are derived from one female and three surviving pups dug from their den in Syria in 1930 (Hoffman, 1982). Thus, the hamster provides a very uniform domesticated model to work with.

Under natural environments in the northern hemisphere, hamsters are fertile throughout the spring and summer, then decrease in fertility through fall. During late fall and winter, hamsters are completely infertile. Fertility returns spontaneously in the spring and is unaffected by photoperiod until the next fall (Stetson and Tate-Ostroff, 1981). During the fertile time, the testes weigh approximately 3,000 mg and decrease to less than 300 mg after ten weeks of short daylengths (Turek and Ellis, 1981). The male hamster undergoes these changes around the fall equinox (late September). Testes remain regressed until late March when testicular recrudescence (initiation of growth and spermatogenesis) begins (Reiter, 1973; 1975). Photoperiods of more than 12.5 h light per day are required to maintain fertility in the male hamster (Gaston and Menaker, 1967).

During the phase when testes are regressed, concentrations of hormones reflect the decreased size of the testes. Concentrations of LH, FSH and testosterone are all decreased. Testosterone decreases from 3-5 ng/ml serum during the breeding season to less than 1 ng/ml during the regressed phase (Berndtson and Desjardins, 1974; Reiter and Johnson, 1974c; Reiter, 1975; Turek et al., 1975b; 1976; Tamarkin et al., 1976a; Bex et al., 1978). Once gonadal regression has occurred, the hamster remains nonreproductive for some weeks and gametogenesis is absent (Stetson and Tate-Ostroff, 1981).

The hamster returns to a reproductive state by spontaneous recrudescence of the testes. This phase of the reproductive cycle is not influenced by the environment. Gametogenesis is re-established, as well as all the endocrine events needed to support spermatozoa production (Turek et al., 1975b; Matt and Stetson, 1979; 1981). Initially,

concentrations of plasma FSH increase followed by increases in LH and testosterone. After spontaneous recrudescence, a photorefractory period is established, during which short daylengths (less than 12.5 h light) will not induce testicular regression (Reiter, 1973). The photorefractory period ends following prolonged exposure to long photoperiods (Reiter, 1975: Bittman, 1978a). No distinction can be made between the photorefractory period and the start of the photosensitive state. The hamster remains reproductively fertile through the photosensitive stage until a photoperiod of less than 12.5 hours is encountered, at which time the cycle repeats.

Hypothalamic Regulation. Duration of photoperiod influences the effects of steroid hormones on gonadotropins. During short days, castrated hamsters are extremely sensitive to the negative feedback effects of testosterone compared to long days (Tamarkin et al., 1976a; Turek, 1977, 1979). A possible mechanism for photoperiodic regulation is variation in sensitivity of negative feedback effects of gonadal steroids. Increased sensitivity to testosterone occurs gradually over a period of two months. Extreme sensitivity to steriods that suppresses FSH and LH to very low concentrations cannot be maintained past 18 weeks. Spontaneous recrudescence occurs after 18 weeks of increased steriod sensitivity (Matt and Stetson, 1979; Ellis et al., 1979).

Photoperiodic regulation is not totally dependent on the negative feedback effects of steroid hormones. In the castrated hamster, gonadotrophins are greatly reduced during short photoperiods (Tamarkin et al., 1976a; Pickard and Silverman, 1979; Turek et al., 1975a; Ellis and Turek, 1980). This suggests that short days inhibit pituitary gonadotropin release independently of steroid hormones. Spontaneous

recrudescence also occurs, and serum gonadotropin concentrations increase in the castrated hamster to greater concentrations than in fertile intact males (Turek et al., 1975a; Matt and Stetson, 1979).

The Pineal Gland. Steroid independent and dependent mechanisms exist for photoperiodic control of hamster reproduction. The pineal is a possible regulator of both these mechanisms. Removal of the pineal gland will maintain a hamster in a photo-stimulated state (Hoffman and Reiter, 1965). Neural efferents do not appear to originate in the pineal, so effects of the pineal are probably hormonal (Elliott and Goldman, 1981). Output from the pineal is mediated by the nervous system. The superior cervical ganglion is the source of the noradrenergic pathways that innervate the pineal. Disruption of these pathways change seasonal influences on hamster reproduction (Reiter, 1972b).

The pineal gland converts serotonin to melatonin, the principal indoleamine produced by the pineal. Melatonin, depending on photoperiod, has specific effects on the reproductive cycle of the hamster. The same amount of melatonin will cause testicular regression under long photoperiods and testicular recrudescence under short photoperiods (Tamarkin et al., 1976b, 1977). Secretions of melatonin follow a diurnal pattern (Klein and Weller, 1970; Rollag and Niswender, 1976). Melatonin administration that mimics the natural melatonin secretion for a set light-dark ratio will result in variation in LH and FSH similar to that for natural photoperiods (Tamarkin et al., 1979; Panke et al., 1979).

Summary. The reproductive cycle of the male hamster can be divided into four periods; fertile, regressed, spontaneous recrudescence and a photorefractory. Testicular weight is greatest during the fertile time until a photoperiod of less than 12.5 h is encountered, then the testes

regress. The male hamster, unlike the short daylength breeder, remains fertile indefinitely providing a photoperiod of less than 12.5 h is not encountered. Spermatozoa production and hormone secretion follow the same seasonal trends as testicular weight.

Seasonal Reproduction in the Stallion

The stallion has maximal spermatozoa output and libido during spring and summer, which coincides with the natural breeding season of the mare (Skinner and Bowen, 1968; Picket et al., 1970, 1976). However, data are limited on seasonal effects on stallion reproduction. In the wild, horses have a limited breeding season. Breeding occurs by harem stallions and foals are born between late spring to early summer (Feist and McCullough, 1975). The stallion maintains his herd group or territory all year long (Klingel, 1975). In contrast, most ungulates do not maintain family groups or territories outside of the breeding season.

Photoperiod Effects. Information on seasonal changes in scrotal circumference or testicular size is limited. Testicular size is difficult to obtain for stallions compared to bulls or rams. Testicular weight decreases from long to short photoperiods. Stallions exposed to short photoperiods had testes that averaged 203 g/paired testes, while testes of breeding stallions averaged 271 g/paired testes (Johnson and Thompson, 1983). In an earlier trial, testes weight was 30 percent less for those stallions exposed to short daylengths versus long daylengths (Johnson and Neaves, 1981).

Semen Production. Fertility problems and seasonal effects on sperm production have been observed in stallions (Wagenaar and Grootenhuis,

1953). Seminal concentration of ergothioneine, citric acid and semen volume vary with season (Mann et al., 1956). Spermatozoa concentration, motility, ejaculate volume and citric acid decrease in Welsh ponies when exposed to short photoperiods (Skinner and Bowen, 1968). In a detailed study of the cycle of seminiferous epithelium, Swierstra et al. (1974) found no seasonal differences in the frequency of stages within the spermatogenic cycle or in testis composition. Seminal components are affected more by season than are spermatozoa traits (Gebauer et al., 1976). Seminal pH, total carbohydrate, dry weight, total nitrogen and lactic acid all decreased with short versus long photoperiods in quarterhorse stallions (Pickett et al., 1975).

Van der Holst (1975) found a marked seasonal influence on ejaculate volume, sperm motility, total number of spermatozoa per ejaculate and morphological abnormalities. Seminal volume decreased 40% from a maximum in May and June to a minimum in December and January (Pickett, 1979; Byers, 1983). Spermatozoa output also decreased 50% from a maximum in July to a minimum in January and the number of mares the stallion settled was affected (Johnson and Neaves, 1981). Motility did not change with seasonal changes in daylength. Pickett (1979) concluded that the most limiting factor was the decrease in spermatozoa during the nonbreeding season, but spermatozoa that are produced are normal and capable of fertilization.

Hypothalamic Regulation. Both mean concentration and frequency of pulses of plasma testosterone in stallions vary with season (Byers et al., 1983). Plasma testosterone concentrations decreased more than 25% for Quarterhorse stallions in Colorado from October through January (Pickett, 1979). Maximal testosterone concentrations occurs during

periods of long photoperiods (Berndtson et al., 1974; Thompson et al., 1977; Irvine and Alexander, 1982; Johnson and Thompson, 1983). Plasma LH concentrations are also depressed during short photoperiods (Thompson et al., 1977; Burns et al., 1982; Johnson and Thompson, 1983).

As with other ungulates that are seasonal breeders, there is an interaction between steroid feedback mechanisms and the duration of photoperiod. This phenomena is not clarified in the horse. Castrated male horses have slight seasonal changes in plasma LH concentrations. Stallions during the breeding season, in contrast to castrated males, have increased concentrations of LH in plasma three to four times greater than concentrations before the breeding season. Testicular steriods apparently modify the seasonal concentrations of LH in the stallion. The pineal gland is suspected to play a central role since pinealectomy will alter the seasonal breeding patterns of the mare (Sharp et al., 1979). The role of melatonin is not defined in the stallion.

Overall Conclusions

Obvious testicular changes occur with season in many species. Seasonal changes in testicular size, spermatogenesis and androgen secretion occur. Most certainly, testicular size is reduced and androgen production is decreased in the nonbreeding season of seasonal reproducing mammals. A decrease in spermatogenesis follows the regression of the testis and the lack of hormone support. Gonadotropic hormones from the anterior pituitary are associated with the seasonal testicular changes. LH secretion changes from a pattern of infrequent

release with large spikes in concentration to frequent pulses of lesser concentration as the breeding season approaches.

The stimulus for FSH and LH release in both long and short day breeders is GnRH, which is released from the hypothalamus. The rate of GnRH release from the hypothalamus regulates LH secretion. Infrequent release of GnRH decreases the plasma concentrations of LH or FSH. Steroid hormones interact with the hypothalamus and anterior pituitary to modify LH secretion in response to GnRH. The photoperiod modifies hypothalamic responses to steroids. Stimulatory light treatments decrease the sensitivity of the hypothalamus and pituitary to negative feedback effects of steriods, while nonstimulatory light treatments increase the sensitivity. Extreme sensitivity during the nonbreeding season reduces LH release. The mechanism appears to be the same in both long and short daylength breeders except that for short daylength breeders, short photoperiods are stimulatory and the opposite is true for long daylength breeders.

The pineal gland is a key element for the regulation of seasonal reproduction. Pinealectomy alters the normal reproductive response in all photoperiodic mammals studied. The principal product of the pineal is melatonin which is tightly coupled to the light-dark cycle. In the physiological chain of events, the pineal must receive neural innervation in order to monitor environmental cues. The pineal is connected to the environment by means of the circadian system of photoperiodic time measurement. A photoperiodic circadian time keeper receives the photic information from the eye and regulates pineal melatonin which influences the hypothalamic-pituitary-gonadal activity.

CHAPTER III

ASSOCIATION OF PHOTOPERIOD WITH SCROTAL CIRCUMFERENCE, INGUINAL CUTANEOUS HYPEREMIA AND ENDOCRINE FUNCTION IN MATURE F_2 FINN X DORSET RAMS SELECTED FOR EXTREME OR SLIGHT SEASONAL CHANGES IN SCROTAL CIRCUMFERENCE

Summary

Thirty-one mature Finn X Dorset F_2 rams were classified as seasonal or nonseasonal based on the decrease in scrotal circumference from October, 1982 to April, 1983. The eight rams with the greatest decrease in scrotal circumference (seasonal) and the seven rams with the least decrease in scrotal circumference (nonseasonal) were selected to evaluate changes in serum LH and testosterone during April, July and October of 1983 and January of 1984. Seasonal rams attained maximal scrotal circumferences during September of 1982 and 1983 (34.18 and 34.39 cm) and minimal scrotal circumferences during March of 1983 and 1984 (29.07 and 28.58 cm). The nonseasonal rams had less change in scrotal circumference from September to March than seasonal rams ($P<.01$). Maximal scrotal circumferences of nonseasonal rams occurred in November, 1982 and October, 1983 (30.74 and 31.59 cm) and minimal scrotal circumferences were in April, 1983 and March, 1984 (29.83 and 30.28 cm). Change in scrotal circumference of individual rams was consistant from the first year to the second (Spearman rank correlation=.82, $P<.001$). Both ram classes had seasonal changes in

inguinal cutaneous hyperemia (ICH), but nonseasonal rams had greater ($P<.05$) intensity and quantity of ICH throughout the year. Within April July and October, serum testosterone before and after two infusions of 1 ug of GnRH, at an hour interval, was similar for both ram classes. During January, serum testosterone was greater ($P<.05$) before GnRH infusion for nonseasonal rams but the response to GnRH was similiar. Within a ram class, both ram classes had greater ($P<.05$) serum testosterone during October than April and seasonal rams had greater ($P<.05$) testosterone during October compared to January. Nonseasonal rams had greater ($P<.05$) serum LH concentrations than seasonal rams during October and January. The magnitude of LH spikes was greater ($P<.05$) for nonseasonal rams than for seasonal rams in April. For both ram classes, April was the month of greatest ($P<.05$) serum LH concentrations and the magnitude of LH spikes. The LH response to the second infusion of GnRH was the same as the response to the first GnRH infusion for nonseasonal rams during all four months. However, the increase in LH in serum was greater ($P<.05$) after the 2nd infusion than after the first in seasonal rams during July. In October, the LH response after the 2nd GnRH infusion was also greater ($P=.13$) for the seasonal rams. In conclusion, external cues stimulate the reproductive system of both ram classes by increased LH in serum during April and increased testosterone during October. Reponse of LH in serum 15 min after the first or second infusion of GnRH is not affected by month for nonseasonal rams, but is for seasonal rams. Reduced LH secretion in seasonal rams during the transition from short to long natural photoperiods may be related to the difference in scrotal circumference change between the two ram classes.

Introduction

Biochronometry of the ram involves circadian endocrine changes that interact with photoperiodic cues (Turek et al., 1984). An expression of biochronometric activity in the ram is oscillating scrotal circumference since changes in scrotal circumference reflect a summation of internal response of a ram to the photoperiod (Lincoln and Short, 1980). If rams with less change in scrotal circumferences are more independent of the photoperiod, these rams may sire daughters that are less seasonal in their reproductive cycles. Breeds vary as to the amount of change in scrotal circumference throughout the year(Islam and Land, 1977; Mickelsen et al., 1982) but the ability to identify rams with less change in scrotal circumference and verify that they are less responsive to photoperiodic cues has not been reported. The purposes of this study were to identify rams which have the least change in scrotal circumference from fall through spring and to compare endocrine changes of these rams to rams that demonstrate considerable change in scrotal circumference during the same period.

Materials and Methods

Thirty-one F_2 Finn x Dorset rams, born during the springs of 1980 and 1981, were maintained under Oklahoma native bermuda pasture conditions until the spring of 1984. Rams were managed in a single group throughout the study, with the exception of the May and June breeding period. Rams were weighed each month and supplemented with alfalfa and grain when forage was limited during dry and(or) winter periods. Condition scores (on a scale of 1= extremely emaciated to 9=

fat deposits over the lumbar vertebrae and ribs) were assigned each month.

Starting in May, 1982, two independent scrotal circumference measurements were made on each ram while the ram was resting on his rump. The testes were held firmly in the lower portion of the scrotum and measured with a fiberglass tape measure. The testes were palpated between scrotal circumference measurements for testicular or epididymidal abnormalities.

Inguinal cutaneous hyperemia (ICH) is a very conspicuous flushing of the inguinal region and was scored for quantity and intensity. The intensity of the ICH was scored from 0 = no color, 1 to 3 = shades of pink, 4 to 5 = light reds, 6 to 7 = reds, 8 = dark red, 9 = purple. The quantity of the ICH was scored: 0 = none, 1 = a band of color no wider than 1 cm within each inguinal region, 2 = a band of color no wider than 3 cm within each inguinal region, 3 = a band of color wider than 3 cm but still within each inguinal region and not including the teat, 4 = a band of color which includes the inguinal area, the teat and spotting of color between the two teats, and 5 = a solid band of color across the two teats and including both ingunial regions.

For the purpose of evaluating endocrine function as related to changes in scrotal circumference, rams with the greatest (n=8) and least (n=7) change in scrotal circumference between October and April were selected from the original 31 rams. Unequal numbers between ram classes resulted from ram death. The degree of change was calculated by subtracting the mean March to April scrotal circumference from the mean October to November scrotal circumference. Rams that had the greatest decrease in scrotal circumference from fall to spring were classified as

seasonal and rams with the least change were classified as nonseasonal. The classification of the rams was based on measurements from October, 1982 to April, 1983.

Intravenous catheters were placed in the venae cavae of seasonal and nonseasonal rams in April, July and October of 1983 and January of 1984. Rams were maintained under continuous light during sampling, isolated from ewes and fed at 0600 h and 1300 h. Blood samples (10 ml) were obtained at 30 min intervals from 0730 h to 1530 h. After a blood sample was taken at 1530 h, 1 ug of GnRH (courtesy of National Hormone and Pituitary Program, Baltimore, Maryland) was infused into the cannulae. Blood samples were obtained at 15 min intervals until 1630 h, then an additional 1 ug of GnRH was infused. Blood samples were obtained every 15 min until 1730 h, then blood samples were taken every 30 min until 2030 h. Blood samples were immediately placed on ice, stored at 4 C for 24 h, centrifuged at 2000 X g for 30 min and serum was frozen until hormones were quantified.

Testosterone was quantified (Wettemann and Desjardins (1979) in samples obtained at 1130, 1330, 1530, 1600, 1630, 1700, 1730, 1830, 1930 and 2030 h. The intra-assay and inter-assay coefficients of variation were 6.7% and 10.2%, respectively. When 5 ng of testosterone were added to a serum sample from a castrated ram, 5.1$\pm$.1 ng (n=25) were recovered.

LH concentrations were quantified by radioimmunoassay (Niswender et al., 1969). Radiolabeled ligand was prepared from LER-1374A-ovine LH and I^{125}. Ovine LH (NIH-LH-S18) was used as the standard. Phosphate buffered saline (PBS, .1 M, pH 7.0) plus 1% lypholyzed egg white (1% EW-PBS) was used as the assay buffer. Dose response curves for dilutions of ram serum were parallel to the standard curve between .05

and 1.6 ng LH/tube. The antisera (#15, supplied by Dr. G. D. Niswender, Colorado State University, Fort Collins, Colorado) had less than 2% crossreactivety with ovine FSH, bovine growth hormone and bovine prolactin.

Serum samples were assayed in duplicate. The lower limit of sensitivity of the assay was .15 ng LH/ml serum. When 5 ng of LH (LER-1374A-ovine) were added to a serum sample from a lactating ewe, 5.0$\pm$.5 ng (n=15) of LH were recovered. The intra-assay and inter-assay coefficients of variation were 5.2 and 10.0%, respectively, for ewe plus 5ng LH.

Data were analyzed by multivariate analysis of variance (MANOVA) performed on the regression coefficients (Allen, 1983; Allen et al., 1983). A full sinusoidual regression model with 12 months per period was fit to each ram for the variables scrotal circumference, inguinal cutaneous hyperemia, body weight and condition score (Mendenhall and Rienmuth, 1982). Least square means of intercepts and slopes for each ram class are listed in appendix table 1 for scrotal circumference, inguinal cutaneous hyperemia, body weight and condition scores. The independent variables for the model were month, sine of month, cosine of month, month * sine of month and month * cosine of month.

One way analysis of variance was used to evaluate the effects of ram class within date or date sampled within ram class for LH and testosterone concentrations prior to GnRH infusion, the magnitude of LH spikes (serum LH concentration greater than two standard deviations above the mean for the individual ram within a date) and the responses in serum LH concentrations at 15 min after the first and second infusion with GnRH. The serum LH response to GnRH was calculated as the

difference between the serum LH concentration of the serum sample prior to the infusion of GnRH and the serum sample obtained 15 min post GnRH infusion.

Polynomial equations were fit to LH and testosterone concentrations in serum after infusion of GnRH with time as a continuous independent variable. The initial degree of polynomial choosen was one less than the number of time periods or until the error matrix was singular. The minimum degree necessary to describe each treatment profile was the degree when the mean of the regression coefficients of the q^{th} degree polynomial and higher powers were zero for each treatment. Least square means of intercepts and slopes for each ram class for the responses of LH and testosterone following GnRH infusion are in appendix table 2 and 3. The test of significance was determined by MANOVA.

The tests of coincident or parallel profiles were performed on the individual ram regression coefficients for the sinusoidal and polynomial regression models. To test the hypothesis that there was no effect of ram type, MANOVA was performed on the regression coefficients $b_0, b_1, \ldots b_q$. Parallel treatment effects were determined by MANOVA on $b_1, b_2, \ldots b_q$. Intercept differences were tested by a univariate analysis of variance for B_0. Ram ranks for change in scrotal circumference and body weight were analyzed by the Wilcoxon (Mann-Whitney) test (Steel and Torrie, 1960).

Results

Scrotal circumferences for seasonal rams changed at a greater rate each month during two complete circannual photoperiods ($P<.01$, figure 1, appendix table 4). Seasonal rams had maximal scrotal circumferences

during September of each year (34.18 and 34.39 cm). In contrast, nonseasonal rams had maximal scrotal circumferences of 30.74 cm in November of the first year and 31.59 cm in October of the second year. The seasonal rams had minimal scrotal circumferences during March of both years (29.07 and 28.58 cm) and the minimal scrotal circumferences for nonseasonal rams were 29.83 cm during April of the first year and 30.28 cm during March of the second. The only time of year that nonseasonal rams had larger scrotal circumferences than seasonal rams was from February through April (figure 1).

The classification of the individual rams based on the degree of scrotal circumference change from fall to spring was essentially the same for both years. The Spearman correlation coefficient for ram ranks between years was .82 ($P<.001$). Initially, when ranked from the least scrotal circumference change to the greatest, nonseasonal rams ranked 1st to 7th, while seasonal rams were 8th to 15th. Except for two rams, all seasonal rams remained in the upper half, and nonseasonal rams remained in the lower half when ranked on scrotal change the second year. The rams were not reclassified based on scrotal change during the second year, but maintained their seasonal and nonseasonal designation from the first year.

The influence of season on intensity of inguinal cutaneous hyperemia (ICH) is summarized in figure 2 and appendix table 5. Maximal ICH intensity preceded maximal scrotal circumference by one month for both ram classes. The ICH intensity profiles were different for the two ram classes ($P<.05$). Seasonal rams had maximal ICH intensity prior to nonseasonal rams during May to August of the first year and less ICH during the subsequent October to May. The quantity of ICH was also

affected by ram class (P<.05, figure 3, appendix table 5). Nonseasonal rams had a larger area of ICH during the fall which was also the time of maximal ICH intensity (figure 3).

Nonseasonal rams had heavier body weights throughout the study (P<.05, figure 4, appendix table 6). However, there were no significant differences in seasonal weight changes between the two ram classes. Body condition also tended to be greater (P<.10) for nonseasonal rams during the two year study (figure 5, appendix table 6).

Concentrations of testosterone in serum were compared between each ram class during April, July, October and January. Prior to the GnRH infusion, nonseasonal and seasonal rams had similar concentrations of testosterone during April, July and October (table 1). In January, nonseasonal rams had greater testosterone in serum than seasonal rams (4.24 vs 2.53 ng/ml, P<.05). Average concentrations of testosterone in serum in response to GnRH infusion were similar for both classes of rams during April, July and October (figures 6,7 and 8). During January (figure 9), the intercept was greater (P<.05) for nonseasonal rams but the LH response curves to both infusions of GnRH were parallel for both ram classes. Overall, serum testosterone concentrations were very similar between seasonal and nonseasonal rams except during January, when seasonal rams had reduced (P<.05) testosterone before GnRH infusion. However, seasonal and nonseasonal rams had similar increases in testosterone after GnRH, even in January.

A comparison between months for nonseasonal rams indicated pre-GnRH concentrations of testosterone in serum were similar during April, July and January (table 1) but less than concentrations in October (3.49, 4.20, 4.24 versus 6.41 ng/ml, respectively, P<.01). Concentrations of

testosterone after GnRH in October and July were greater than the responses during April or January (figure 10, P<.01). Concentrations of testosterone after GnRH in nonseasonal rams were similar in October and July. The mean testosterone concentrations in serum after infusion of GnRH for both ram classes are presented in appendix table 8.

Variation between months in serum testosterone concentrations for seasonal rams were similar to those for nonseasonal rams (figure 11). Concentration of testosterone before GnRH was greatest during October compared to July, April and January (5.69 versus 3.99, 3.29, 2.50 ng/ml, respectively, table 1, P<.01). Except for the difference in intercept, concentration of testosterone after infusion of GnRH were similar during October and July. Testosterone concentrations after GnRH in April and January were less than that observed in October (P<.01).

Concentrations of LH in serum were compared between ram classes during April, July, October and January. Nonseasonal rams had greater (P<.05) serum LH concentrations than seasonal rams during October and January (table 1). In April and July, nonseasonal rams tended to have greater serum LH, however, the difference was not significant. Seasonal trends were evident within each ram class for serum LH concentrations prior to GnRH infusion. Concentrations of LH were greatest in April (P<.05) followed by a decline in July for both ram classes. Nonseasonal rams reached a minimal concentration of LH in July and LH gradually increased through October and January (table 1). In contrast, concentrations of LH in seasonal rams continued to decline until October and remained at low concentrations in January (table 1).

Nonseasonal rams had greater concentration of LH during spikes than seasonal rams in April (P<.05) and October, but the ram classes had

similar concentrations during July and January (table 1). The magnitudes of the LH spikes for nonseasonal rams were greatest ($P<.05$) during April and then declined to similar concentrations during July, October and January (table 1). The magnitudes of LH spikes for seasonal rams were greater ($P<.05$) for April and July than October and January (table 1).

Mean LH concentrations in serum after infusion of GnRH are presented in appendix table 7. The increase in LH following the first and second infusions with GnRH were similar between classes of rams (table 1) during April. In addition, the LH response curves were similar for both seasonal and nonseasonal rams after the initial infusion of GnRH and following the second infusion 1 h later (figure 12).

In July, nonseasonal and seasonal rams had similar increases in serum LH concentrations following the initial infusion of GnRH, but seasonal rams had the greater increase in LH concentrations following the second infusion (table 1, $P<.11$). Within nonseasonal rams, the LH concentration in serum in response to the second infusion of GnRH was not greater than the first infusion of GnRH. Within seasonal rams the LH response to the second infusion of GnRH was greater than the first infusion during July (table 1, $P<.05$). The decrease in serum LH concentrations following the initial and second LH response to GnRH was very similar between the two ram classes (figure 13).

The response in serum LH to the first treatment with GnRH was less for seasonal rams in October ($P<.05$) than for nonseasonal rams (table 1) but the LH response to the second infusion of GnRH was similar for both classes of rams (table 1). Within ram class, the response of LH concentration in serum following the second infusion GnRH compared to

the first infusion was similiar for nonseasonal rams but greater (P=.13) for seasonal rams. Nonseasonal rams maintained serum LH at a greater concentration following the second infusion of GnRH than seasonal rams (figure 14, P<.05).

Nonseasonal rams had a greater (P<.05) LH response than seasonal rams to the first infusion of GnRH in January and the response was similar for both classes of rams following the second infusion (table 1). The difference in response of serum LH to the second versus the first infusion of GnRH was similar within both ram classes (table 1). The decrease in serum LH following GnRH was also similar between the two ram classes during January (figure 15).

The difference in seasonal influence on serum LH concentrations in response to GnRH was also evident when the different months were compared within nonseasonal rams (figure 16) and seasonal rams (figure 17). Nonseasonal and seasonal rams had greatest LH responses (P<.05) to the first infusion of GnRH during April and the LH response was similar during July, October and January (table 1). The LH response to the second infusion was maximum (P<.05) during April for nonseasonal rams and during April and July for seasonal rams. The serum LH response of the first compared to the second infusion of GnRH was similar for all months in nonseasonal rams. In contrast, the LH response to the second infusion of GnRH was greater than the first during July (P<.05) and October (P=.13), for seasonal rams (table 1).

Discussion

Rams classified as seasonal or nonseasonal based on change in scrotal circumference from October to April of one year, were classified similarly the following year. The overall scrotal circumference changes were similar to previous breed comparisons (Skinner and van Heerden, 1971; Islam and Land, 1977; Dyrmundsson et al., 1981; Mickelsen et al., 1982; Sanford and Yarney, 1983; Tulley and Burfening, 1983;). However, there was an interaction for scrotal circumference between ram classification and month. Seasonal rams had the largest scrotal circumference during the fall months, but the smallest during the early winter months. During the normal fall breeding season, rams less responsive to season had smaller scrotal circumferences.

Inguinal cutaneous hyperemia (ICH) varied with season in both ram classes. The intensity of coloring within the inguinal area was similar for the two ram classes, but seasonal rams had a reduced area of ICH. Both ram types had a seasonal pattern in ICH, but nonseasonal rams generally had greater intensity and quantity of ICH throughout the year. Inguinal cutaneous hyperemia is associated with testosterone concentrations in serum (Lincoln, 1976). The maximal concentrations of testosterone in serum occurred in October, which coincided with maximal area of inguinal cutaneous hyperemia but not the maximal intensity. The greatest intensity occurred during August and September, months when no serum samples were collected.

The seasonal change in body weight and condition score were expected since the rams were maintained under pasture conditions and subjected to seasonal changes in pasture forage. However, two sources of evidence

indicate that change in scrotal circumference was not strongly influenced by change in body weight. Nonseasonal and seasonal rams were similar in body weight change, but the scrotal circumference profiles were distinctly different between the two ram types. In addition, change in scrotal circumference for individual rams was consistant from the first year to the second (Spearman rank correlation=.82, $P<.001$) but individual change in body weight was not consistant (Spearman rank correlation=-.39, $P>.5$)

In agreement with previous reports (Schanbacher and Ford, 1976; Sanford et al., 1978; Barrell and Lapwood, 1978/1979; Sanford and Yarney, 1983; Barenton and Pelletier, 1983; Occhio and Brooks, 1983) concentration of testosterone in serum was maximal for rams in October. The increase during the fall in scrotal circumference for both ram classes coincides with increased concentrations of testosterone in serum. These findings agree with those of Courot and Ortavant (1981) which indicate a positive relationship between testicular size and testosterone concentration. However, the large increase in scrotal size of seasonal rams compared to nonseasonal rams during October is not reflected in greater serum testosterone concentrations. The only difference between the two ram classes was in January, nonseasonal rams had greater serum testosterone concentrations than seasonal rams. The scrotal circumferences of seasonal rams were decreasing at a greater rate during January than nonseasonal rams.

Maximal LH concentrations were in April for both seasonal and nonseasonal rams. Early reports indicated that maximal LH concentration coincided with high levels of serum testosterone in the fall (Johnson et al., 1973; Schanbacher and Ford, 1976). However, subsequent reports

suggest that the increase in LH concentrations occurs prior to the increase in testosterone concentrations (Sanford et al., 1978; Barrell and Lapwood, 1978/1979). Lincoln and Short (1980) demonstrated that LH is released infrequently as large surges prior to the fall breeding season and as frequent small surges in the fall breeding season.

Following maximal concentration of serum LH in April, both ram classes had reduced LH during July, October and January. In contrast to seasonal, nonseasonal rams had progressively increasing concentrations of LH in serum after July, while seasonal rams had minimal concentrations. The progressive increase in LH of nonseasonal rams through the fall suggests a difference in gonadotropin support of testes between seasonal and nonseasonal rams during October and January.

The ability of an initial infusion of GnRH to influence the release of LH following a second infusion of GnRH has been demonstrated in rams (Stelmasiak and Galloway, 1977). The LH responses after the 1st and 2nd infusions were similar in nonseasonal rams during all months. The LH response to the 2nd infusion of GnRH was greater than the response to the 1st infusion in July and October for seasonal rams.

The maximal response of LH concentrations in serum was in April for both ram classes, which agrees with Lincoln (1977). Lincoln studied LH response in Soay rams and found the maximal response was during the period of testicular regression. The maximal response of LH concentrations in serum to 1 ug GnRH was at 15 min, which is earlier than studies that infuse greater quantities of GnRH (Galloway and Pelletier, 1975; Bremner et al., 1976)

In conclusion, testosterone concentrations are greatest in October for both ram classes and the only difference in testosterone

concentrations between the two classes is that seasonal rams have decreased testosterone concentrations in January. LH concentrations in serum are similar for both ram classes in April, when serum LH is maximal, and in July. Following July, concentrations of LH in nonseasonal rams progressively increase through January, while concentrations in seasonal rams decrease. Nonseasonal and seasonal rams also respond to GnRH infusion differently during July and October. Seasonal rams have an increase in serum LH response to a second GnRH infusion compared to the first GnRH infusion, while nonseasonal rams do not. Endocrine changes in seasonal rams agrees with the concept that rams which have extreme changes in scrotal circumference due to season have corresponding changes in endocrine function.

TABLE 1

MEAN SECRETORY PATTERNS OF LH AND TESTOSTERONE IN SERUM DURING APRIL, JULY, OCTOBER AND JANUARY IN NONSEASONAL (N) AND SEASONAL (S) MATURE F_2 FINN-DORSET RAMS

Hormone ng/ml	Ram class	April	July	October	January
LH concentration					
Mean	N	3.04[a]	1.24	1.45[b]	1.69[b]
	S	1.86[a]	1.03	.72[b]	.74[b]
Spikes/8h	N	1.88	1.50	2.25	2.38
	S	2.29	1.86	2.57	1.71
Spike magnitude[d]	N	8.92[a]	5.82	4.51[b]	5.67
	S	5.22[a]	4.68[a]	2.49[b]	3.41
LH response to GnRH[e]					
1st infusion	N	32.67[a]	22.69[ac]	24.14[b]	23.00[b]
	S	30.40[a]	17.44[ac]	13.01[b]	17.90[b]
2nd infusion	N	32.86[a]	23.54	21.73	23.07
	S	32.11[a]	32.40[ac]	20.16	24.00
Testosterone concentration					
Mean	N	3.49[a]	4.20	6.41	4.24[b]
	S	3.28[a]	4.18	5.61	2.53[ab]

[a]Concentration within a row are different from October ($P<.05$).
[b]Concentrations in the same column with the same trait are different ($P<.05$).
[c]Response to 1st and 2nd infusion of GnRH are different within seasonal rams ($P<.05$).
[d]Serum LH concentration greater than two standard deviations above individual ram mean LH concentration.
[e]Serum LH concentration 15 minutes following infusion of 1 ug GnRH.

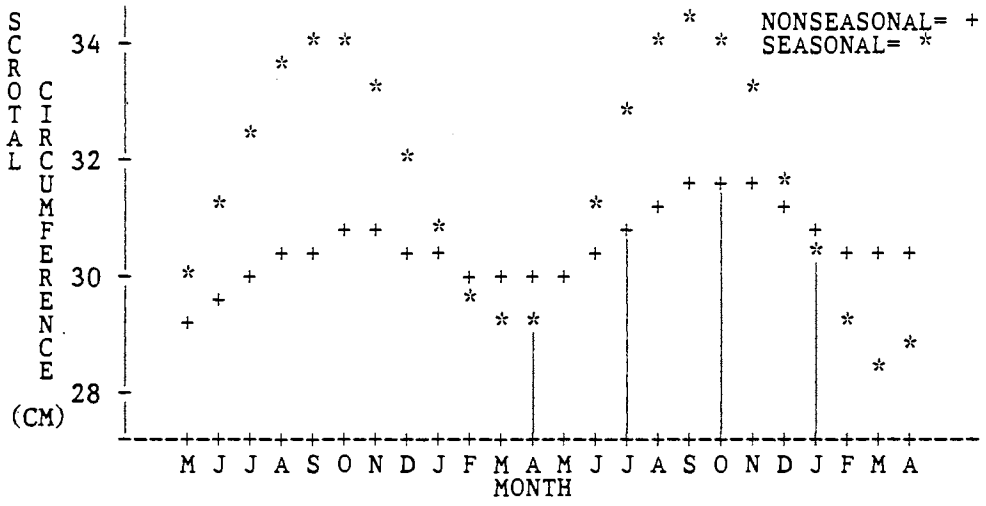

FIGURE 1. SCROTAL CIRCUMFERENCE OF SEASONAL AND NONSEASONAL RAMS SELECTED FOR ENDOCRINE PROFILE ANALYSIS DURING APRIL, JULY, OCTOBER AND JANUARY (|)

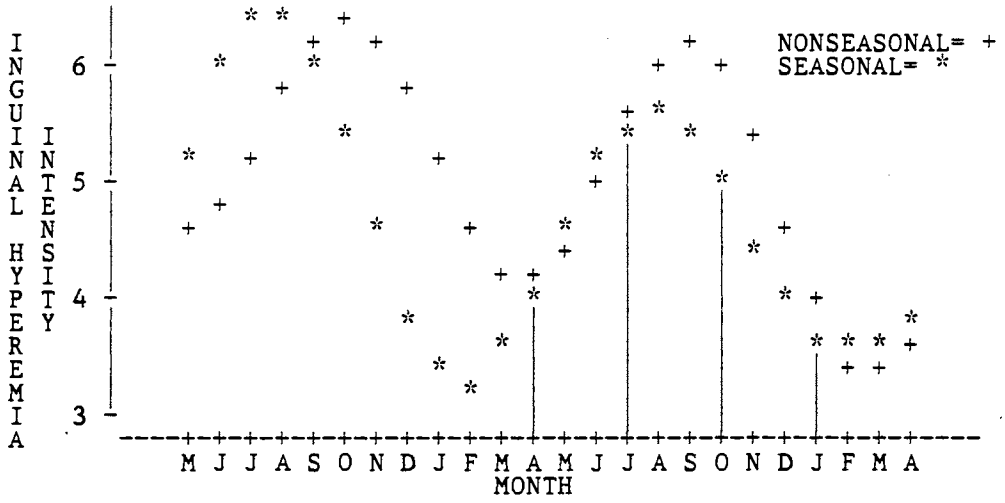

FIGURE 2. INGUINAL HYPEREMIA (INTENSITY) OF SEASONAL AND NONSEASONAL RAMS SELECTED FOR ENDOCRINE PROFILE PROFILE ANALYSIS DURING APRIL, JULY, OCTOBER AND JANUARY (|)

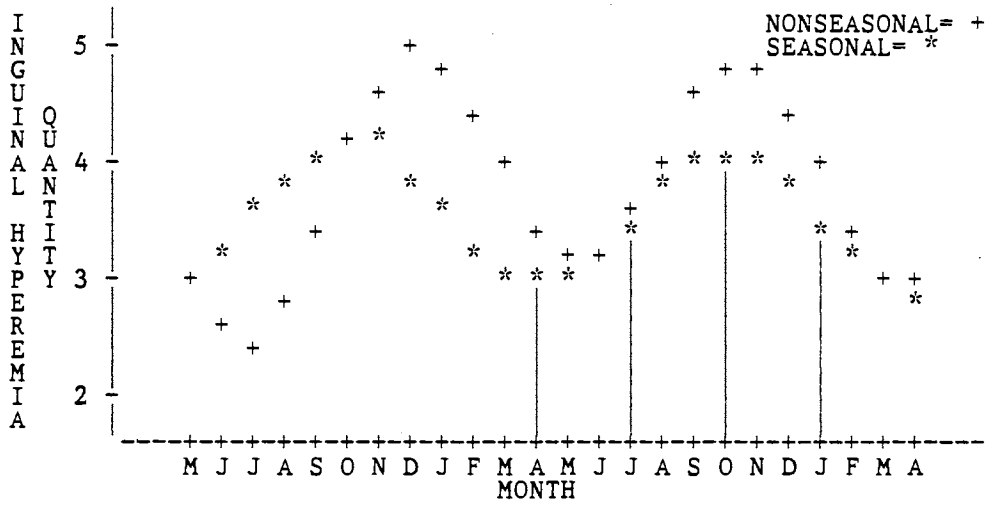

FIGURE 3. INGUINAL HYPEREMIA (QUANTITY) OF SEASONAL AND NONSEASONAL RAMS SELECTED FOR ENDOCRINE PROFILE ANALYSIS DURING APRIL, JULY, OCTOBER AND JANUARY (|)

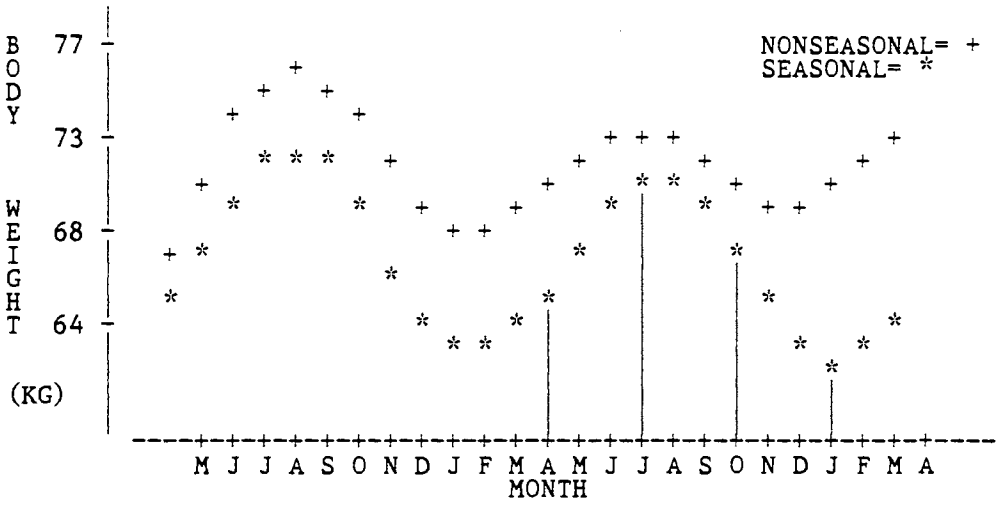

FIGURE 4. BODY WEIGHT OF SEASONAL AND NONSEASONAL RAMS SELECTED FOR ENDOCRINE PROFILE ANALYSIS DURING APRIL, JULY, OCTOBER AND JANUARY (|)

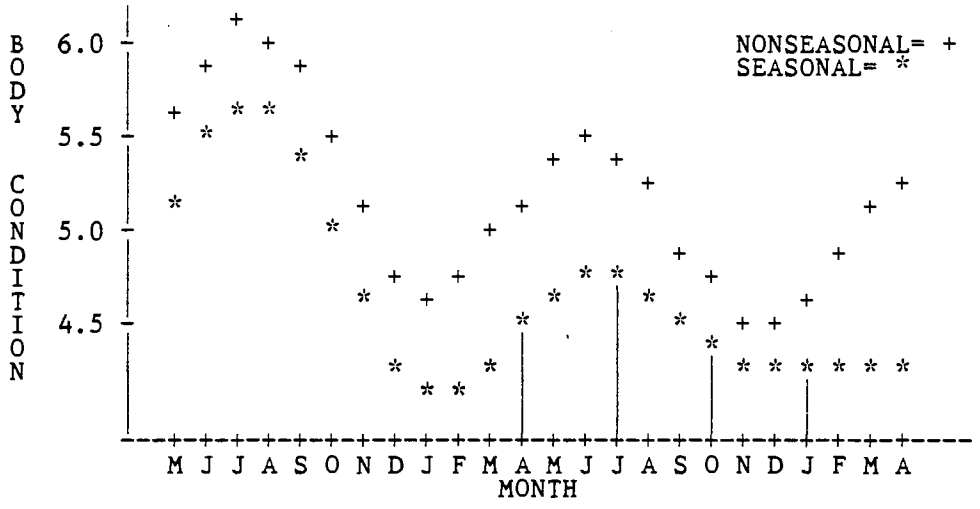

FIGURE 5. BODY CONDITION OF SEASONAL AND NONSEASONAL RAMS SELECTED FOR ENDOCRINE PROFILE ANALYSIS DURING APRIL, JULY, OCTOBER AND JANUARY (|)

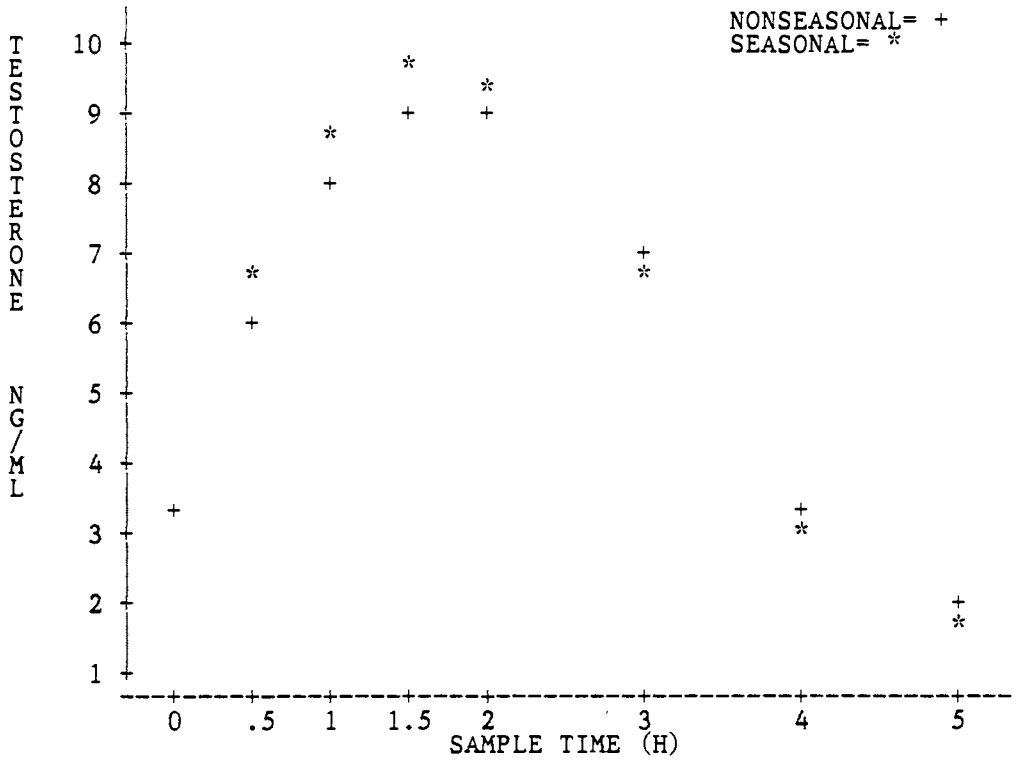

FIGURE 6. CONCENTRATIONS OF TESTOSTERONE IN SERUM AFTER INFUSION OF 1 UG OF GNRH AT 0 AND 1 H DURING APRIL FOR SEASONAL VERSUS NONSEASONAL FINN-DORSET RAMS

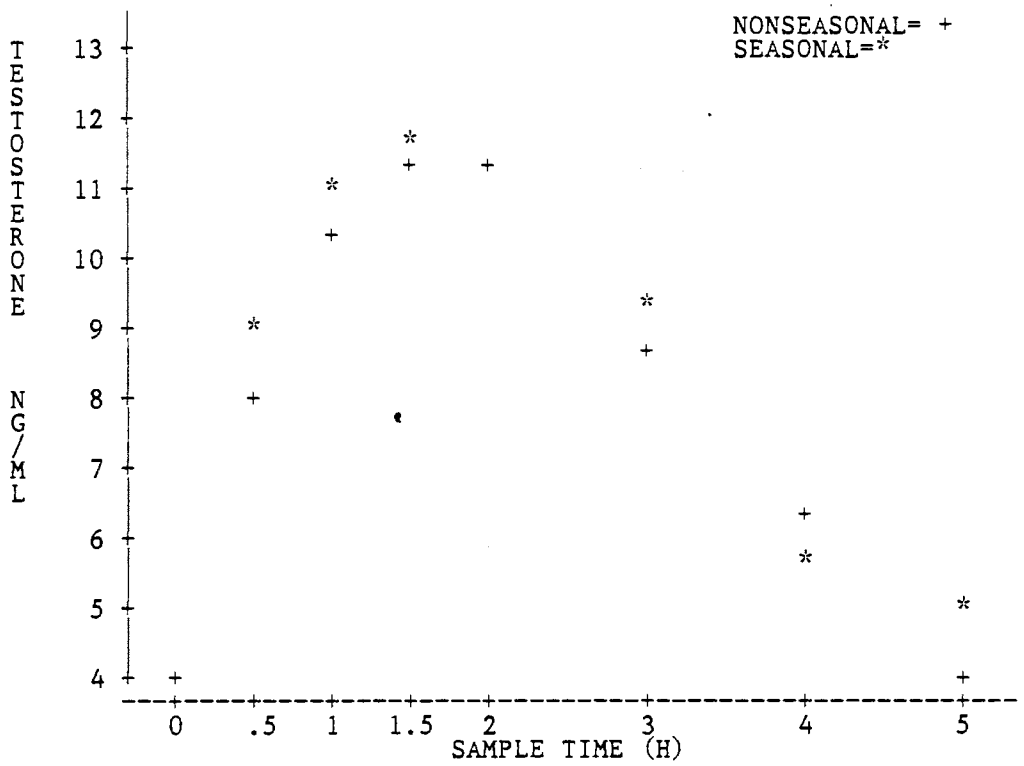

FIGURE 7. CONCENTRATIONS OF TESTOSTERONE IN SERUM AFTER INFUSION OF 1 UG OF GNRH AT 0 AND 1 H DURING JULY FOR SEASONAL VERSUS NONSEASONAL FINN-DORSET RAMS

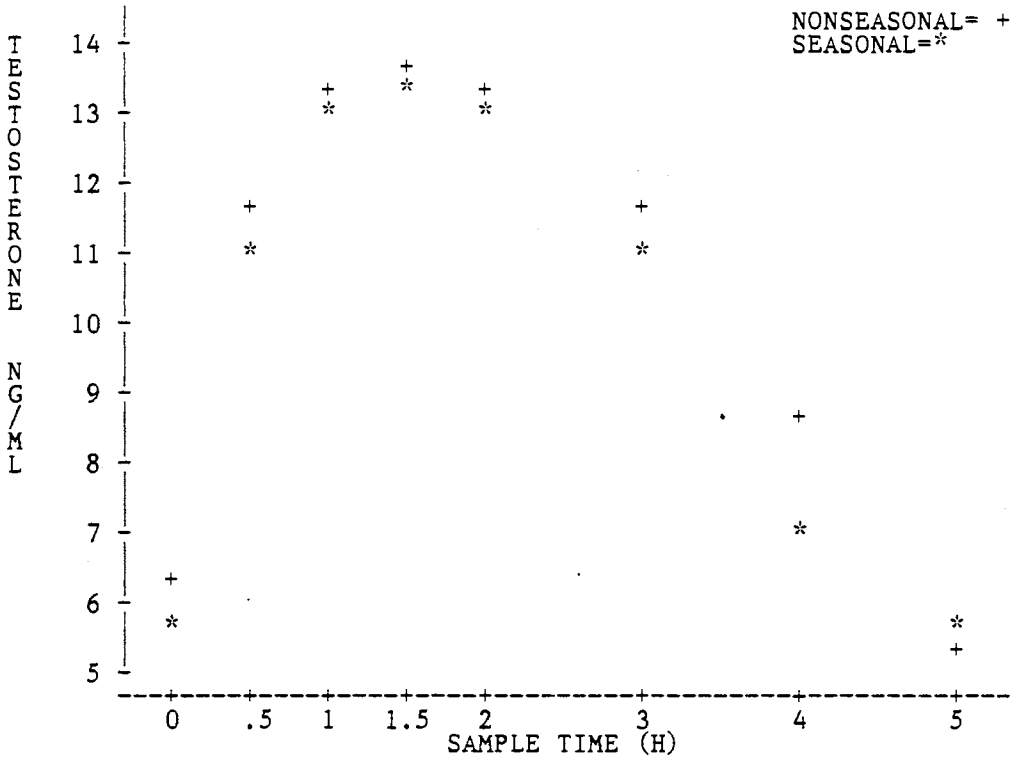

FIGURE 8. CONCENTRATIONS OF TESTOSTERONE IN SERUM AFTER INFUSION OF 1 UG OF GNRH AT 0 AND 1 H DURING OCTOBER FOR SEASONAL VERSUS NONSEASONAL FINN-DORSET RAMS

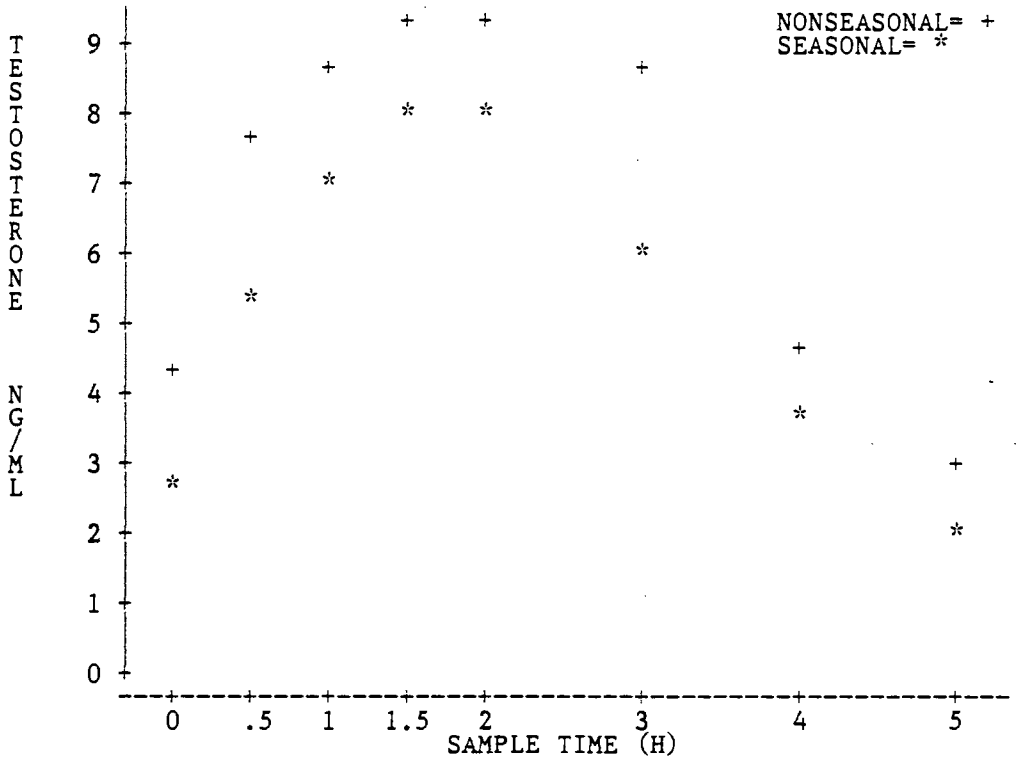

FIGURE 9. CONCENTRATIONS OF TESTOSTERONE IN SERUM AFTER INFUSION OF 1 UG OF GNRH AT 0 AND 1 H DURING JANUARY FOR SEASONAL VERSUS NONSEASONAL FINN-DORSET RAMS

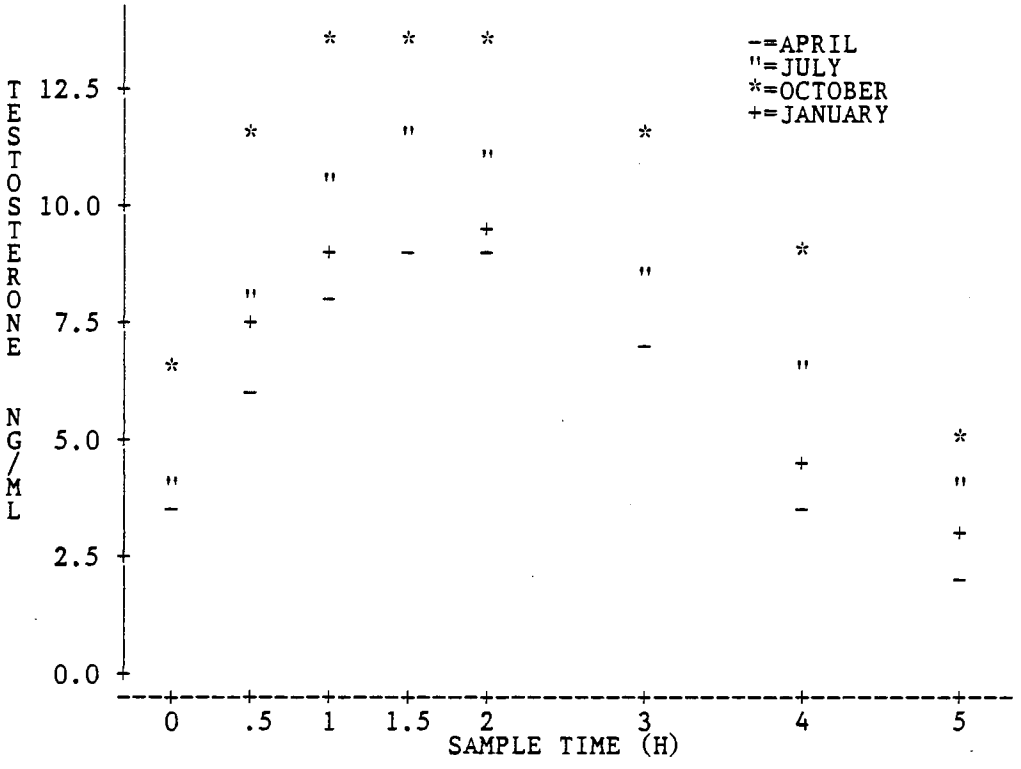

FIGURE 10. CONCENTRATIONS OF TESTOSTERONE IN SERUM AFTER INFUSION OF 1 UG OF GNRH AT 0 AND 1 H DURING APRIL, JULY, OCTOBER AND JANUARY FOR NONSEASONAL FINN-DORSET RAMS

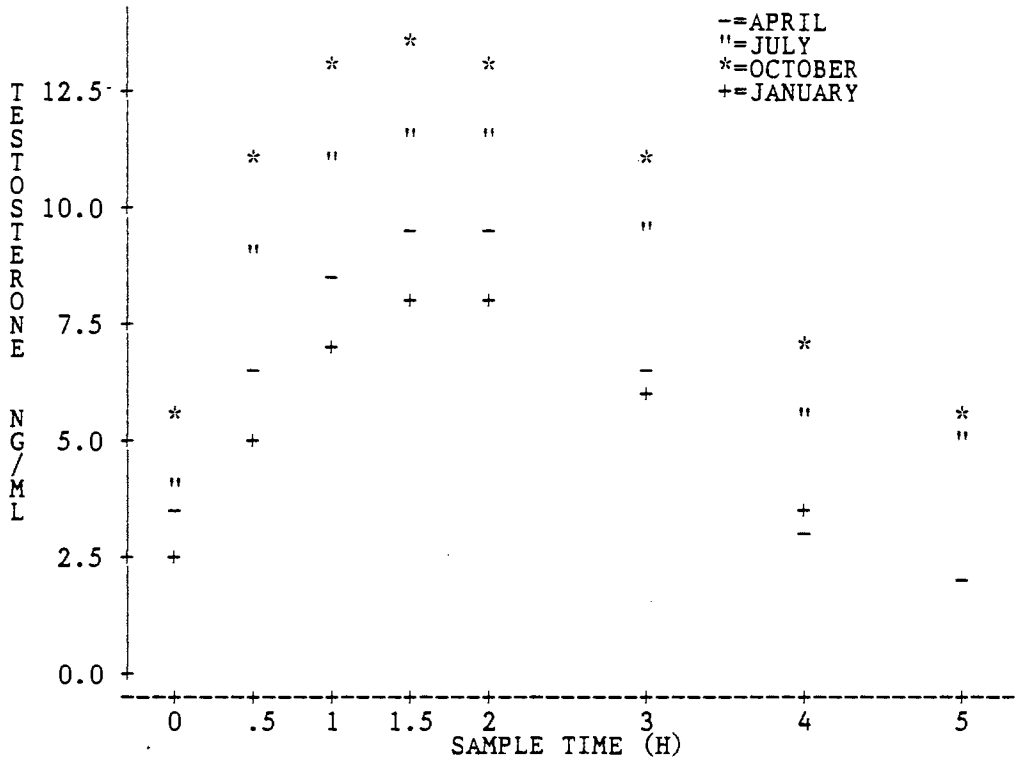

FIGURE 11. CONCENTRATIONS OF TESTOSTERONE IN SERUM AFTER INFUSION OF 1 UG OF GNRH AT 0 AND 1 H DURING APRIL, JULY, OCTOBER AND JANUARY FOR SEASONAL FINN-DORSET RAMS

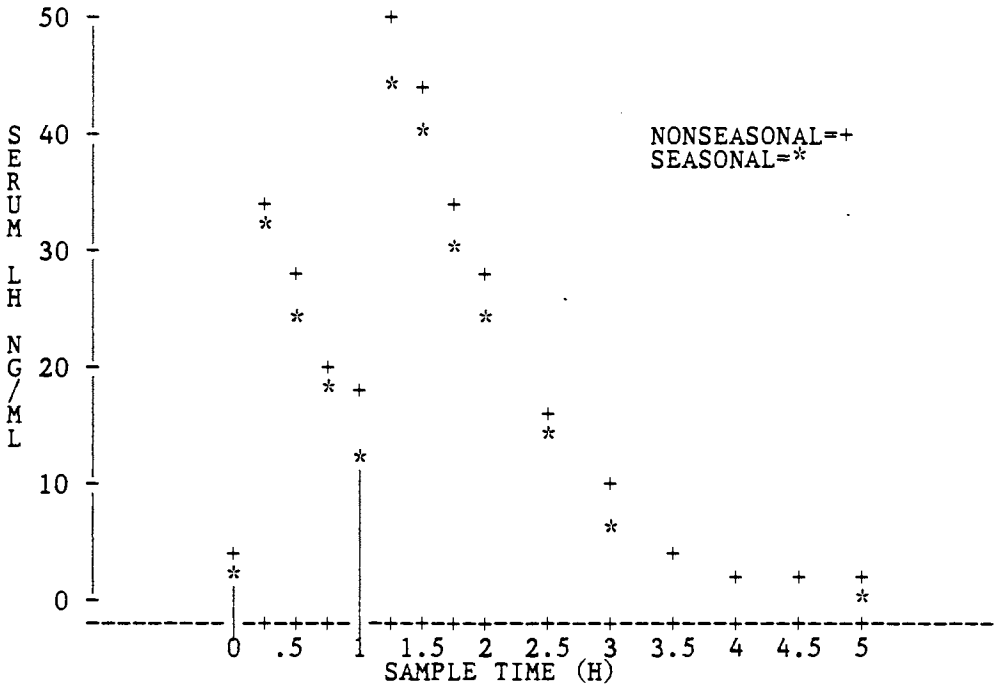

FIGURE 12. CONCENTRATIONS OF SERUM LH AFTER INFUSION (|) OF 1 UG OF GNRH AT 0 AND 1 H DURING APRIL FOR MATURE FINN-DORSET SEASONAL VERSUS NONSEASONAL RAMS

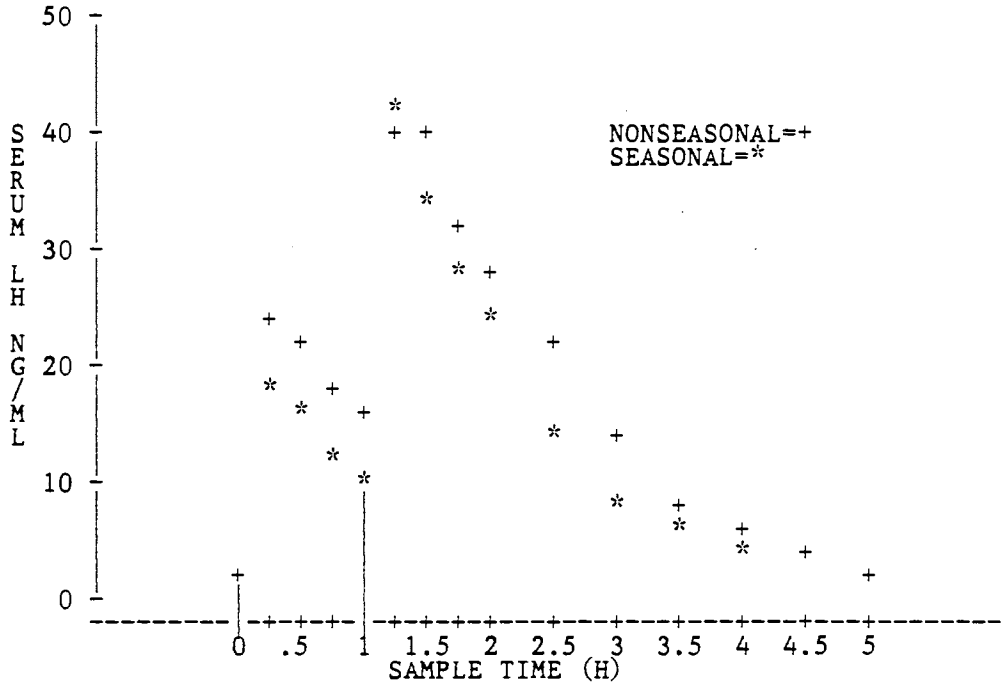

FIGURE 13. CONCENTRATIONS OF SERUM LH AFTER INFUSION (|) OF 1 UG OF GNRH AT 0 AND 1 H DURING JULY FOR MATURE FINN-DORSET SEASONAL VERSUS NONSEASONAL RAMS

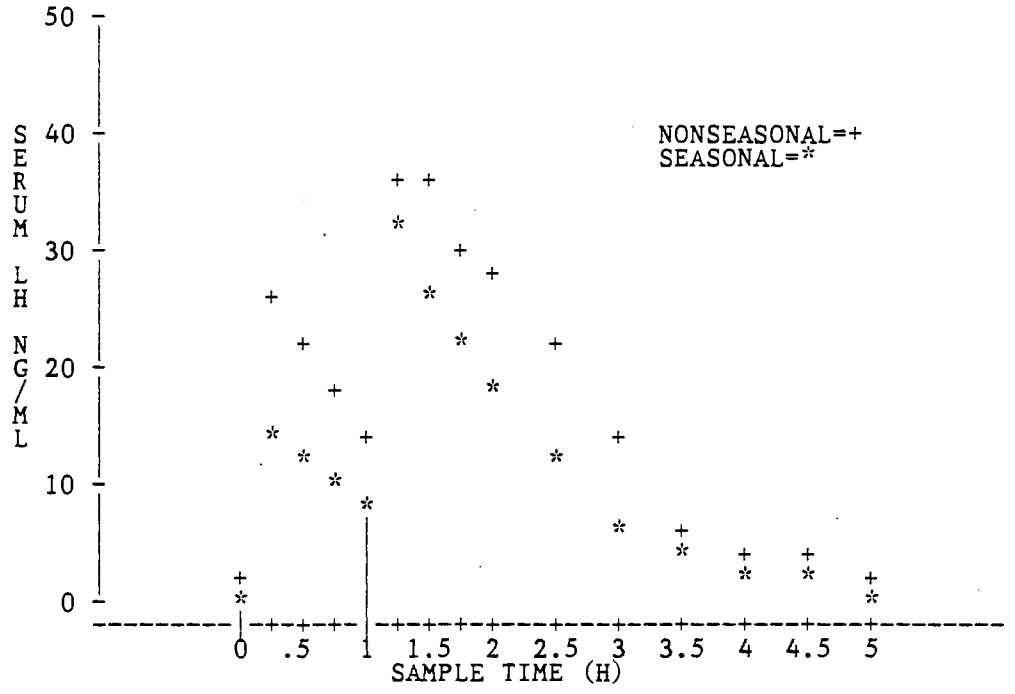

FIGURE 14. CONCENTRATIONS OF SERUM LH AFTER INFUSION (|) OF 1 UG OF GNRH AT 0 AND 1 H DURING OCTOBER FOR MATURE FINN-DORSET SEASONAL VERSUS NONSEASONAL RAMS

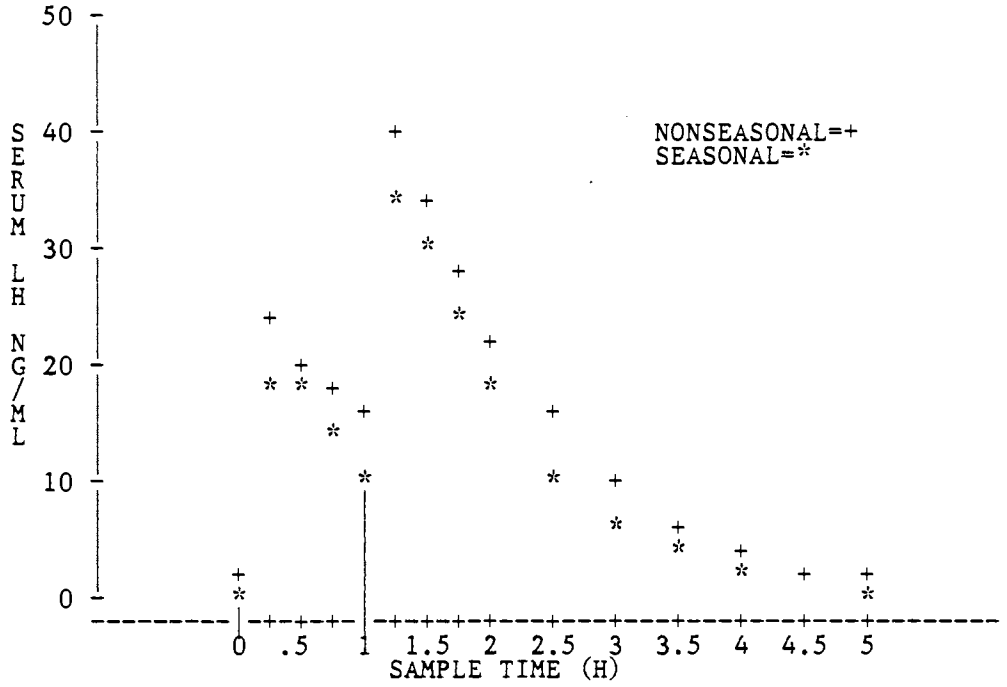

FIGURE 15. CONCENTRATIONS OF SERUM LH AFTER INFUSION (|) OF 1 UG OF GNRH AT 0 AND 1 H DURING JANUARY FOR MATURE FINN-DORSET SEASONAL VERSUS NONSEASONAL RAMS

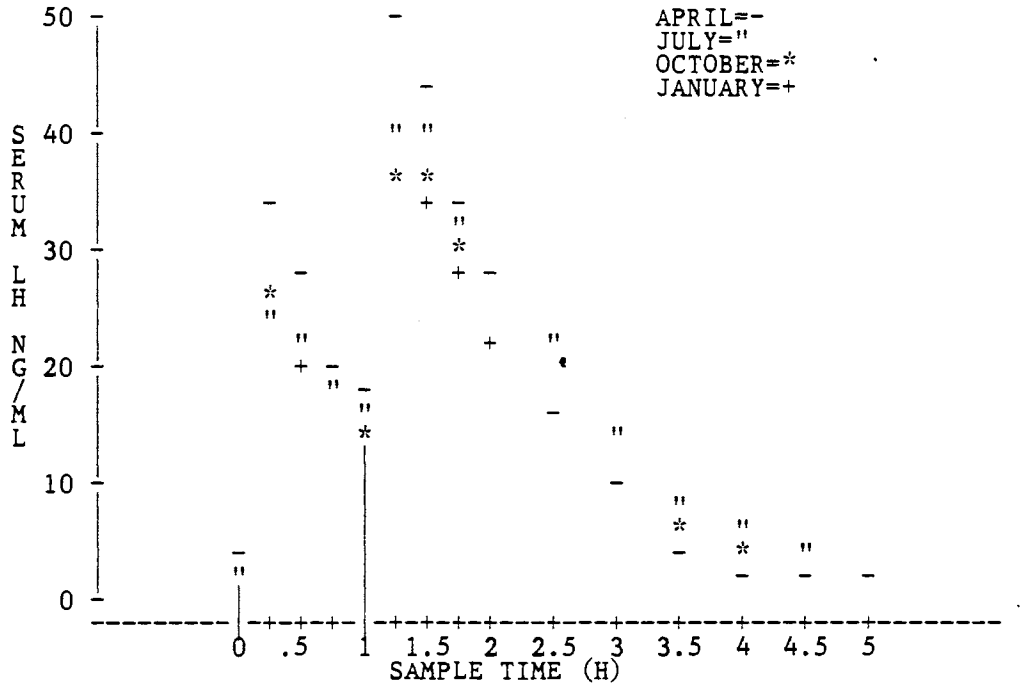

FIGURE 16. CONCENTRATIONS OF SERUM LH AFTER INFUSION (|) OF 1 UG OF GNRH AT 0 AND 1 H DURING APRIL, JULY, OCTOBER AND JANUARY FOR NONSEASONAL MATURE FINN-DORSET RAMS

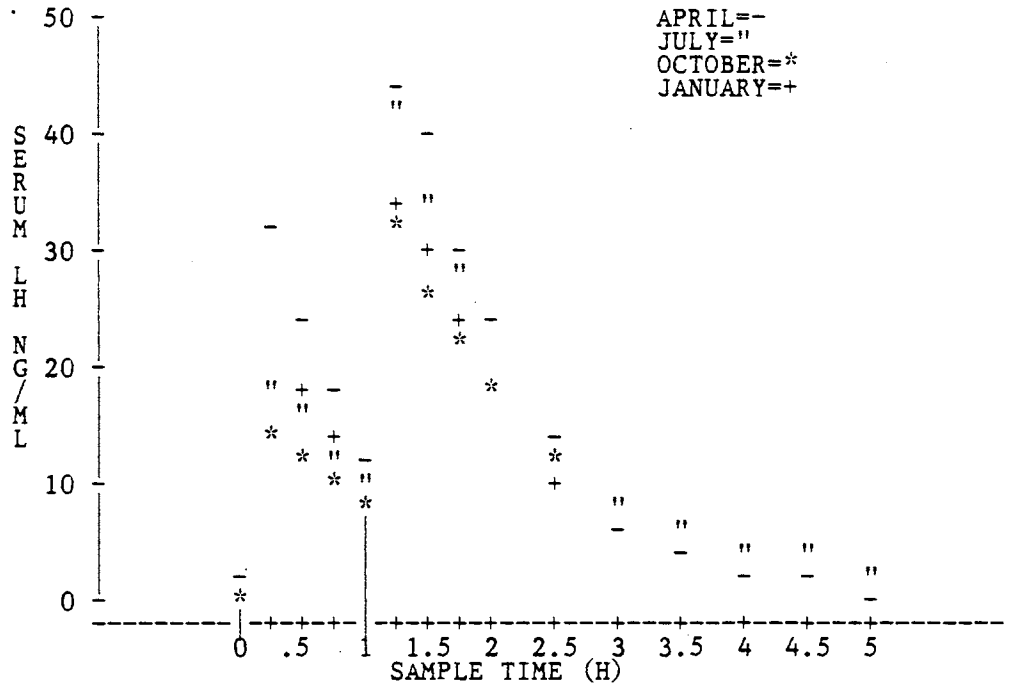

FIGURE 17. CONCENTRATIONS OF SERUM LH AFTER INFUSION (|) OF 1 UG OF GNRH AT 0 AND 1 H DURING APRIL, JULY, OCTOBER AND JANUARY FOR SEASONAL MATURE FINN-DORSET RAMS

CHAPTER IV

MAY-JUNE REPRODUCTIVE PERFORMANCE OF RAMS SELECTED FOR EXTREME OR SLIGHT SEASONAL CHANGES IN SCROTAL CIRCUMFERENCE

Summary

Sixty-four mature Finn x Dorset F_2 rams were classified as seasonal or nonseasonal based on the decrease in scrotal circumference from October to April. The 15 rams with the greatest decreases in scrotal circumference (seasonal) and the 14 rams with the least decreases in scrotal circumference (nonseasonal) were selected during a three year period and each was mated with at least 25 white-faced ewes from May 1 to June 15. Scrotal circumference decrease from October to April was greater ($P<.001$) for seasonal rams ($-3.60 \pm .27$ cm) than for nonseasonal rams ($-0.33 \pm .27$ cm). Nonseasonal rams mated more ewes (48.9 vs 37.0%, $P<.15$) and a greater percentage of the ewes exposed to nonseasonal rams lambed (35.9 vs 21.7%, $P<.05$) compared to seasonal rams. Conception rate (percentage of ewes mated that lambed) was also greater (73.4 vs 58.6%, $P<.05$) for ewes mated to nonseasonal compared to seasonal rams. The number of lambs per ewe lambing was not influenced by ram classification ($\bar{x} = 1.19$), but ewes exposed to nonseasonal rams lambed an average of 4 days earlier than ewes mated by seasonal rams ($P<.05$). These data indicate that the response of scrotal circumference to season varies between rams. Rams with testes that responded less to daylength (nonseasonal rams) tended to be more aggressive during the

breeding season and had greater conception rates. In conclusion, Finn X Dorset rams with greater decreases in scrotal circumference from October to April have reduced fertility during May and June breeding.

Introduction

Sheep alternate between periods of infertility and fertility on a circannual cycle (Yeates, 1949; Hafez, 1952). These annual changes occur in rams as well as in ewes (Mickelsen et al., 1982; Sanford and Yarney, 1983; Tulley and Burfering, 1983). Change in scrotal circumference is one trait that is a direct consequence of the photoperiodic effects on endocrine functions (Lincoln and Short, 1980) and selection of rams with minimal changes in scrotal circumference during the year may expand the reproductive periods of sheep (Land, 1978). This experiment was designed to determine the monthly changes in scrotal circumference of mature F_2 Finnish Landrace x Dorset rams and to evaluate if the degree of change in scrotal circumference was related to mating ability and fertility during May and June breeding.

Materials and Methods

During three consecutive May to June breeding seasons, a flock of 450 ewes consisting primarily of Rambouillet but also Rambouillet X Dorset, Rambouillet X Dorset X Finnish Landrace and Dorset X Finnish Landrace ewes, and 64 F_2 Finn x Dorset rams were used. Prior to the breeding season, the ewes were managed similarly in native bermuda pastures each year and randomly allotted to single ram breeding pastures by breed type, previous lambing history and condition score. Ewes were

only exposed to rams during May-June breeding for the first and second years, but ewes that were not mated during the 1982 spring breeding season were mated to lamb during January and February, 1983. This accounted for 79% of the total ewes exposed during May-June, 1983. Each year, rams were individually exposed to ewes (n=27 to 29) from May 3 to June 15.

During the three year period, 29 F_2 Finn x Dorset rams were selected from 64 rams based on the degree of scrotal circumference change from October through March. The degree of change was calculated by subtracting the mean March-April (Spring) scrotal circumference from the mean October-November (Fall) scrotal circumference during the seven months prior to the May-June breeding season. Rams that had the greatest decrease in scrotal circumference from fall to spring were classified seasonal and rams with the least change were classified nonseasonal.

Scrotal circumference and structural soundness were evaluated monthly and only rams greater than 18 months of age and structurally sound were used. Different rams were evaluated each year. Two independent scrotal circumference measurements were made on each ram while the ram was resting on his rump. The testes were held firmly in the lower portion of the scrotum and a fiberglass tape measure was used for the measurement. The testes were palpated between scrotal circumference measurements for testicular and(or) epididymidal abnormalities. Rams indicating any abnormality were removed from the study.

Rams were weighed and a body condition score (BCS) was given each month. The BCS scores ranged from one (extremely emaciated) to nine (fat deposits over the lumbar vertebrae and ribs). Each ram was fitted

with a "Sire-Sine" (Mid States Wool, Hutchinson, Kansas) marking harness to monitor daily mating activity.

Mating and lambing dates were recorded and percentage ewes mated, percentage ewes conceived, percentage ewes lambed and lambs per ewe lambing were calculated. Percentage ewes mated and percentage ewes lambed were based on the number of ewes exposed at breeding. Percentage ewes conceived was the percentage of the mated ewes that lambed. Because of reduced fertility during the third breeding season (explanation in Appendix A), lambing dates and lambs per ewe lambing from the third year were not included in the analyses. Least squares means were calculated for scrotal circumference and body weight change. The model used was:

$$\text{Scrotal circumference or Body weight change} = B_0 + B_1 \text{ Ram Class} + B_2 \text{ Year} + B_3 \text{ Ram Class} * \text{Year} + \text{Random Error.}$$

Ewe breeds were equally distributed across ram types and no interactions were present between ram type and ewe breed. All ewes were considered one type for the analysis and were called white-faced ewes. The Wilcoxon (Mann-Whitney) test (Steel and Torrie, 1960) determined the level of significance for differences between ram classes for percentage ewes mated, percentage ewes conceived, percentage ewes lambed, lambs per ewe lambing and average lambing date.

Results

Characteristics of the rams used during the three years are summarized in table 1. Change in body weight from October to April was similar for seasonal and nonseasonal rams during 1981-82 and 1982-83. But during 1983-84, seasonal rams lost 4.36 kg more weight ($p<.05$) than

the nonseasonal rams. Since the rams were selected for extreme changes in scrotal circumference, the scrotal circumference of seasonal rams for three years decreased an average of 3.27 cm more from October to April than did the circumference of nonseasonal rams ($P<.001$). The year by ram class interaction was not significant but change in scrotal circumference in the third year was greater ($P<.05$) than changes during the first two years.

Nonseasonal rams had similar scrotal circumferences in March-April as in October-November during the first two years (table 1). However, during the third year, nonseasonal rams had reduced scrotal circumference ($P<.01$) in March-April compared to the scrotal circumference in October-November. Seasonal rams consistently had smaller scrotal circumferences in March-April when compared to scrotal circumferences the previous fall ($P<.001$).

Reproductive performance for the F_2 Finn x Dorset rams used for the three seasons is summarized by year in table 2. The difference between ram classes for percentage of ewes mated and percentage of ewes lambed was not constant between years (year * ram class interaction, $P<.15$). In 1981 and 1982, nonseasonal rams mated 41.1 and 9% more ewes ($P<.05$), respectively, than seasonal rams and 34.5 and 17.4% more ewes ($P<.05$) lambed in the fall. The reproductive performance was similar between the two ram classes for 1983. Only 7.2% of the ewes exposed to seasonal rams lambed in 1983 and 5.4% of the ewes exposed to nonseasonal rams lambed. Seasonal rams mated 19.8% of the ewes versus 11.9% for the nonseasonal rams. Nonseasonal rams had greater ($P<.05$) conception rates for all three years of the study (11.3, 19.9, and 8.6%).

During the three years, nonseasonal rams found and mated 11.9% more estrus ewes ($P<.15$) than seasonal rams. Plus, nonseasonal rams settled 14.8% (conception rate) more of the ewes mated ($P<.05$) compared to seasonal rams. Overall, 14% more ($P<.05$) ewes mated with nonseasonal rams and lambed in the fall compared to seasonal rams. Ewes exposed to nonseasonal rams also lambed on an average of four days earlier ($P<.05$) than the ewes bred to seasonal rams; however, the number of lambs born per ewe that lamb was not influenced by class of rams.

Discussion

A distinct advantage existed with May-June breeding for those rams that had less change in scrotal circumference from October to April the first two years. Data from 1983 does not disprove the idea that nonseasonal rams are more fertile, but cannot offer evidence that supports the concept because of low fertility for both ram classes. Overall, seasonal rams minimal fertility during all three years of the study.

The reduced fertility of nonseasonal rams during the last year may be related to the extra scrotal circumference loss by the rams during the winter of 1983 and(or) the ewes may have been anestrous since over 70% of the ewes lambed during January and February. If the reduced reproductive performance was related to anestrous ewes in 1983, there was less opportunity for the more fertile rams to mate and the difference between seasonal and nonseasonal rams would be expected to be smaller in 1983.

Changes in scrotal circumference measurements between fall and spring identify rams that were more fertile during May to June. As

suggested by Land (1973), by selecting more fertile rams and mating the rams to ewes that will breed in the spring, progress should be made towards increased reproductive performance with spring matings.

Scrotal circumference is currently the best external measurement to evaluate the response of rams to duration of photoperiod (Islam and Land, 1977; Lincoln and Short, 1980; Mickelsen et al., 1982; Sanford and Yarney, 1983; Tulley and Burfering, 1983). These data indicate individuals exist within breeds that have different reproductive response to duration of photoperiod. If this is a heritable trait, selection of rams for minimal seasonal changes in scrotal circumference may improve yearlong reproductive performance of sheep.

TABLE 1

LEAST SQUARES MEANS FOR SCROTAL CIRCUMFERENCE AND BODY WEIGHT CHANGES FROM OCTOBER THROUGH APRIL FOR SEASONAL AND NONSEASONAL RAMS THAT WERE EXPOSED TO WHITE-FACED EWES DURING MAY AND JUNE

Year	Ram type	No. rams	Average change: Scrotal circumference (cm)	Average change: Body weight (kg)
1981[b]	Seasonal	3	-2.69	10.91
	Nonseasonal	4	.04	15.23
1982[b]	Seasonal	5	-2.50	9.55
	Nonseasonal	4	.24	9.32
1983[c]	Seasonal	7	-5.60	-10.18
	Nonseasonal	6	-1.27	-5.82
Overall	Seasonal	15	-3.60	3.41
	Nonseasonal	14	-0.33	6.23

[a]Average change equals the average October-November measurement of scrotal circumference and body weight minus the average March-April measurement.
[b]Scrotal circumference differ between seasonal and nonseasonal rams within year ($P<.01$).
[c]Scrotal circumference and body weight differ between seasonal and nonseasonal rams ($P<.05$).

TABLE 2

REPRODUCTIVE PERFORMANCE OF SEASONAL AND NONSEASONAL F_2 FINN X DORSET RAMS EXPOSED TO WHITE-FACED EWES DURING MAY AND JUNE

Year	Ram type	No. rams	No. ewes exposed	% ewes mated	% ewes lambed	% ewes conceived
1981	Seasonal	3	82	54.3	31.7	57.8
	Nonseasonal	4	115	95.4	66.2	69.1
1982	Seasonal	5	134	47.8	33.6	70.3
	Nonseasonal	4	108	56.8	51.0	90.2
1983	Seasonal	7	167	19.8	7.2	36.4
	Nonseasonal	6	168	11.9	5.4	45.0
Overall	Seasonal	15	383	37.0	21.7[a]	58.6[a]
	Nonseasonal	14	391	48.9	35.9[a]	73.4[a]

[a]Means in the same columns differ ($P<.05$).

CHAPTER V

SUMMARY AND CONCLUSIONS

While I reviewed studies conducted by R. B. Land and co-workers in the United Kingdom, I became aware of the large amount of variation that existed for scrotal circumference in rams and the relative changes in scrotal circumference that occurred over a period of months. Seasonal trends were very apparent for scrotal circumference and breed comparisons suggested that change in scrotal circumference throughout the year was a reliable indicator of the physiological response of a ram to the photoperiod.

A review by Lincoln and Short (1980) confirmed that enough was known about changes in scrotal circumference in the ram to incorporate scrotal circumference measurements into efforts to develop a prolific line of sheep based on a Dorset and Finnish Landrace foundation that would breed readily during May and June in Oklahoma.

Initially, scrotal circumferences were measured on older F_1 Finn X Dorset rams at El Reno, Oklahoma that were used for the production of F_2 progeny. Within this group of rams, a consistent pattern of scrotal circumference change developed over the years. The subsequent methods for evaluation of F_2 rams were derived from the early observations made on the mature F_1 rams. Maintaining a large group of healthy rams was difficult. Epididymitis, internal parasites and fighting reduced ram numbers by over 50%.

Although F_2 rams were born in the fall and spring, the majority of F_2 rams utilized for my studies were born during the spring of 1980 and 1981. Scrotal circumference was measured on rams from weaning to over three years of age. The most difficult aspect of the study was determining how to classify rams so change in scrotal circumference could be evaluated.

The majority of F_1 rams had maximal scrotal circumferences during October and November and scrotal circumferences decreased at various rates starting in December. Minimal scrotal circumferences occurred from January through March. I decided to use the average scrotal circumference for October and November minus the average scrotal circumference for March and April to separate the F_2 rams into two classes. Seasonal rams were those with the greatest change in scrotal circumference and nonseasonal rams were those with the least change.

Although this classification system clearly produced two distinct ram types, a note of caution must be expressed. I only evaluated the extremes of the rams in the herd. The one type of ram that could be classified incorrectly with this system is the ram that had an extreme decline in scrotal circumference in December and January, but regains scrotal circumference so the March value was similar to the October and November average circumference. A February and March average may be an alternative method to classify rams.

Seasonal rams had a consistent annual cycle in scrotal circumference. The majority of nonseasonal rams followed the same 12 month pattern of scrotal change as seasonal rams, but the magnitude of the changes were greatly reduced. Additional selection could have been made within nonseasonal rams since some rams had cycles that

approximated six months, while four rams had no seasonal pattern of monthly change in scrotal circumference.

There was a difference in fertility between the two classes of rams. Seasonal rams had minimal fertility during May and June. Nonseasonal rams generally had greater fertility than seasonal rams during May and June, but fertility was less than that which would be expected during the fall. Nonseasonal and seasonal rams should be evaluated at other months of the year to confirm seasonal fertility differences.

The annual changes in scrotal circumference also reflected a difference in the endocrine system of the two classes of rams. The reproductive cycle of both classes of rams was timed for maximal fertility during the fall. Maximal concentration of testosterone during October allows maximal support of androgen dependent tissues (i.e., inguinal cutaneous hyperemia) and sexual behavior during the fall breeding season.

April was the month when rams had the greatest concentrations of LH in serum. The reason for maximal LH concentration to occur in April is unclear. By extrapolating information from research obtained from Soay rams (Lincoln and Short, 1980) and Suffolk ewes (Karsh et. al, 1984), we can speculate on what mechanisms are involved. Soay rams go through four distinct testicular phases, regressed, developing, developed and regressing. Finn X Dorset rams only have three phases, developing, developed and regressing. No period of sustained testicular regression occurs.

LH is released in conspicuously large surges with high amplitudes prior to an increase in scrotal circumference in the Soay ram. Unlike

the Finn X Dorset ram, the Soay ram does not have greater mean concentration of LH in serum during this period. The difference between the two breeds could be in the ability of the pituitary to produce LH. Therefore, when GnRH is released in the Soay ram only the initial response is great during the testicular regressed phase, a phase the Finn X Dorset does not have. In the Finn X Dorset ram, the pituitary may maintain LH production so even infrequent releases of GnRH may affect mean concentration of LH in serum.

In those breeds of sheep which undergo complete gonadal regression during the nonbreeding season, a steriod independent system may prevail for regulation of the neuroendocrine axis. In more domesticated breeds, complete gonadal regression does not occur and steriod production can interact with the neuroendocrine axis. Therefore, if Finn X Dorset rams depend on steriod regulation, the low concentrations of testosterone during April may allow the increased concentration of LH in serum.

A critical test of difference between seasonal and nonseasonal rams was the infusion of two 1 ug doses of GnRH. Endogenous GnRH release is apparently less during April for nonseasonal rams and during April and July for seasonal rams since maximal response of serum LH to the infusion of GnRH was during these months. Further insight can be gained into the LH synthetic activity of both ram classes by comparing the serum LH response to the second GnRH infusion to that after the first.

In the Soay ram, the response in serum LH to the second infusion of GnRH is the same as the first during periods of maximal LH synthesis and secretion. Nonseasonal rams had a similar response of LH in serum

during all four months tested, but seasonal rams only had such a response during April and January. During testicular regression in the Soay ram, the second GnRH infusion increased serum LH greater than the first treatment, suggestive of decreased LH synthesis and secretion when testes are regressing. Seasonal rams had a similar response of serum LH as the Soay ram from July through October.

A scenario of each ram type would be as follows. The seasonal ram initiates a reproductive cycle prior to April, when scrotal circumference starts to increase. LH synthesis and secretion is maximal during April, but testosterone concentrations are still minimal. Scrotal circumference continues to increase through July, but LH synthesis and secretion has declined compared to April. By October, scrotal circumference and subsequent testosterone concentrations are maximal, but LH synthesis has decreased even more since July and remains minimal through January. Scrotal circumference rapidly decreases after October and testosterone concentration also decreases to complete the reproductive cycle.

Nonseasonal rams follow a similar reproductive cycle as seasonal rams but do not have the extreme oscillations in scrotal circumference. Rather than initiate the reproductiuve cycle prior to April, nonseasonal rams only undergo a revitalization. Just like the seasonal ram, LH synthesis and secretion is great during April and has declined by July. Then, maximal testosterone concentrations coincide with maximal scrotal circumferences during October. But in distinct contrast, nonseasonal rams maintain constant LH synthesis and secretion throughout the year. Therefore, only minor changes in scrotal circumference are noted.

In conclusion, greater variation exists between months in the seasonal effect on scrotal circumference for seasonal rams compared to nonseasonal rams. The sustained reproductive system of nonseasonal rams is capable of greater fertility during May and June, than for seasonal rams. Seasonal rams, when compared to nonseasonal rams have reduced concentration of LH in serum during October and January, reduced testosterone concentration during January and increased response to a second GnRH infusion compared to the first during July and October. Rams, classifed as seasonal or nonseasonal based on change in scrotal circumference, have different physiological responses to change in photoperiod. Individual rams can be identified that are less responsive to photoperiodic cues by recording change in scrotal circumference.

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APPENDIX A

1983 FERTILITY TRIAL MODIFICATIONS

Modification of the Fertility Test of Seasonal Versus Nonseasonal Rams Exposed to White-Faced Ewes the Spring 1983.

The trial (chapter 4) was modified slightly in 1983 because less ewes exhibited estrus during May and early June. The 1983 breeding season was divided into two separate periods, May 3 to June 14 and June 15 to July 8. During the first period, the protocol was the same as that used the previous two years. An attempt was made to induce estrus in the anestrous ewes in mid-June. Only the first period of the 1983 breeding season was analyzed with the data from 1981 and 1982 and was reported in chapter four. The data from period two is presented in this section to offer an explanation for the 1983 results.

Starting on June 15, 1983, ewes which had not been mated in the 12 pastures were randomly divided into three groups in an attempt to determine if the ewes were anestrus. One group (n=6) in each pasture received an injection of 600 IU of pregnant mare serum (PMS) on June 18, a second group (n=6) received an injection of 20 mg progesterone on June 15 and 17 plus an injection of 600 IU of PMS on June 18. The remaining non-mated ewes in each pasture were untreated controls.

Rams had been exposed to ewes for an equivalent of three estrous cycles before June 14, and only 32% of the ewes had been mated. Besides those rams already with the ewes, three seasonal and three nonseasonal rams, that were mated in previous seasons, were selected to help determine if the ewes were anestrus. The group of seasonal rams from

previous years and the group of nonseasonal rams from previous years replaced one seasonal and one nonseasonal ram and were placed in these ewe groups just prior to treatment of the ewes.

Percentage of ewes mated, percentage of ewes lambed, and percentage of ewes conceived of those mated were similar between the controls and progesterone or progesterone plus PMS treated ewes (table 1). The treatment and(or) handling of the ewes did induce more ewes to express estrus (table 2) following injections. However, most of the mating marks only indicated one or two mounts by a ram and did not suggest repeated mating activity.

The treatment regime did not significantly effect the number of ewes lambing for seasonal and nonseasonal rams that were assigned to the 1983 breeding pastures (table 3). Prior to the injection regime, seasonal rams had a greater percentage of ewes mated and subsequently had a greater percentage of ewes lamb. The same trend was evident following the hormone injections. Conception rate increased for both ram classes after June 15. The trio of seasonal and trio of nonseasonal rams performed similar to the reproductive performance of those rams the year before. The nonseasonal rams mated more ewes (100 vs 65.2%, table 3) and had greater conception rates (76 vs 53.3%).

A combination of events probably contributed to the reduced reproductive performance. Approximately two thirds of the ewes lambed during January to March of 1983, thus a percentage of the ewes were anestrus due to a relatively short postpartum period. The rams also had reduced libido. For some unknown reason, the rams lost additional body weight during the spring of 1983 and March-April scrotal circumference was not equivalent to October-November measurements even in the

nonseasonal rams. In the two previous years, the scrotal circumference of nonseasonal rams in the spring was equivalent to their fall scrotal circumference. In conclusion, hormone injections did not induce estrus in a sufficient number of anestrous ewes to evaluate reproductive response of seasonal and nonseasonal rams.

TABLE 1

REPRODUCTIVE PERFORMANCE AFTER PMS OR PROGESTERONE PLUS PMS TREATMENT OF ANESTROUS RAMBOUILLET EWES DURING LATE JUNE, 1983 EXPOSED TO F_2 FINN X DORSET RAMS

Treatment	Date	Total ewes	% ewes mated[1]	% ewes lambed	% ewes conceived[2]
1. PMS	June 18	72	25.0	16.7	66.7
2. Progesterone	June 15	72	33.3	13.9	41.7
Progesterone	June 17				
PMS	June 18				
3. Nontreated		162	30.9	17.9	58.0

[1]21 days (June 19-July 8) following PMS injection.
[2]Percent ewes lambed of ewes mated.

TABLE 2

WEEKLY MATING ACTIVITY AND CONCEPTION OF RAMBOUILLET EWES DURING MAY AND JUNE OF 1983

Week[1]	% ewes mated[2]	% ewes conceived[3]
1	2.2	1.0
2	1.8	0.0
3	4.3	1.8
4	2.6	0.7
5	2.2	0.1
6	2.6	2.3
7	4.9	2.3
8	32.8	3.5
9	9.2	3.6
10	22.0	1.2

[1]Week 1 = May 3-6, subsequent weekly intervals are seven days.
[2]Includes light and questionable mating marks.
[3]Percent ewes lambed of ewes mated.
[4]PMS injection day 1 of week 8.

TABLE 3

THE REPRODUCTIVE PERFORMANCE OF SEASONAL OR NONSEASONAL RAMS EXPOSED TO RAMBOUILLET EWES WHICH WERE TREATED TO INDUCE ESTRUS

Ram class	No. ewes exposed	% ewes mated	% ewes lambed	% ewes conceived[3]
Seasonal[1]	23	65.2	34.8	53.3
Nonseasonal[1]	25	100.0	76.0	76.0
Seasonal[2]	127	30.7	13.3	43.6
Nonseasonal[2]	103	20.3	5.8	24.0

[1]Rams that were used the previous year and exposed to ewes in June one week before hormone injections in 1983.
[2]Rams assigned for evaluation in 1983.
[3]Percent ewes lambed of ewes mated.

APPENDIX B

DATA MEANS

TABLE 1

LEAST SQUARE MEANS OF INTERCEPTS AND SLOPES OF THE SINUSOIDAL MODEL USED TO ANALYZE SCROTAL CIRCUMFERENCE, SEXUAL FLUSH QUANTITY, SEXUAL FLUSH INTENSITY, BODY WEIGHT AND CONDITION SCORE IN FINN X DORSET RAMS

Dependent variable	Ram type	Intercept	SE	Month	SE	Sine/12 of month	SE	Cosine/12 of month	SE	Sine X month	SE	Cosine X month	SE
Scrotal	N	30.522	.759	.058	.026	0.263	.241	-0.620	.254	.026	.033	-.005	.028
circumference	S	31.659	.710	-.012	.025	1.622	.225	-2.129	.238	.035	.031	-.006	.027
Flush	N	3.977	.271	.010	.021	-0.448	.161	-0.651	.232	.091	.027	-.023	.013
quantity	S	3.516	.254	-.009	.020	0.120	.150	-0.564	.217	.000	.026	.005	.012
Flush	N	5.158	.545	-.039	.032	0.592	.306	-0.861	.394	.068	.055	.014	.025
quality	S	4.576	.510	-.027	.030	1.209	.286	-0.248	.369	-.047	.052	-.002	.023
Body	N	166.838	5.65	.031	.122	5.406	1.166	-3.142	.748	-.252	.165	.631	.096
weight	S	156.406	5.29	-.147	.114	8.147	1.091	-5.615	.700	.027	.154	.256	.090
Condition	N	5.119	.200	-.029	.012	0.401	.081	0.182	.063	-.037	.015	.025	.007
score	S	4.544	.187	-.034	.012	0.391	.076	-0.008	.059	-.044	.014	.004	.006

TABLE 2

LEAST SQUARE MEANS OF INTERCEPTS AND SLOPES OF THE POLYNOMIAL MODEL USED TO ANALYZE TESTOSTERONE RESPONSE TO GnRH INFUSION IN FINN X DORSET RAMS

Ram type	Date	Intercept	Time post infusion	$Time^2$	$Time^3$	$Time^4$	$Time^5$	$Time^6$
Nonseasonal	April	9.007	0.048	-.358	.014	-.006	.002	-.0000
	July	11.059	-1.828	-.328	.526	-.045	-.026	.0033
	October	13.381	-1.344	-.141	.332	-.039	-.015	.0021
	January	9.316	0.122	-.044	.015	-.024	-.001	.0003
	± Std err	1.126	.825	.275	.201	.027	.011	.0014
Seasonal	April	9.640	-0.102	-.496	.002	.003	.003	-.0003
	July	11.332	-1.763	-.165	.493	-.055	-.025	.0035
	October	13.292	0.250	-.289	-.149	-.002	.014	-.0014
	January	7.970	-0.133	-.370	.057	-.002	.001	.0001
	± Std err	.932	.363	.130	.089	.012	.005	.0007

TABLE 3

LEAST SQUARE MEANS OF INTERCEPTS AND SLOPES OF POLYNOMIAL MODELS USED TO ANALYZE LH RESPONSE TO GnRH INFUSIONS IN FINN X DORSET RAMS

		First infusion response		Second Infusion Response		
Ram type	Date	Intercept	Time post infusion 1	Intercept	Time post infusion 2	$Time^2$
Nonseasonal	April	25.339	-6.019	14.078	-8.119	1.239
	July	19.735	-2.461	16.694	-6.717	.811
	October	19.715	-3.809	16.655	-5.684	.505
	January	19.764	-2.526	12.992	-6.131	.844
	± Std err	3.795	.781	2.769	.852	.108
Seasonal	April	21.653	-6.744	10.522	-7.493	1.268
	July	14.163	-2.795	12.386	-6.344	.993
	October	11.013	-1.851	9.232	-4.904	.711
	January	14.706	-3.127	8.962	-5.520	.889
	± Std err	3.000	.867	1.799	.708	.106

TABLE 4

MEAN MONTHLY SCROTAL CIRCUMFERENCE FOR SEASONAL AND NONSEASONAL MATURE F_2 FINN X DORSET RAMS FOR TWO YEARS

Month	Nonseasonal scrotal circumference	SE	Seasonal scrotal circumference	SE
May	29.3	.95	31.0	1.00
June	29.7	.96	31.5	1.15
July	29.9	.87	32.6	1.14
August	29.8	.77	32.8	.84
September	30.2	.77	33.5	.94
October	31.0	.77	34.6	.76
November	31.0	.89	33.9	.74
December	30.3	.85	32.3	.77
January	30.6	.99	31.0	.65
February	30.1	1.02	29.6	.67
March	29.9	.95	28.1	.72
April	29.3	.90	28.5	.55
May	29.7	.96	29.6	.65
June	30.9	.81	31.5	.75
July	31.2	1.17	32.9	.83
August	31.0	.62	33.4	.72
September	32.1	.59	35.2	.74
October	31.7	1.02	34.2	.86
November	30.5	.82	33.0	.80
December	30.8	.68	30.9	1.04
January	31.2	.86	30.3	.72
February	30.7	1.06	29.3	.88
March	30.7	1.13	29.6	.85
April	29.8	.91	28.8	1.25

TABLE 5

MEAN MONTHLY SEXUAL FLUSH QUANTITY AND INTENSITY FOR SEASONAL AND NONSEASONAL MATURE F_2 FINN X DORSET RAMS FOR TWO YEARS

	Nonseasonal				Seasonal			
Month	Flush Quantity	SE	Flush Intensity	SE	Flush Quantity	SE	Flush Intensity	SE
May	2.9	.59	5.4	1.21	3.6	.62	6.0	1.04
June	2.6	.72	5.0	1.57	3.4	.59	7.1	1.09
July	2.3	.75	4.1	1.42	3.6	.46	6.0	1.00
August	3.0	.58	5.6	1.29	3.1	.74	4.5	1.15
September	3.7	.36	6.7	.78	4.1	.40	6.3	.53
October	4.4	.30	7.2	.64	4.5	.27	7.2	.44
November	4.0	.49	5.3	1.06	4.1	.44	3.8	.45
December	4.9	.14	5.4	.75	4.4	.32	4.4	.56
January	5.0	0	5.4	.53	3.5	.50	3.0	.38
February	4.7	.18	5.1	.59	2.5	.57	2.8	.67
March	3.9	.34	4.3	.52	3.1	.40	4.0	.57
April	3.4	.30	3.4	.37	2.5	.38	3.3	.80
May	3.6	.43	3.4	.87	3.0	.53	3.3	.92
June	3.7	.36	4.7	.92	3.3	.56	4.8	1.15
July	3.3	.56	6.2	1.30	3.4	.53	6.1	1.11
August	3.6	.53	6.7	1.06	3.6	.73	5.8	1.19
September	4.7	.28	6.7	1.08	3.6	.50	5.1	1.11
October	4.7	.29	4.9	.80	4.8	.25	5.0	.27
November	4.6	.20	4.7	.52	3.6	.42	4.6	.50
December	4.9	.14	4.7	.42	3.8	.31	3.8	.53
January	4.4	.30	4.6	.78	3.1	.64	3.1	.77
February	3.0	.72	4.0	1.09	3.5	.38	3.8	.65
March	2.6	.78	2.6	.95	3.0	.65	4.0	.96
April	3.3	.36	4.1	.91	3.3	.53	4.6	1.07

TABLE 6

MEAN MONTHLY BODY WEIGHT AND CONDITION SCORE FOR SEASONAL AND NONSEASONAL MATURE F_2 FINN X DORSET RAMS FOR TWO YEARS

	Nonseasonal				Seasonal			
Month	Body weight	SE	Condition score	SE	Body weight	SE	Condition Score	SE
May	154	8.0	5.7	.42	150	7.6	5.5	.19
June	172	7.4	5.9	.26	162	7.3	5.3	.16
July	169	7.1	6.4	.30	159	6.6	6.0	.33
August	172	6.6	5.4	.30	164	5.8	4.9	.13
September	184	6.5	6.3	.18	174	6.0	5.6	.18
October	172	6.2	5.1	.14	165	5.2	5.0	.19
November	166	6.0	5.1	.26	158	5.4	4.8	.16
December	165	5.8	5.0	.38	156	5.5	4.2	.23
January	168	5.9	4.9	.26	157	5.0	4.5	.19
February	165	5.5	4.4	.20	151	5.3	3.8	.25
March	163	5.9	4.7	.29	147	4.9	4.3	.16
April	148	6.6	5.3	.52	136	4.1	4.1	.23
May	168	6.4	5.4	.37	153	5.0	4.5	.19
June	170	6.6	5.6	.48	165	5.1	4.9	.13
July	166	8.7	5.2	.40	167	4.9	5.0	.19
August	176	7.2	5.0	.44	166	4.1	4.3	.31
September	172	5.3	5.0	.38	165	4.8	4.5	.19
October	172	5.8	5.3	.29	163	5.2	4.8	.25
November	163	5.4	4.4	.30	154	4.7	4.3	.25
December	154	5.0	4.1	.26	145	4.2	3.9	.30
January	162	4.4	4.4	.20	149	5.8	4.3	.16
February	173	5.4	5.3	.36	154	6.4	4.5	.27
March	174	5.6	5.4	.37	154	7.3	4.4	.26
April	163	5.2	5.0	.22	140	7.1	4.3	.31

TABLE 7

MEAN LH CONCENTRATION IN SERUM AFTER INFUSION OF 1UG GnRH AT 0 AND 1 H FOR NONSEASONAL AND SEASONAL MATURE F_2 FINN X DORSET RAMS DURING APRIL, JULY, OCTOBER AND JANUARY

Ram type	Time(h)	April	SE	July	SE	October	SE	January	SE
Nonseasonal	0	1.83	1.40	.65	.10	1.49	.48	1.25	.53
	.25	34.50	4.21	23.35	3.93	25.62	3.96	24.25	3.83
	.50	28.85	5.68	21.14	3.75	21.52	3.65	20.63	3.27
	.75	20.90	4.32	18.40	4.25	17.42	3.45	17.19	3.52
	1.00	17.09	3.72	16.06	4.02	14.29	2.50	16.98	4.50
	1.25	49.95	3.58	40.18	4.81	36.02	5.25	40.05	6.14
	1.50	43.32	4.11	40.01	5.34	35.14	5.05	34.37	5.56
	1.75	34.37	3.32	32.07	5.28	29.68	4.08	27.45	5.31
	2.00	28.11	3.48	27.84	4.99	27.99	4.89	22.76	5.28
	2.50	16.56	2.52	22.37	4.60	21.64	5.06	15.63	3.56
	3.00	10.37	1.81	13.41	3.08	14.27	3.09	10.78	3.03
	3.50	4.42	.78	7.80	1.30	6.32	1.10	5.72	1.76
	4.00	2.71	.58	5.52	.98	4.89	1.10	3.91	1.22
	4.50	1.76	.44	3.79	.55	3.13	.74	2.59	.75
	5.00	1.48	.49	2.30	.45	2.26	.48	1.40	.32
Seasonal	0	1.86	1.10	.85	.33	.84	.42	.79	.45
	.25	32.26	5.04	18.29	4.76	13.86	2.80	18.69	3.56
	.50	24.31	4.17	15.85	3.31	11.78	2.37	17.32	4.33
	.75	18.24	4.08	12.39	2.27	10.21	1.89	13.16	2.78
	1.00	11.81	1.79	10.12	1.93	8.21	1.34	9.65	2.07
	1.25	43.91	3.91	42.52	3.99	31.34	3.74	33.65	5.90
	1.50	39.93	4.06	33.86	3.32	26.23	2.50	29.10	5.23
	1.75	29.73	3.71	27.69	3.37	22.02	2.71	24.64	4.90
	2.00	23.82	3.60	23.91	3.35	18.18	2.95	17.56	3.30
	2.50	13.21	2.61	14.65	2.99	11.39	1.67	10.60	2.23
	3.00	5.51	.94	8.61	1.50	6.33	.83	5.59	1.41
	3.50	3.20	.68	5.83	1.34	3.75	.91	3.92	1.23
	4.00	1.43	.30	4.51	1.22	1.91	.34	1.89	.54
	4.50	1.23	.43	3.86	1.06	1.35	.19	1.19	.39
	5.00	.66	.11	1.93	.43	.95	.16	.93	.27

TABLE 8

MEAN TESTOSTERONE CONCENTRATION IN SERUM AFTER INFUSION OF 1UG GnRH AT 0 AND 1 H FOR NONSEASONAL AND SEASONAL MATURE F_2 FINN X DORSET RAMS DURING APRIL, JULY, OCTOBER AND JANUARY

Ram type	Time(h)	April	SE	July	SE	October	SE	January	SE
Nonseasonal	0	2.14	.53	3.85	1.17	7.72	2.14	4.25	1.16
	.5	5.85	.60	7.09	.87	11.09	1.67	7.63	1.07
	1.0	8.25	.69	10.96	.98	13.86	1.89	8.69	.76
	1.5	8.31	.57	12.24	1.35	14.01	2.00	9.45	.86
	2.0	9.26	.82	9.90	1.61	12.69	1.62	9.25	.64
	3.0	6.96	.47	9.26	.55	11.86	1.78	8.82	2.19
	4.0	3.36	.46	6.13	.38	8.70	1.38	4.62	.46
	5.0	2.07	.42	4.15	.61	5.25	.79	3.09	.61
Seasonal	0	2.46	.80	5.46	1.60	5.19	1.09	1.95	.66
	.5	6.60	.47	8.20	1.04	11.39	1.78	5.07	.54
	1.0	8.62	.47	11.70	.88	12.75	1.56	7.36	.76
	1.5	9.62	.58	12.35	.79	12.98	1.53	7.68	.72
	2.0	9.44	.65	10.34	.79	13.40	1.45	7.96	.79
	3.0	6.62	.50	9.89	.58	10.66	1.18	6.04	.43
	4.0	2.92	.51	5.50	.68	7.08	1.09	3.54	.29
	5.0	1.82	.53	4.99	.89	5.71	1.13	2.01	.30

VITA 2

Kris Alan Ringwall

Candidate for the Degree of

Doctor of Philosophy

Thesis: ASSOCIATION OF NATURAL PHOTOPERIOD WITH SCROTAL CIRCUMFERENCE, INGUINAL CUTANEOUS HYPEREMIA, ENDOCRINE FUNCTION AND MAY-JUNE FERTILITY IN MATURE F_2 FINNISH LANDRACE X DORSET RAMS

Major Field: Animal Breeding

Biographical:

Personal Data: Born in Crosby, North Dakota, September 22, 1953, the son of Chester and Lillie Ringwall; married Marian E. Dhuyvetter April 2, 1977; father of Kirstin and Kristofor.

Education: Graduated from Columbus High School, Columbus, North Dakota, May 1971; received the Bachelor of Science degree from North Dakota State University, February 1975 with a major in Animal Husbandry; received the Master of Science degree at Oklahoma State University, December 1982; completed requirements for the Doctor of Philosophy degree at Oklahoma State University in May, 1985.

Experience: Raised and worked on a livestock and crop farm; 1971-1975 worked part-time at the North Dakota State University sheep barn; 1975-1979 County Agricultural Agent, North Dakota Extension Service; 1979-1984 graduate assistant, Department of Animal Science, Oklahoma State University; 1984 Animal Husbandman, North Dakota Extension Service.

Professional Organizations: Alpha Zeta, Phi Kappa Phi, Amerian Society of Animal Science.