

THE INFLUENCE OF DURATION OF PHOTOPERIOD ON  
GROWTH AND HYPOPHYSEAL-GONADAL  
FUNCTION OF YOUNG BOARS

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## CHAPTER I

### INTRODUCTION

Duration of the daily light period regulates seasonal sexual cycles of some domestic animal species and the effects of photic induced changes on their reproductive function have been studied extensively. On the other hand, species of farm animals which do not exhibit dramatic seasonal decreases in reproductive capacity have traditionally been regarded as being insensitive to changes in the length of the daily light period. Therefore, limited information is available to suggest whether light participates, even subtly, in physiological functions of such animals.

As more swine are produced indoors in partial or total confinement systems, the opportunity exists for manipulating and more closely controlling such environmental factors as ambient temperatures and daily light exposure. The possibility of increasing productivity of swine in confinement by manipulating lighting systems is attractive since essentially no changes in physical facilities would be required. Yet, our knowledge relative to photic effects on pigs is limited. Therefore, we evaluated the effects of duration of photoperiod on growth and reproductive function of young boars. We chose boars as our experimental animal in an effort to (1) more carefully characterize photic effects on reproductive function of boars, (2) gain insight into the optimum length of photoperiod to maximize growth and reproductive

development of boars, and (3) obtain information which could be applicable to reproductive development of gilts since photic control of gonadotropin secretion should be similar, but not confounded by variations due to estrous cycles.

Throughout the body of this dissertation, the word photoperiod is extensively used. This word denotes the duration of the light period in a day. Therefore, if a photic environment is described as having a long photoperiod, it implies long hours of light such as those observed for the days of summer in the temperate zones of the northern hemisphere. The reverse meaning is true for short photoperiods.

Photoperiodic influences on growth and sexual development of swine could have profound practical implications. Decreasing the age at puberty of boars could aid swine producers in evaluating reproductive soundness at an earlier age and help to increase the effectiveness of boar selection. This information could also be useful for decreasing the age of first estrus in gilts, a problem often encountered for confinement reared females. Thus, photoperiodic manipulation could help to increase the efficiency of swine production.

## CHAPTER II

### LITERATURE REVIEW

#### Introduction and Scope of Review

Light participates in the timing of seasonal reproductive phenomena in many species and other physiological functions (e.g., average daily gain or feed efficiency) may also be influenced by variations in daily light exposure. Extensive information is available for species of animals which display pronounced sensitivity to variations in photoperiod and the characteristics of photic perception and biochronometry for these species have been evaluated in great detail. It is not surprising that the same information is not available for domestic animals which are not as obviously influenced by light since no overt, easily assayable response is observed. For this reason, the data evaluating photic influences on growth and reproductive function of boars are relatively limited. Therefore, the scope of this review has been expanded to include areas of experimentation which not only address photoperiodic effects in boars, but also related areas which contributed to the design of experiments comprising this dissertation research.

## Photoperiodic Time Measurement (Biochronometry)

### Circadian Organization of Photoperiodic Time Measurement (PTM)

Several species of mammals which inhabit the temperate zones of the world have adapted annual reproductive cycles in order to maximize the probability of survival of their young. This type of seasonal reproductive strategy remains essentially invariant from year to year and therefore must be cued by stable environmental factors for such precision to recur. It is now generally agreed that the adaptive timing of breeding seasons depends largely (but perhaps not exclusively) on annual changes in length of the daily light period as the stable, "noise-free" cue. The reliance of mammals on the length of the light period as their primary cue implies that somehow they are capable of measuring the length of the day, yet our understanding of the physiological nature of PTM remains obscure.

Two general classes of theories of PTM have developed. The first assumes a so-called hourglass mechanism for the measurement of the length of day. According to this theory, a photochemical process occurs during the light hours (or dark) and this process yields a hypothetical reaction product which is reversed in the other portion of the light-dark cycle. If sufficient reaction product accumulates, a threshold is reached and the organism perceives the day as long (conversely, if too little accumulates, a short day is perceived). According to this theory, the animal literally measures the length of light or dark (Elliott, 1976; Whitsett et al., 1983). Such an hourglass timer appears to operate as the clock for the aphid, Megoura

viciae (Lees, 1966; found in Elliott, 1976) and the male lizard, Anolic carolinensis (Underwood, 1981).

The second theory of PTM was originally proposed by Bünning (1936; found in Pittendrigh, 1972; Elliott, 1976; Earnest and Turek, 1983; Whitsett et al., 1983) to explain photoperiodic measurement in plants and suggests that photoperiodic time is measured by a circadian (24-h) rhythm of photoproducible photosensitivity. According to this theory, the organism is sensitive to light only during certain portions of the circadian rhythm and that photosensitive photoinducibility occurs when this photoinducible phase ( $\phi_i$ ) is illuminated. Therefore the effect that a certain light-dark (LD) cycle has depends on whether or not the light portion of the cycle extends into  $\phi_i$  (Elliott, 1976). Within the framework of circadian oscillations of photosensitivity, two models have been proposed for PTM (Pittendrigh, 1972). In the "external coincidence" model, light serves to entrain the circadian rhythm of photosensitivity ( $\phi_i$ , an internal rhythm) and when light (an external stimulus) coincides with  $\phi_i$ , photoinducibility occurs (Earnest and Turek, 1983; Whitsett et al., 1983). In the "internal coincidence" model, light serves to entrain two (or more) circadian oscillators so that exposure to photoinductive lighting systems alligns the phases of the oscillators and the proper photoperiodic response is evoked (Turek and Campbell, 1979; Pittendrigh, 1981; Earnest and Turek, 1983; Whitsett et al., 1983).

The nature of PTM has been most extensively studied in the male golden (Syrian) hamster (Mesocricetus auratus) and it is clear that a circadian system is involved in PTM in this species (Elliott, 1976; Elliott, 1981). The involvement of the circadian system in PTM in

the hamster has been evaluated by using ahemoral (non-24-h), resonance light treatments. Groups of mature, male golden hamsters were subjected to 6 h of light followed by 18, 30, 42, or 54 h of darkness (LD, 6:18, 6:30, 5:42, or 6:54). These treatments generated LD cycles of 24, 36, 48, and 60 h, respectively. Following 89 d of exposure, testicular regression occurred in hamsters exposed to LD 6:18 and LD 6:42. However, the testes of hamsters exposed to LD 6:30 and LD 6:54 remained large and were similar to those of hamsters in stimulatory (LD 14:10) long days (Elliott et al., 1972; Stetson et al., 1975). The results of these studies rule out the possibility that an hourglass system of PTM occurs for hamsters since all hamsters were exposed to 6 h of light per LD cycle. Further, these experiments exclude the possibility that the duration of darkness or the light:dark ratio is the key to PTM since stimulated hamsters were exposed to different durations of dark and different light:dark ratios (Stetson et al., 1975; Elliott, 1981). Photic entrainment of circadian systems has also been described for laboratory rats, Rattus norvegicus (Nelson et al., 1982), Djungarian hamsters, Phodopus sungorus (Hoffmann, 1979; Yellon et al., 1982), deer mice, Peromyscus maniculatus bairdii (Whitsett et al., 1983), and rams (Schanbacher and Crouse, 1981; Almeida and Lincoln, 1982). A circadian rhythm of photosensitivity has also been suggested for bulls (Petitclerc et al., 1980).

The results of experiments demonstrating the involvement of a circadian system in PTM clearly emphasize that the circadian time of light exposure is far more important than the frequency or duration of exposure. Indeed, as little as 15 min of light every 10 days will induce gonadal growth in hamsters when the timing of the light burst

is coincident with  $\phi_1$  (Elliott, 1981). A photoperiod of LD 6:18 interrupted by a 1 s light burst 8 h after lights-off maintains testicular function in mature golden hamsters transferred from photostimulatory LD 14:10 (Earnest and Turek, 1983).

The characteristics of the circadian rhythm of photosensitive photoinducibility have been most completely described for golden hamsters. The photoinducible phase ( $\phi_1$ ) is closely related temporally to the hamsters activity cycle (circadian rhythm of wheel running), and  $\phi_1$  commences about .5 h before the onset of wheel running and extends for 10.5 to 12 h, almost the entire subjective night (Elliott, 1981; Earnest and Turek, 1983). The extreme demarkation of  $\phi_1$  is demonstrated by the observation that about a 30-fold increase in testicular weight is observed when hamsters are exposed to 12.5 h light/24 h compared with hamsters in 12 h light/24 h (Elliott, 1976).

#### Anatomical Location of the

#### Circadian Pacemaker

The paired suprachiasmatic nuclei (SCN) of the anterior hypothalamus have been identified among rodents as the probable circadian pacemaker. Ablation of the SCN interrupts normal photic entrainment of circadian rhythms and inconsistently alters the periodicity of the free-running activity rhythm in continuous darkness (DD; Stephen and Zucker, 1972; Moore and Klein, 1974; Stetson and Watson-Whitmyre, 1976; Rusak and Zucker, 1979). Hypothalamic islands produced by Halász knife cuts which contain the SCN maintain circadian rhythms of electrical activity while other areas of the brain lose rhythmicity (Inouye and Kawamura, 1979). Mature male golden hamsters with SCN



lesions do not undergo testicular atrophy when exposed to short photoperiods (LD 2:22; Rusak and Morin, 1976) or DD (Stetson and Watson-Whitmyre, 1976). In addition, testicular growth occurred in lesioned hamsters whose testes were previously regressed by short photoperiod (Rusak and Morin, 1976) and the time course of spontaneous recrudescence was more rapid in SCN lesioned than intact hamsters chronically exposed to short days (Rusak, 1980). Lesions of the SCN also reverse short day induced hypersensitivity to steroid feedback on gonadotropin secretion (Turek et al., 1980; Turek and Ellis, 1981) and prevent melatonin delayed spontaneous recrudescence (Rusak, 1980).

Photic information for entrainment of circadian rhythms is thought to reach the SCN via the retinohypothalamic tract (RHT). Moore and Lenn (1972) demonstrated the existence of the RHT in the rat. The RHT originates in ganglion cells of the retina and its projections transverse the optic tract and chiasm and terminate bilaterally in the SCN. Integrity of the neural connections between the retina and the SCN is essential for entrainment of circadian rhythms. Destruction of all visual pathways by blinding abolishes the circadian rhythm of serotonin N-acetyltransferase activity in rats (Moore and Klein, 1974) and induces testicular regression in golden hamsters (Rusak and Morin, 1976). However, these responses are not observed when the primary optic tracts (Moore and Klein, 1974; Rusak and Morin, 1976) or the accessory optic tracts (Moore and Klein, 1974) are interrupted.

Photoperiodic Influences on Reproductive  
Function of Rodents

Effects on Testicular Function, Onset of  
Refractoriness and Spontaneous  
Recrudescence of the Testes

Several species of rodents exhibit annual cycles of reproductive competence as a result of exposure to short days and have therefore been useful as models for studying seasonal breeding. In particular, the male golden (Syrian) hamster (Mesocricetus auratus) has been extremely useful because of its extremely repeatable and uniform responses to variations in photoperiod and the ease with which these animals are maintained under standard laboratory conditions. The extensive literature characterizing this species will be surveyed and, where applicable, supporting or contrasting information from other rodent species will be included.

The detrimental effects of short days on testicular function in golden hamsters have been well documented. Gaston and Menaker (1976) systematically exposed mature golden hamsters to photoperiods ranging from LD 0:24 to LD 24:0. They found that a minimum of 12.5 h of light daily was required for maintenance of testicular size and this photic requirement has since been repeated and confirmed (Elliott, 1976). Exposure of hamsters to less than 12.5 h of light daily results in a dramatic decrease (about 10-fold) in testicular size within 10 wk of exposure to short days (for reviews see Turek and Campbell, 1979; Turek and Ellis, 1981). Among other species that undergo testicular atrophy in response to short days are Djungarian hamsters, Phodopus

sungorus (Hoffmann, 1979; Simpson et al., 1982), Chinese hamsters, Cricetulus griseus (Bartke and Parkening, 1981), white-footed mice, Peromyscus leucopus (Gram et al., 1982), deer mice, Peromyscus maniculatus bairdii (Desjardins and Lopez, 1983), and laboratory rats, Rattus norvegicus (Nelson et al., 1982). The decrease in testicular weight observed following exposure to short days is accompanied by diminished spermatogenic function (Berndtson and Desjardins, 1974; Desjardins and Lopez, 1983), and the seminiferous tubules eventually became devoid of mature spermatozoa (Turek and Ellis, 1981).

Following extended exposure to short days (< 12.5 h light/24 h for 20 to 25 wk) the involuted testes of hamsters "escape" photic inhibition and eventually return to mature size (Turek and Ellis, 1981). Complete recovery of the testes is observed after about 30 wk of exposure to short days (Reiter, 1972; Turek et al., 1975) and this phenomenon has been termed spontaneous recrudescence. This term is functionally significant since exposure to long days following testicular regression can stimulate recovery of the testes well in advance of spontaneous recrudescence (Berndtson and Desjardins, 1974; Zucker and Morin, 1977). However, a time-dependent increase in the hamster's sensitivity to the stimulatory effects of long days following testicular collapse is observed. Hamsters which are exposed to 9 to 10 wk of non-stimulatory short days (i.e., those whose testes have just regressed) are less responsive to transfer into stimulatory long days (demonstrate less growth) than hamsters exposed to short days for 12 to 15 wk (Turek et al., 1975; Zucker and Morin, 1977).

Hamsters which have been exposed to 20 to 30 wk of non-stimulatory short days and have undergone spontaneous recrudescence of the testes

become refractory to the detrimental effects of exposure to short days since a second regression of the testes can not be induced until testicular growth has been induced by long days (Elliott, 1981; Turek and Ellis, 1981). There is a time-dependent requirement of long day exposure for the termination of refractoriness. Return of hamsters with newly recrudescing testes to LD 14:10 for 1 to 10 wk followed by transfer to LD 1:23 is not sufficient to induce a second involution of the testes (Reiter, 1972). However, 11 to 22 wk of exposure to LD 14:10 is sufficient to terminate refractoriness and return of hamsters to short days induces testicular regression a second time (Stetson et al., 1977; Reiter, 1972).

#### Endocrine Correlates of Reproductive Responses to Photoperiod

Mature hamster testes weigh about 3 g and are capable of secreting sufficient testosterone to maintain concentrations in serum between 3 and 5 ng/ml (Turek and Ellis, 1981). However, short day induced testicular regression results in a dramatic reduction in serum testosterone concentrations (to about 1 ng/ml) and a reduced ability of the involuted testis to convert progesterone to testosterone (Berndtson and Desjardins, 1974). Reduced endocrine function of the testes may be in part due to a reduction in testicular receptors for LH (Bartke et al., 1980). Concentrations of LH and FSH in serum are also decreased when hamsters are maintained in non-stimulatory short days (Berndtson and Desjardins, 1974; Turek et al., 1975; Tamarkin et al., 1976; Bartke et al., 1980; Tate-Ostroff and Stetson, 1981; Steger et al., 1982). The hypothalamic content of gonadotropin releasing hormone (GnRH)

increases while gonadotropins in serum decrease during reproductive decline of hamsters, suggesting that GnRH release is reduced in these animals (Steger et al., 1982). However, spontaneous recrudescence of the testes (Klemcke et al., 1981; Tate-Ostroff and Stetson, 1981; Steger et al., 1982) or transfer of hamsters with regressed testes from short to long days (Turek, 1982) is occasioned by a return of circulating titers of LH and FSH to concentrations reminiscent of hamsters maintained on long days. In addition, increasing serum concentrations of gonadotropins and spontaneous recrudescence of the testes are associated with decreasing concentrations of GnRH in the hypothalamus, indicating that stimulation of the hypophyseal-gonadal system may be the result of increasing GnRH release (Steger et al., 1982).

Concentrations of prolactin (PRL) in serum are also reduced in hamsters maintained in short days (Bartke et al., 1980; Goldman et al., 1981; Klemcke et al., 1981). Homologous pituitary grafts placed under the kidney capsule of hamsters prior to transfer to short days maintain concentrations of PRL in serum and truncate testicular atrophy normally induced by short days. The reduced severity of testicular regression in hamsters with pituitary grafts following transfer to short days may be due to an increase in testicular LH receptors since hamsters on both long and short days with pituitary grafts have increased testicular LH binding capacity (Bartke et al., 1980). However, increased concentrations of PRL in serum can not solely account for delayed and incomplete testicular regression observed by Bartke et al. (1980) since hamsters with pituitary grafts also had increased concentrations of gonadotropins in serum.

Concentrations of PRL in serum eventually increase in hamsters undergoing spontaneous recrudescence in short days (Goldman et al., 1981; Klemcke et al., 1981; Tate-Ostroff and Stetson, 1981; Steger et al., 1982). Therefore, a refractoriness to the inhibition of PRL secretion is developed during extended exposure of the hamster to short days and appears to be independent of the testis since the spontaneous increase in PRL in serum occurs at the same time (after about 20 wk of short days) in intact, castrated and castrated hamsters with testosterone implants (Goldman et al., 1981).

As noted previously, hamsters exposed to less than 12.5 h of light daily have reduced concentrations of gonadotropins in serum. This reduction in gonadotropins may be due to altered responsiveness of the hypothalamo-hypophyseal axis of hamsters in short days to the negative feedback effects of gonadal steroids. Hamsters maintained on short days are more sensitive to the negative feedback effects of testosterone (Tamarkin et al., 1976; Turek, 1977; Ellis and Turek, 1979; Sisk and Turek, 1983), 5  $\alpha$ -dihydrotestosterone and 17  $\beta$ -estradiol than hamsters exposed to long days (Ellis and Turek, 1980b). A gradual increase in the sensitivity to testosterone is observed when hamsters are transferred from long to short days while a gradual decrease in sensitivity to testosterone accompanies transfer from short to long days (Ellis and Turek, 1979). Prolonged exposure to non-stimulatory short days results in decreased sensitivity to testosterone feedback, suggesting that when hamsters become refractory to short days, a shift in hypothalamo-hypophyseal sensitivity to gonadal steroids also occurs (Ellis et al., 1979).

Reduced neuroendocrine-gonadal function observed in hamsters maintained in non-stimulatory photoperiods can not be solely attributed to short day induced hypersensitivity to the negative feedback effects of gonadal steroids. Reduced gonadotropin secretion following transfer of hamsters to short days appears to have a steroid-independent as well as a steroid-dependent component (Turek and Ellis, 1981). Castrated hamsters transferred from long to short days have reduced concentrations of gonadotropins in serum (Urbanski and Simpson, 1982; Simpson et al., 1982) and gonadotropin secretion is increased when castrated hamsters are transferred from short to long days (Ellis and Turek, 1980b; Simpson et al., 1982). Taken together, these studies and the observation that neither adrenalectomy nor low-steroid diets alter gonadotropins in castrated hamsters maintained on short days (Ellis and Turek, 1980a) suggest that both steroid-dependent and steroid-independent mechanisms contribute to alterations in gonadotropin secretion when hamsters are exposed to non-stimulatory photoperiods. Urbanski and Simpson (1982) suggest that since reduced gonadotropin secretion follows exposure to short days independently of the testes in the intact animal, less testosterone would be required to oppose such gonadotropin secretion in the intact animal. The reverse of this argument is applicable to hamsters exposed to stimulatory long days.

#### Role of the Pineal Gland

The role of the pineal gland in photic-induced changes in neuroendocrine-gonadal function of several species of mammals has been extensively evaluated (for review, see Turek and Campbell, 1979;

Reiter, 1980a and b; Hoffmann, 1981). The importance of pineal integrity for reproductive function of hamsters has been repeatedly confirmed by observations that pinealectomy can block the inhibitory effects of short days on the gonads (Turek and Campbell, 1979; Hoffmann, 1981). Removal of the pineal also diminishes the reduction in gonadotropins in the serum that is observed following exposure to short days and can cause premature spontaneous recrudescence (Hoffmann, 1981). In fact, interruption of the neural connections at any point between the SCN and the pineal gland mimics the effects of pinealectomy. Transection of the nervi conarii or superior cervical ganglionectomy, decentralization of the superior cervical ganglia (by cutting preganglionic sympathetic efferents from the SCN) and ablation of the SCN all prevent testicular involution of hamsters exposed to short days (Reiter, 1980a).

The pineal factor most commonly implicated as a regulator of reproductive function is N-acetyl-5-methoxytryptamine (melatonin) since injection or implantation of melatonin results in alterations of neuroendocrine-gonadal function. A wide variety of effects are observed following melatonin administration, depending on the time of day and the duration of photoperiod under which melatonin is administered. For example, daily melatonin injections given near the end of the light period (but not near the beginning) can block the stimulatory effects of long days on gonadotropins and testicular function in golden hamsters (Tamarkin et al., 1976; Tamarkin et al., 1977; found in Turek and Campbell, 1979). Hamsters which were maintained on LD 6:18 and implanted with melatonin filled capsules did not undergo testicular degeneration and non-treated hamsters with regressed testes in LD 6:18



underwent premature testicular recrudescence following melatonin implantation. However, melatonin greatly delays testicular growth normally seen in hamsters moved from LD 6:18 to LD 14:10 (Turek and Losee, 1978) and regresses the testes of hamsters already in LD 14:10 (Sisk and Turek, 1982). Melatonin administered to Djungarian hamsters maintained in long days failed to induce testicular collapse (Hoffmann, 1981). It has been suggested that in golden hamsters, melatonin administration has the opposite effect of the photoperiod. That is, in short days, administration of melatonin is stimulatory while in long days, administration of melatonin is inhibitory to gonadal function (Hoffmann, 1981).

The role of the pineal gland in photic-induced changes in the sensitivity of the hypothalamo-hypophyseal system to the negative feedback effects of gonadal steroids has also been explored. Testosterone suppresses serum LH and FSH to a greater extent in sham-pinealectomized hamsters in LD 6:18 than sham-pinealectomized hamsters in LD 14:10. However, the increased sensitivity to negative feedback effects of testosterone on gonadotropin secretion are lost when hamsters are pinealectomized (Turek, 1979). The loss of increased sensitivity to steroidal feedback observed in pinealectomized hamsters may be mediated through melatonin since melatonin given to castrated hamsters maintained in LD 14:10 increases the suppressive effects of testosterone on gonadotropin secretion (Sisk and Turek, 1982).

Although it is clear that the pineal gland and its products play a role in the mediation of photoperiodic effects on reproductive function in the hamster, resolution of some of the perplexing effects

observed following removal of the pineal or administration of melatonin will require further investigation.

Influences of Photoperiod on Reproductive  
Function of Domestic Animals

Light and Seasonality in Sheep

Influence of Light on Reproductive

Phenomena of Rams

Variations in Size and Spermatogenic Function of the Testes.

Domestic sheep (Ovis aries) are generally regarded as seasonally breeding animals although some breeds of sheep are reproductively active throughout the year. Ewes of most breeds which inhabit the temperate zones of the northern hemisphere are stimulated by short days and have regular estrous cycles in the fall. Recently, seasonal components of ram fertility have been the target of extensive investigation and the concept of "ram seasonality" can now be defined more quantitatively.

Perhaps the most striking feature of the yearly reproductive cycle of the ram is the variation observed in testis size. Rams of the Soay breed have served as useful animal models for evaluating photic effects on testicular function since the stimulatory effects of short days on this breed are marked and consistent. Exposure of Soay rams with fully active testes to LD 16:8 results in decreased testicular size with the testes attaining minimum diameter in about 15 wk (Lincoln and Davidson, 1977). However, about 2 wk after exposure to short days (LD 8:16), testicular diameter begins to increase and the testes reach maximum

size in about 10 wk (Lincoln and Davidson, 1977). Similarly, Soay rams maintained outdoors exhibit yearly cycles of testicular size with a nadir occurring during the late spring followed by the return of active testes in mid-summer, just prior to the breeding season (Lincoln, 1979a). Seasonal variations in testicular size occur in rams of other breeds but the seasonal effect is not as pronounced as that observed in Soay rams. Préalpes du Sud and Ile-de-France rams also have increased testicular size just prior to the breeding season (Pelletier et al., 1982; Howles et al., 1982; Barenton and Pelletier, 1983) and growth of the testes (increased scrotal circumference) has been demonstrated in Suffolk (Schanbacher, 1979) and Suffolk x Hampshire (Schanbacher and Ford, 1979) rams after exposure to LD 8:16. Clearly, exposure to either natural or experimentally short days stimulates gonadal function of rams.

Seasonal changes in testicular size in the ram may reflect an endogenous rhythm which is merely entrained by the photoperiod. When mature rams are maintained under constant photoperiodic conditions for long periods of time (3 yr), a rhythm of testicular changes still persists but becomes free-running. Rams continually exposed to long days (LD 16:8) have cycles of changes in testicular volume with a periodicity of about 35 wk (Howles et al., 1982). These data are consistent with the observation that following 16 wk of exposure to LD 16:8, rams with regressed testes "escape" photic-inhibition and the testes spontaneously redevelop (Almeida and Lincoln, 1982).

Variations in testicular size throughout the year, and particularly testicular collapse observed during long days, can be attributed to (at least in part) insufficient gonadotropic stimulation of the testis. The result of decreased gonadotropin secretion is manifested as

decreased testicular size and depressed spermatogenic function of the testes of rams. Suffolk x Hampshire rams exposed to LD 16:8 produced nearly half as many sperm per day and had reduced epididymal sperm reserves when compared with rams in LD 8:16 (Schanbacher and Ford, 1979). Regressed ram testes contain seminiferous tubules with reduced diameter and fewer germ cells that mature past spermatocyte stages (Schanbacher and Ford, 1979; Mortimer and Lincoln, 1982). The seminiferous epithelium appears disorganized and the Leydig cells have reduced content of smooth endoplasmic reticulum (Mortimer and Lincoln, 1982). The amount of smooth endoplasmic reticulum in Leydig cells has been identified as the best predictor of testosterone production by in vitro perfused rat, rabbit, guinea pig, dog and hamster testes (Zirkin et al., 1980; Ewing et al., 1983). Taken together, these ultrastructural data provide a histological basis for reduced testosterone in serum of rams with regressed testes.

Endocrine Function and Hypothalamic and Hypophyseal Sensitivity to Gonadal Steroids. Variations in concentrations of gonadotropins and testosterone in serum are observed in rams under conditions of long and short days. In general, long days are inhibitory while short days are stimulatory to the hypothalamo-hypophyseal-gonadal axis. Repeated investigations confirm that when rams are observed throughout the year under natural photoperiodic conditions (Schanbacher and Lunstra, 1976; Schanbacher and Ford, 1976; Pelletier et al., 1982) or are exposed to experimentally controlled photoperiods (Pelletier and Ortavant, 1975a and b; Lincoln, 1976; Lincoln and Davidson, 1977; Lincoln and Peet, 1977; Lincoln et al., 1977; Schanbacher and Ford, 1979) a positive effect of short days is observed on gonadotropin

and testosterone secretion. Concentrations of LH (Pelletier and Ortavant, 1975a; Lincoln and Davidson, 1977; Schanbacher and Ford, 1979) and FSH (Lincoln and Davidson, 1977; Schanbacher and Ford, 1979) in serum are increased when rams are exposed to LD 8:16, probably as a result of increased frequency of episodic discharges of LH (Lincoln, 1976; Lincoln and Peet, 1977; Lincoln et al., 1977) and FSH (Lincoln et al., 1977; Lincoln and Peet, 1977) from the pituitary. Increases in episodic releases of gonadotropins from the pituitary probably reflect concomitant increases in GnRH secretion from the hypothalamus, although this has not been specifically evaluated. Concentrations of LH in serum (Schanbacher and Lunstra, 1976), the frequency of episodic surges of LH (Pelletier et al., 1982) and the number of testicular LH receptors (Barenton and Pelletier, 1983) increase during mid- to late-summer in rams maintained under conditions of natural light. This stimulation in endocrine function occurs shortly after the onset of decreasing daylight and in advance of the breeding season.

The testes of rams exposed to LD 8:16 respond to increased LH secretion with increased testosterone secretion (Lincoln and Peet, 1977; Lincoln et al., 1977). Not surprisingly, increases in concentrations of testosterone in the serum essentially parallel increases in testicular size for rams exposed to artificially short days (Lincoln and Davidson, 1977; Lincoln and Peet, 1977; Lincoln et al., 1977; Schanbacher and Ford, 1979) or for rams in naturally decreasing photoperiods (Schanbacher and Lunstra, 1976; Pelletier et al., 1982). A lag time exists of about 6 to 8 wk from the onset of photic-induced LH secretion to the occurrence of maximum testosterone secretion.

Increases in libido (Schanbacher and Lunstra, 1976; Lincoln and Davidson, 1977), ram-ram aggressive behavior and development of sexual flush of ventral flank skin (Lincoln and Davidson, 1977; Lincoln, 1979a) are all temporally correlated with photic-induced endocrine events in rams. In fact, infusion of rams that have regressed testes with pulses of GnRH results in increased pulsing of LH and testosterone in the serum and stimulates testicular growth and sexual skin flush that is characteristic of rams during the breeding season (Lincoln, 1979b).

In rodents, seasonal cycles in sexual activity reflect not only changes in neuroendocrine-gonadal activity but also changes in the sensitivity of gonadotrophs (and perhaps the hypothalamus) to gonadal steroids (Turek and Campbell, 1979). In addition, there is compelling evidence that seasonal estrous activity in ewes involves increased sensitivity to gonadal steroids during the anestrous period (Legan et al., 1977). This phenomenon has been less extensively evaluated in rams, but injections of testosterone propionate suppress LH secretion to a greater extent in rams exposed to LD 16:8 than in rams exposed to LD 8:16 (Pelletier and Ortavant, 1975b). However, photic-induced changes in LH secretion also occur in the absence of the testes, since wethers in LD 8:16 have greater concentrations of LH in serum than wethers in LD 16:8 (Pelletier and Ortavant, 1975a).

Exposure of rams to LD 16:8 stimulates PRL secretion compared with rams maintained on LD 8:16 (Pelletier, 1973; Lincoln, 1979c; Almeida and Lincoln, 1982; Lincoln et al., 1982) and rams maintained under ambient photoperiod conditions have greatest concentrations of PRL in serum during the summer months (Ravault, 1976). Although PRL has been demonstrated to increase the sensitivity of rat testes to LH (Bartke

and Dalterio, 1976) and to increase the number of testicular LH receptors (Chan et al., 1981). PRL has not been associated with the number of testicular receptors for LH in rams or the affinity of LH for its receptor (Barenton and Pelletier, 1983). Therefore, if PRL is involved with the seasonal sexual cycle of rams, its involvement is probably independent of secretion of LH.

Role of the Pineal Gland in Reproductive Function. Surgical removal of the pineal gland abolishes the increase that is normally observed in episodic secretion of LH during decreasing light periods in intact rams (Kennaway et al., 1981). Pinealectomized rams maintained in long days had increased episodic secretion of LH (Barrell and Lapwood, 1978). Similarly, when cranial sympathectomy of rams is performed by removal of the superior cervical ganglia, secretion of LH does not change when the animals are exposed to alternating short and long days (Lincoln et al., 1981; Lincoln et al., 1982). In addition, short days do not have a detrimental effect on testicular size or serum concentrations of testosterone in ganglionectomized rams.

Denervation of the pineal also abolishes the diurnal rhythm in serum melatonin. Melatonin concentrations in the serum increase during the dark phase of the light:dark cycle in intact rams exposed to long and short days. However, removal of the superior cervical ganglia abolishes this rhythm (Lincoln et al., 1981; Lincoln et al., 1982; Lincoln and Almeida, 1982). Further, ganglionectomized rams fail to respond to increased daylight with elevated serum concentrations of PRL (Lincoln, 1979; Lincoln et al., 1982). Conversely, castrated rams maintained in LD 8:16 and implanted with testosterone do not have

decreased PRL secretion following ganglionectomy (Lincoln and Almeida, 1982).

Clearly, when pineal afferents are disturbed or the gland itself is removed, alterations in endocrine secretions of rams follow. Seasonal variations in gonadotropin secretion and gonadal function are interrupted by these manipulations, but elucidation of a definitive role for melatonin and PRL in seasonal reproductive function of rams will require further study.

Photoperiodic Control of Seasonal Breeding in Ewes. Considerable variation exists in the frequency of estrous cycles in ewes throughout the year (Hafez, 1952; Ortavant et al., 1964) and seasonal changes also occur in endocrine secretions. But, the duration of the breeding season varies among breeds of ewes. Although some breeds may miss only a few estrous cycles or none at all during the year, most British breeds have regular estrous cycles primarily during times of decreasing daylight (Ortavant et al., 1964). Estrous cycles usually occur at regular intervals of 16-17 days (McKenzie and Terrill, 1937; found in Karsch and Foster, 1981) from late summer until early spring (Hafez, 1952). Since duration of photoperiod regulates the seasonal reproductive cycle of ewes, estrous cycles can be initiated in anestrus ewes by exposing them to decreased photoperiod (Yeates, 1949).

The nature of PTM in ewes has not been demonstrated directly, but may involve a circadian rhythm of photosensitivity since there is evidence for this in rams (Schanbacher and Crouse, 1981; Almeida and Lincoln, 1982). Preception of photoperiodic time by the retino-hypothalamic tract, the involvement of the SCN in integrity of



circadian rhythms and the role of the pineal gland still remain questioned as components of seasonal reproductive function in ewes.

The endocrine mechanisms governing seasonal breeding in ewes have been evaluated in detail. The underlying cause of seasonal anestrus appears to be a lack of discharges of LH from the pituitary that are frequent enough to elicit a sustained increase in estradiol and initiate an ovulatory surge of LH (Goodman and Karsch, 1981; Karsch and Foster, 1981). Suppression of frequent pulses of LH is a result of increased potency of estradiol as an inhibitor of gonadotropin secretion during long days. The heightened sensitivity of the hypothalamo-hypophyseal system of ewes to estradiol continues until the transition into the breeding season (i.e., mid-summer). At this time, estradiol gradually becomes a weak inhibitor of tonic LH secretion, and allows more frequent secretion of LH and therefore a substantial increase in estradiol that is sufficient to trigger an ovulatory surge of LH. During the breeding season, progesterone replaces estradiol as the primary inhibitor of LH secretion and the secretion of progesterone governs the estrous cycle of ewes (Legan et al., 1977; Goodman and Karsch, 1981; Karsch and Foster, 1981).

Effects of Photoperiod on Growth of Lambs. Body weight gain increases when lambs are exposed to long (LD 16:8) photoperiods (Forbes et al., 1979; Schanbacher and Crouse, 1980; Schanbacher and Crouse, 1981) and the beneficial effect of long days on lamb growth can not be accounted for solely by increased feed intake, although this does occur (Forbes et al., 1979; Schanbacher and Crouse, 1980; Schanbacher and Crouse, 1981). When lambs are limit-fed and exposed

to LD 16:8, they grow faster than those in LD 8:16. This suggests that longer photoperiods result in increased feed efficiency (Forbes et al., 1979).

In experiments where feed intake was measured (Schanbacher and Crouse, 1980; Schanbacher and Crouse, 1981), lambs in longer photoperiods converted feed to body weight more efficiently than lambs exposed to shorter photoperiods. In contrast to the results obtained by others, Hackett and Hillers (1979) did not observe beneficial effects of supplemental lighting on lamb performance. Light was supplemented during various times at night and the exact duration of daylight and the time of light supplementation relative to dawn was not specified. Perhaps these variables or other unknown environmental factors could explain the lack of photoperiodic stimulation of growth in this experiment.

When lambs were exposed to a split-photoperiod (LDLD 7:9:1:7) but received a total of only 8 h of light per 24 h, they performed like lambs exposed to LD 16:8 and had increased daily gain, feed intakes, feed efficiencies and PRL in serum compared to lambs in LD 8:16 (Schanbacher and Crouse, 1981). This experiment provided evidence that photoperiodic time is measured by a circadian clock in sheep and that a photosensitive phase exists, at least in part, during the 17th h after dawn.

Accelerated growth of lambs exposed to long photoperiods may be due to elevated concentrations of PRL in serum (Forbes et al., 1975). Prolactin has been suggested to stimulate growth in cattle (McAtee and Trenkle, 1971) but growth rate was not affected when lambs were treated with 2-bromo- $\alpha$  ergocryptive, a drug which lowers PRL

concentrations in serum (Ravault et al., 1977). Therefore, the mechanism responsible for increased growth rate of lambs exposed to long photoperiods remains to be determined.

### Photoperiodic Influences on Growth, Milk

#### Production and Endocrine Function

##### of Cattle

Growth, Puberty and Lactation in Heifers. Most studies suggest a beneficial effect of long days on growth of heifers. Holstein heifers grew faster when exposed to LD 16:8 than heifers exposed to ambient photoperiods of 9 to 12 h of light daily (Peters et al., 1978; Peters et al., 1980) or continuous light (Peters et al., 1980). Increased gains of heifers exposed to 16 h of light daily may be due to increased dry matter intake (Peters et al., 1980; Peters et al., 1981) and improved feed efficiency (Peters et al., 1980). Increased PRL in serum, normally associated with longer days, probably is not the mechanism by which light increases growth of heifers, since concentrations of PRL in serum were suppressed by cold weather and the stimulatory effect of long photoperiods was still observed (Peters et al., 1980). Similarly, Schillo et al. (1983) found that heifers born in September grew faster from 6 to 9 mo of age (March to June) than heifers born in March. This suggests that longer days may stimulate growth of heifers prior to puberty.

Information concerning the influence of duration of photoperiod on pubertal attainment of heifers is inconsistent. Heifers born in the fall and exposed to increasing photoperiods between 6 and 12 mo of age reached puberty at a younger age than heifers born in March

(Schillo et al., 1982; Schillo et al., 1983). Similarly, exposure of heifers to LD 16:8 tended to hasten attainment of puberty compared with heifers exposed to winter photoperiods in Michigan (Peters et al., 1978). The apparently positive effects of increased photoperiod during the late prepubertal period may be due to increased growth rate of heifers (Peters et al., 1978; Peters et al., 1980; Schillo et al., 1983) which results in a more rapid attainment of the body weight necessary to initiate estrous cycles (Menge et al., 1960; Grass et al., 1982). In contrast, some investigators found that heifers born in the spring and exposed to shorter photoperiods during the late prepubertal period, reached puberty at a younger age than heifers born in the fall (Menge et al., 1960; Roy et al., 1980). Thus, the influence of season of birth (duration of photoperiod or other environmental factors) on the age at which heifers begin to exhibit regular estrous cycles is a question still to be resolved.

Exposure of lactating cows to LD 16:8 increased milk yield above that for cows exposed to natural photoperiods (Peters et al., 1978; Peters et al., 1981). Cows exposed to LD 16:8 consumed more dry matter than cows in shorter photoperiods (Peters et al., 1981). Although milk yield is increased when cows are exposed to longer photoperiods, the percentage of fat in the milk is not influenced by duration of photoperiod (Peters et al., 1981).

Endocrine Function of Cows. One consistent feature associated with exposure of cows and heifers to varying photoperiods is that PRL concentrations in serum are positively correlated with the duration of the light period (Karg and Schams, 1974; Peters and Tucker, 1978; Peters et al., 1981; Rzepkowski et al., 1982; Schillo et al., 1983).

However, ambient temperature and photoperiod interact so that PRL is suppressed for animals exposed to long photoperiods and cold temperatures (Peters and Tucker, 1978; Peters et al., 1980). Cows in LD 16:8 secrete more PRL in response to injection of thyrotropin releasing hormone (TRH; Peters et al., 1981) but photoperiod does not influence the release of PRL associated with milking (Peters et al., 1981) or the characteristic increase of PRL in serum between diestrus and estrus (Rzepkowski et al., 1982).

Duration of photoperiod has little, if any, effect on secretion of reproductive hormones in cows. The magnitude and the time of day of preovulatory surges of LH and FSH were similar for cows exposed LD 8:16 and LD 16:8 (Rzepkowski et al., 1982). Schillo et al. (1983) found greater concentrations of LH in the serum of prepubertal heifers (6 to 9 mo of age) born in September than in heifers born in March and this effect was consistent whether fall-born heifers were exposed to increasing or decreasing photoperiods. However, no consistent effects of photoperiod on concentrations of FSH in serum were observed between 6 and 12 mo of age. Concentrations of growth hormone (GH; Peters and Tucker, 1978; Peters et al., 1980; Peters et al., 1981), glucocorticoids (Peters et al., 1980; Peters et al., 1981) and thyroxine (Schillo et al., 1983) in cows are not influenced by duration of photoperiod.

Endocrine Function of Bulls. Longer photoperiods consistently increase concentrations of PRL in the serum of bulls (Karg and Schams, 1974; Bourne and Tucker, 1975; Leining et al., 1979; Petitclerc et al., 1980; Stanisiewski et al., 1982). After one week of exposure to LD 24:0, PRL in serum was increased above that observed in LD 8:16. But, following continued exposure to LD 24:0, concentrations of PRL

decreased to values not significantly different from those observed in bulls exposed to LD 8:16 (Leining et al., 1979). Bulls apparently do not distinguish red light (550 to 750 nm) or blue light (300 to 425 nm) from cool-white light (Leining et al., 1979). Bulls in LD 16:8 with 8 h of light supplied either as red or blue light (the other 8 h from cool-white fluorescent light) had increased concentrations of PRL (Leining et al., 1979).

In contrast to PRL, concentrations of LH in the serum of bulls appears to be unaffected by photoperiod (Bourne and Tucker, 1975; Stanisiewski et al., 1982). However, testosterone was elevated in serum of prepubertal bull calves which had been exposed to LD 16:8 for 12 wk. Even though LH secretion was not altered by photoperiod, the authors speculate that LH may have synergized with elevated PRL to increase testosterone secretion (Stanisiewski et al., 1982).

Photoperiodic effects on other endocrine parameters in bulls have not been investigated fully. Bulls exposed to 16 or 20 h of light daily tended to have reduced concentrations of glucocorticoids in serum compared to bulls exposed to only 8 h of light (Leining et al., 1980). However, average concentrations of GH, thyroid stimulating hormone and thyroxine were not affected by duration of light exposure. In addition, neither intensity of light (a range of 22 to 540 lx) nor wavelength (300 to 750 nm) affected concentrations of GH, glucocorticoids or thyroxine in bulls.

Photoperiodic Influences on Growth, Maternal  
Performance and Reproductive Function  
of Swine

Growth, Pubertal Attainment and Incidence of Seasonal Anestrous.

Duration of photoperiod clearly does not affect growth rate or feed efficiency of gilts (Braude et al., 1958; Dufour and Bernard, 1968; Ntunde et al., 1979; Berger et al., 1980; Wheelhouse and Hacker, 1982), yet its effect on pubertal attainment is less certain. For example, gilts exposed to complete darkness exhibited first estrus earlier than gilts maintained in ambient daylight of unspecified duration (Dufour and Bernard, 1968). However, Hacker et al. (1974) and Ntunde et al. (1979) found that gilts maintained in complete darkness were older at first estrous than gilts in short natural (9 to 10.8 h of light/d) or artificially long (LD 18:6) days. Diekman and Hoagland (1982) concluded that 15 h of light per day hastened puberty when the duration of natural light was decreasing. But, an experiment involving a total of 155 gilts suggested that age at puberty was similar for gilts in LD 18:6 versus LD 8:16 when two different light intensities (67 vs 225 lx) were used (Kelley et al., 1982). Based on these data, no definite conclusions can be reached regarding photoperiodic effects on pubertal attainment of gilts.

A seasonal component may be involved in the regulation of anestrous periods in domestic pigs. In European wild pigs, females usually are anestrous from June through December. If adequate nutrition is available, sows and gilts may initiate regular estrous cycles earlier in the fall (Mauget, 1982). Domestic pigs may exhibit variations in anestrous periods which appear to be independent of temperature

(Hurtgen et al., 1980). A lower percentage of sows returned to estrous after weaning during July through September regardless of whether they were housed in cooled or noncooled environments (Hurtgen et al., 1980). Olfactory bulbectomized domestic gilts also have anestrus periods through the summer and early autumn (Booth and Baldwin, 1983).

Maternal Performance of Sows. Productivity of sows may be increased by exposure to long photoperiods (LD 16:8). Sows exposed to LD 16:8 beginning at day 103 (Mabry et al., 1982b) or day 107 (Mabry et al., 1982a) of pregnancy weaned heavier litters with more pigs per litter than sows exposed to LD 8:16. Increased survival of baby pigs whose dams were exposed to LD 16:8 may have been due to increased milk production (Mabry et al., 1982b) and/or increased suckling activity of piglets (Mabry et al., 1982a). Although Stevenson et al. (1982) found no beneficial effect of increased photoperiod on the number of pigs weaned or survival rate, litter weights at weaning were increased for sows receiving longer photoperiods compared to those maintained in darkness during lactation. Thus, there may be a potential for increasing productivity by exposing sows to longer photoperiods during late gestation and lactation.

Endocrine Function of Sows and Gilts. Luteinizing hormone in serum obtained at weekly intervals was similar for gilts exposed to either continuous darkness, LD 18:6 or natural photoperiods (9 to 10.8 h of light/d) from 100 to 219 d of age (Ntunde et al., 1979). Similarly, gilts exposed to LD 15:9 had LH concentrations in serum which were similar to those found in gilts maintained in natural (decreasing) photoperiods (Diekman and Hoagland, 1982).



Prolactin in serum was not affected by exposure of sows to LD 16:8 just prior to and after parturition (Cunningham et al., 1981) or by exposure of prepubertal gilts to LD 15:9 (Diekman and Hoagland, 1982). However, significant seasonal variations in PRL were observed in wild sows bled at monthly intervals and greatest concentrations were observed during June (Ravault et al., 1982). It should be noted that these data were collected from sows exposed to ambient temperatures and this may account for some seasonal variation. We have demonstrated that PRL in plasma of heat stressed gilts is elevated during early pregnancy (Minton, Wettemann and Bazer, unpublished data). Yet, Ravault et al. (1982) found only isolated increases in PRL in the serum of domestic gilts exposed to ambient temperatures and photoperiods and concluded that season had little effect on PRL.

Growth and Reproductive Function of Boars. Duration of photoperiod does not greatly influence growth rate of young boars (Berger et al., 1980; Minton et al., 1980; Hoagland and Diekman, 1982). Mahone et al. (1979) found that boars exposed to 15 h of light daily grew faster than boars exposed to natural photoperiods (9-13 h of light/d) between 22 and 24 wk of age. However, treatment did not influence growth rate at other times in the experiment. Similarly, feed efficiency of boars is not improved by increasing the duration of photoperiod (Berger et al., 1980; Hoagland and Diekman, 1982).

Exposure of boars to LD 15:9 increased libido scores and decreased the age at which semen was first collected compared with boars exposed to natural daylight in Indiana (Mahone et al., 1979; Berger et al., 1980; Hoagland and Diekman, 1982). However, semen quality was similar for boars exposed to ambient and extended photoperiods (Mahone et al.,

1979; Berger et al., 1980) and sperm content and weights of the testes and epididymides were similar for boars exposed to LD 8:16 and LD 16:8 during pubertal development (Minton et al., 1980).

Concentrations of LH (Minton et al., 1980; Hoagland and Diekman, 1982) and FSH (Hoagland and Diekman, 1982) in serum are not significantly influenced by photoperiodic treatment of young boars. Yet, Minton et al. (1980) observed that at 25 wk of age, testosterone was increased in serum of boars exposed to 16 h of light per day when compared with boars in only 8 h of light. In one experiment, concentrations of testosterone and androstenedione in serum were increased for boars at 25 wk of age by exposure to LD 15:9, but this finding was not corroborated in a follow-up experiment (Hoagland and Diekman, 1982).

Concentrations of PRL in serum are not increased in domestic boars by increased daily light (Hoagland et al., 1981). In contrast, seasonal fluctuations in PRL in serum were observed throughout the year in wild boars and the greatest concentrations occurred in June and July (Ravault et al., 1982).

#### Endocrine Correlates of Sexual

##### Maturation in Boars

Testosterone is detectable in the serum of fetal boars between 40 and 60 d after conception, averages about .5 ng/ml, and decreases to about .2 ng/ml between days 60 and 100 after conception (Colenbrander et al., 1978). Concentrations of testosterone in serum increase between birth and 3 wk of age and average about 1 ng/ml (Colenbrander et al., 1978; Tan and Raeside, 1980). From about 4 to about 17 wk of age, concentrations of testosterone in serum gradually

increase from less than 1 ng/ml to almost 2 ng/ml (Colenbrander et al., 1978; FlorCruz and Lapwood, 1978; Tan and Raeside, 1980). Greater absolute concentrations of testosterone were observed by Allrich et al. (1982) between about 5 and 17 wk of age but this may reflect the more frequent sampling schedule employed in the experiment. Between about 18 and 28 wk of age, concentrations of testosterone in serum increase markedly (Colenbrander et al., 1978; FlorCruz and Lapwood, 1978; Tan and Raeside, 1980; Allrich et al., 1982) as do concentrations of estradiol-17 $\beta$  (Allrich et al., 1982). These endocrine changes correspond temporally with rapid testicular growth, increased volume of individual Leydig cells (FlorCruz and Lapwood, 1978; Allrich et al., 1982) and greater testosterone and estradiol-17 $\beta$  secretion in vitro from testicular tissues of boars (Allrich et al., 1983).

Serum concentrations of LH vary episodically during the early pubertal period in boars (Lapwood and FlorCruz, 1978) but average concentrations of LH in serum collected at frequent intervals did not increase during periods of rapid testicular growth and increased concentrations of testosterone in serum (Allrich et al., 1982). In contrast, FlorCruz and Lapwood (1978) observed increases in LH in plasma prior to pubertal development in boars which were sampled at biweekly intervals. In any event, an underlying mechanism of pubertal attainment in boars appears to be increased sensitivity of the testes to LH. As mentioned earlier, testicular tissue of boars is more sensitive to hCG between 16 and 20 wk of age and secretes more testosterone and estradiol-17 $\beta$  in vitro (Allrich et al., 1983).

Testes of pubertal and mature boars secrete sufficient testosterone to maintain average concentrations in serum between about .8 and 2.0 ng/ml

(Ellendorff et al., 1975; Claus and Gimenez, 1977; Lapwood and FlorCruz, 1978; Kattesh et al., 1979; Claus and Hoffmann, 1980; Tan and Raeside, 1980). Luteinizing hormone (Ellendorff et al., 1975; Lapwood and FlorCruz, 1978) and testosterone (Ellendorff et al., 1975; Lapwood and FlorCruz, 1978; Kattesh et al., 1979; Claus and Hoffmann, 1980; Tan and Raeside, 1980) in boars are secreted in an episodic or pulsatile fashion. Pulsatile secretion of LH and testosterone is thought to occur at random throughout the day since no rhythm of secretion relative to other environmental cues (e.g., lights-on or off) has been identified (Lapwood and FlorCruz, 1978). Association of pulses of LH with testosterone secretion in boars is difficult because of the variations in concentrations over time and the inconsistent and sometimes arbitrary identification of "secretory spikes" of LH and testosterone.

Concentrations of LH and testosterone in serum may decrease as pubertal boars become mature (Lapwood and FlorCruz, 1978). Concentrations of LH and testosterone in serum fluctuated less and were decreased in boars at 8 vs 4 mo of age. In other studies, LH fluctuated below 1 ng/ml from 166 to 240 d of age (FlorCruz and Lapwood, 1978) and testosterone in serum was negatively associated with age (from 160 to 208 d of age), although the magnitude of the correlation was not given (Kattesh et al., 1979). Dehydroepiandrosterone sulfate increased in plasma from 1 to 29 wk of age, declined slightly from 29 to 33 wk, then steadily increased until 46 wk of age (Tan and Raeside, 1980). Concentrations of dehydroepiandrosterone sulfate ranged from 5 ng/ml at 1 wk to about 50 ng/ml at 46 wk (Tan and Raeside, 1980). Average concentrations of cortisol in serum of

boars ranged from 9 to 23 ng/ml between about 5 and 33 wk of age (Allrich et al., 1982). Average concentrations of estradiol-17 $\beta$  in serum remained fairly stable between 5 and 13 wk of age (10-20 pg/ml) and increased sharply from 13 to 21 wk of age (less than 20 pg/ml to  $\sim$  90 pg/ml). Thereafter, concentrations of estradiol-17 $\beta$  in serum increased at a slower rate up to 33 wk of age (Allrich, 1982).

#### Influence of Hemicastration of Testicular Size and Endocrine Function

Removal of one testis, hemicastration (HC), results in a marked increase in size of the remaining testis in boars (Sundby et al., 1981), bulls (Johnson, 1978; Barnes et al., 1980a; Leidl et al., 1980; Barnes et al., 1981; Sundby et al., 1981; Barnes et al., 1983), rams (Voglmayr and Mattner, 1968; Johnson et al., 1971; Hochereau-de Reviers et al., 1976; Walton et al., 1978; Land et al., 1979) and rats (Liang and Liang, 1970; Ojeda and Ramirez, 1972; Ramirez and Sawyer, 1974; Cunningham et al., 1978). In addition, the epididymides may also increase in size in response to HC of bulls (Barnes et al., 1980a; Barnes et al., 1983) and rams (Johnson et al., 1971). Increased testicular size appears to be the result of both increased total tubular (Barnes et al., 1980b) and intertubular areas (Hochereau-de Reviers et al., 1976; Leidl et al., 1980). The diameter (Johnson, 1978; Barnes et al., 1980b) of seminiferous tubules and the height of the seminiferous epithelium and tubular lumen diameter (Barnes et al., 1980b) were also increased following HC.

Most evidence suggests that the testes of HC males have increased spermatogenic function. Increased relative numbers of each germinal

cell type were found in stage VII seminiferous tubules of HC bulls compared with intact bulls (Johnson, 1978). Hochereau-de Reviers et al. (1976) found more total  $A_0$  and  $A_1$  spermatogonia per testis and increased round spermatid production per day in HC rams. More total testicular and epididymal sperm were found in HC rams (Johnson et al., 1971) and bulls (Barnes et al., 1980a). Increased sperm output per testis per day was observed in HC rams (Voglmayr and Mattner, 1968) and with a fixed number of semen collections, more sperm were collected from HC bulls than intact bulls (Barnes et al., 1980a).

The increase in testis size following HC, and perhaps more importantly, the increase in intertubular area, result in testosterone secretion that is adequate to maintain serum concentrations similar to those of intact animals (Johnson, 1978; Barnes et al., 1980b; Barnes et al., 1981; Sundby et al., 1981; Barnes et al., 1983). Testicular tissue from HC animals may secrete more androgens since tissue from HC rams incorporated more  $^{14}\text{C}$ -acetate into testosterone than intact rams (Johnson et al., 1971). Gonadotropic support for the testis appears to be increased in HC males. Increased serum concentrations of FSH have been observed for HC bulls (Leidl et al., 1980; Barnes et al., 1981; Barnes et al., 1983), rams (Walton et al., 1978) and rats (Ojeda and Ramirez, 1972; Ramirez and Sawyer, 1974; Cunningham et al., 1978). Both the content and concentration of LH in the pituitary were increased in HC bulls (Barnes et al., 1980c) and HC bulls released more LH and FSH in response to GnRH (Barnes et al., 1981). So, even though serum LH concentrations are similar for HC and intact males (Barnes et al., 1980c; Barnes et al., 1981; Barnes et al., 1983) more releasable LH may be available in the pituitary. Concentrations of PRL in serum were increased in HC bulls at

1 and 6 wk after removal of one testis, but were similar at 12 and 24 wk (Barnes et al., 1983).

## CHAPTER III

### THE INFLUENCE OF DURATION OF PHOTOPERIOD AND HEMICASTRATION ON GROWTH, TESTICULAR AND ENDOCRINE FUNCTION OF BOARS

#### Summary

Yorkshire boars were used to evaluate the influence of duration of photoperiod and hemicastration on growth and testicular and endocrine function. At 10 wk of age, 5 hemicastrate (HC) and 5 intact (I) boars were assigned to either 8 or 16 h of light daily and remained on these treatments until 6 mo of age. Body weights were recorded biweekly throughout the experiment. Venous cannulae were placed in all boars at 6 mo of age and serum was collected at 30-min intervals from 0800 to 2000 h. Gonadotropin releasing hormone (GnRH) was infused at 2000 h (50  $\mu$ g) and at 2030 h (250  $\mu$ g) and samples of serum were collected until 2400 h. The following day, all boars were castrated and the weight and sperm content of the testes and epididymides determined. At castration, all boars were implanted with 16 cm Silastic tubing filled with crystalline testosterone. Fourteen days later, venous cannulae were inserted into all animals and serum was collected at frequent intervals for 2 h prior to and 6 h after an intramuscular injection of 50 mg of testosterone. Thereafter, serum was collected at 3-h intervals until 24 h after testosterone injection.



Growth of boars was not significantly affected by duration of photoperiod or number of testes. Similarly, duration of photoperiod did not affect testicular or epididymal weights or sperm numbers in these tissues. Hemicastrated boars had greater testicular ( $P < .01$ ) and capita-corpora (C-C) epididymal weights ( $P < .05$ ) and more testicular and C-C sperm ( $P < .01$ ). Basal concentrations of LH in the serum were generally below the sensitivity of the assay for all boars ( $< .5$  ng/ml). Concentrations of prolactin (PRL) and testosterone were similar for I and HC boars. However, concentrations of PRL in the serum of boars exposed to 16 h of light per day tended to be increase ( $P < .13$ ) compared with boars in 8 h of light but concentrations of testosterone were similar for boars exposed to both light treatments. Luteinizing hormone and testosterone secretion after GnRH treatment were not significantly affected by duration of photoperiod and HC and I boars had similar concentrations of testosterone in serum after infusion of GnRH. However, HC boars secreted more LH in response to GnRH than I boars ( $P < .05$ ). We conclude that the testes and epididymides of HC boars contain more sperm than I boars at 6 mo of age, but growth and testosterone in serum are not significantly altered by duration of photoperiod or HC. Hemicastrate boars secrete more LH in response to exogenous GnRH than I boars and increased daily light exposure may result in increased PRL secretion in pubertal boars.

#### Introduction

Even though domestic pigs do not have periods of complete sexual inactivity during the year, their sexual development may be altered by variations in photoperiod. Exposure of growing boars to 15 h of

light daily increases libido and decreases the age at which semen can be collected (Mahone et al., 1979; Berger et al., 1980; Hoagland and Diekman, 1982). Exposure of boars to 16 h of light daily tends to increase testosterone concentrations in the serum (Minton et al., 1980). However, other experiments evaluating testicular endocrine function of boars at similar ages with infrequently collected blood samples yielded inconsistent results (Hoagland and Diekman, 1982).

Increases in PRL in serum are observed during exposure of bulls (Bourne and Tucker, 1975; Leining et al., 1979) and rams (Pelletier, 1973; Lincoln, 1979; Lincoln et al., 1982) to increased photoperiods. Increased concentrations of PRL were observed during the summer months in wild boars (Ravault et al., 1982) yet duration of photoperiod did not alter PRL concentrations in blood collected at weekly or biweekly intervals from domestic boars (Hoagland et al., 1981; Ravault et al., 1982).

The sensitivity of the hypothalamo-hypophyseal axis to feedback from gonadal steroids increases during exposure to long days in male golden hamsters (Turek and Ellis, 1981). A similar increase in the sensitivity to gonadal steroids may also occur in rams during the nonbreeding season (Pelletier and Ortavant, 1975b). However, no information is available concerning whether differences in the sensitivity of the hypothalamo-hypophyseal axis to feedback from gonadal steroids exists for boars exposed to different photoperiods.

The purpose of this study was to evaluate the influence of duration of photoperiod, hemicastration and their interaction on endocrine and testicular functions of pubertal boars.

## Materials and Methods

Experiment 1

Twenty purebred Yorkshire boars from 8 litters farrowed between March 2, 1981 and March 25, 1981 were used in this study. When the boars averaged 8 wk of age, half were hemicastrated (HC) and the other half remained intact (I). One week later, all boars were transferred to the Southwestern Livestock and Forage Research Station, El Reno, Oklahoma. The boars were allotted to one of two temperature and light controlled chambers (3 m x 12 m) so that 5 I and 5 HC boars were raised as a group. Fluorescent and incandescent lighting (600 lx) were provided from 0800 to 2000 h. One week later lighting was abruptly changed to LD 8:16 in one chamber and LD 16:8 in the other chamber and the boars were exposed to these treatments for 16 weeks. Lights were turned on at 0800 h and off at 1600 h (LD 8:16) or 2400 h (LD 16:8). Ambient temperatures were recorded daily and maximum daily temperatures in both chambers averaged  $27 \pm 3$  C.

The boars were weighed every two weeks throughout the experiment. An 18% crude protein growing ration containing .75% lysine was provided in self-feeders until the boars averaged  $53.1 \pm .5$  kg, then a 16% crude protein (.62% lysine) finishing ration was supplied for the remainder of the experiment. Water was continuously available from automatic nipple waterers.

At an average of  $184 \pm 1$  days of age, cannulae were surgically placed in the jugular vein or vena cava of all boars (Kreider, 1973). The next day, samples of blood (10 to 12 ml) were obtained every .5 h and 3 ml of sterile 2.9% sodium citrate were placed in the cannula

between sampling to prevent clotting. A sample of blood was taken at 2000 h, then 50  $\mu$ g of GnRH (Abbott Laboratories, North Chicago, IL) were rapidly infused through the cannula. Ten milliliters of sterile .85% NaCl were flushed through the cannula and the cannula was filled with sterile 2.9% sodium citrate. At 2030 h, another sample of blood was obtained, then 250  $\mu$ g of GnRH were infused and the cannula was again flushed with NaCl and sodium citrate. Samples of blood were taken at .5 h intervals until 2400 h.

Samples of blood were allowed to clot at room temperature for 20 min, then stored at 4 C for 24 h until centrifuged (1000 x g for 30 min). The serum was decanted and stored at -10 C until LH, PRL and testosterone were quantified by radioimmunoassays. The radioimmunoassay for testosterone in porcine serum has been validated in our laboratory (Wettemann and Desjardins, 1979). Concentrations of LH in serum were quantified by the radioimmunoassay described by Hallford et al. (1975) except that USDA-pLH-I-1 and USDA-pLH-B-1 (supplied by Dr. D. J. Bolt, USDA-BARC-Reproduction Lab, Beltsville, MD) were used as radiolabeled ligand and standard, respectively. Phosphate buffered saline (PBS, .1 M, pH 7.0) plus 1% lypholyzed egg whites (1% EW-PBS) was used as the assay buffer. Dose response curves for dilutions of barrow serum and a porcine pituitary homogenate were parallel to the standard curve between .1 and 1.6 ng LH/tube (figure 1). The cross-reactivity of USDA-pGH-B-1, USDA-pFSH-B-1 and USDA-pPRL-B-1 (also gifts from Dr. D. J. Bolt) at quantities that displaced 50% of  $^{125}$ I-pLH bound to antibody ( $B/B_0$ ) was 2.0%, .3%, and <.4%, respectively. Ten-fold more LER 778-4 pLH than USDA-pLH-B-1 was needed to produce 50%  $B/B_0$  (figure 2).

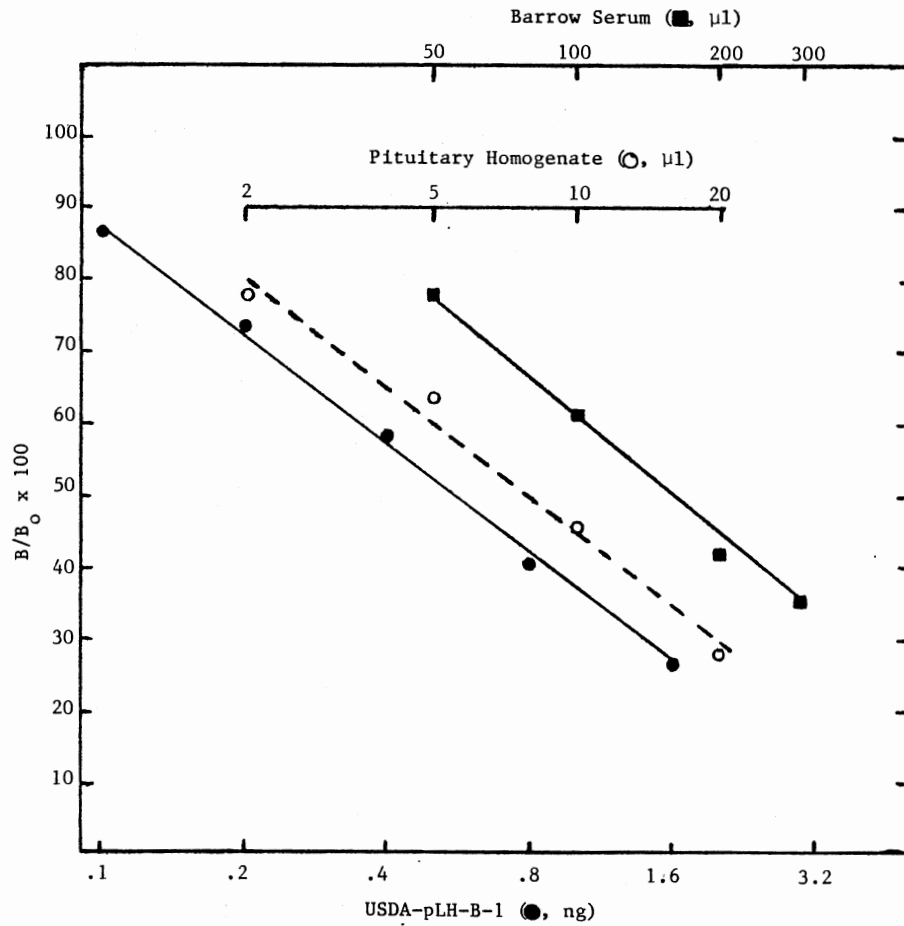


Figure 1. Displacement of  $^{125}\text{I}$ -USDA-pLH-B-1 by USDA-pLH-B-1, Barrow Serum and Porcine Pituitary Homogenate in the Luteinizing Hormone Assay

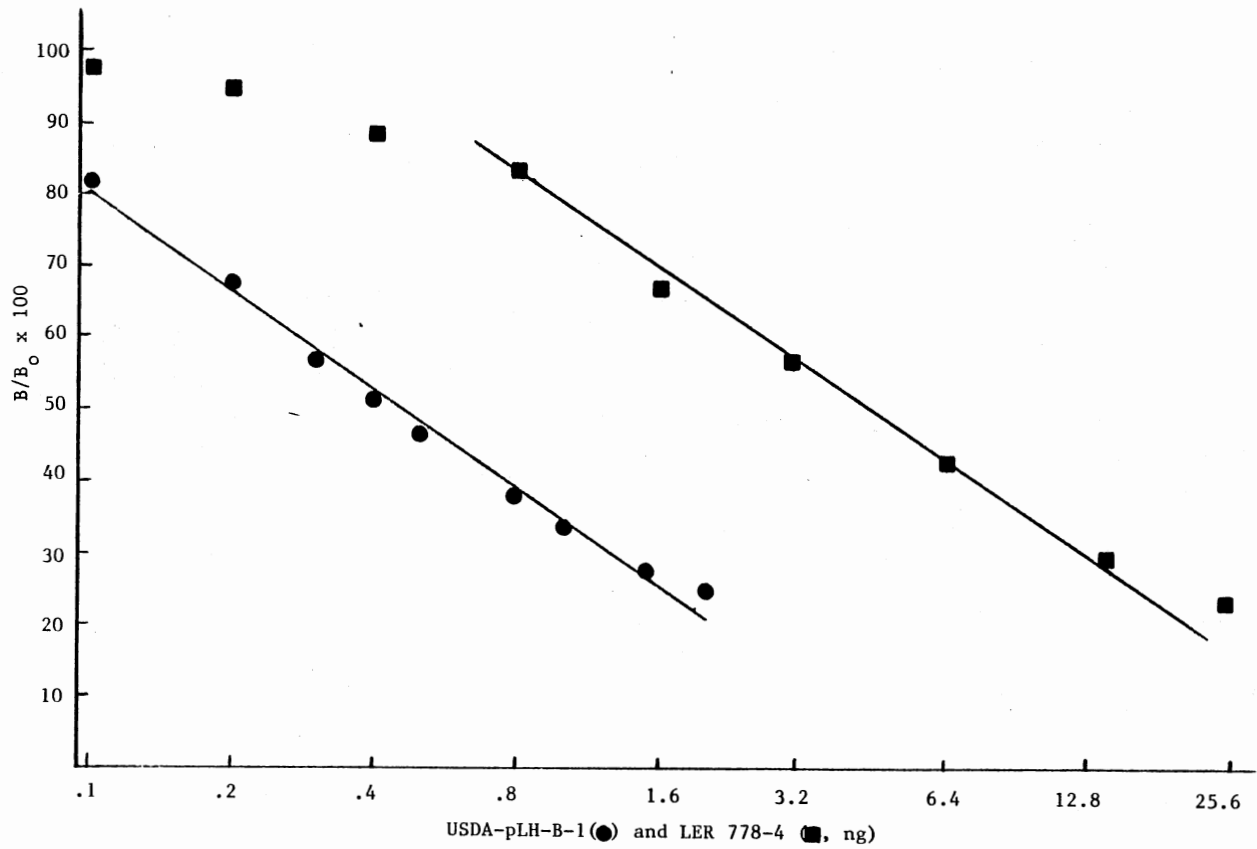


Figure 2. Displacement of  $^{125}\text{I}$ -USDA-pLH-B-1 by USDA-pLH-B-1 and LER 778-4 in Luteinizing Hormone Assay

Standard LH (diluted in 1% EW-PBS) ranging from .1 to 3.2 ng/tube was included in each assay. At a dilution of 1:160,000, the antisera (#566, supplied by Dr. G. D. Niswender, Colorado State University, Fort Collins, Colorado) bound 11% of  $^{125}\text{I}$ -LH in the absence of nonlabeled LH. At this dilution of antibody, the lower limit of sensitivity of the assay was .5 ng LH/ml serum. Increasing quantities (1, 2, 5 and 10 ng) of USDA-pLH-B-1 were added to 1 ml samples of barrow serum and  $1.2 \pm .3$  (n = 10),  $2.4 \pm .2$  (n = 4),  $4.8 \pm .4$  (n = 4), and  $10.5 \pm .6$  ng (n = 4), respectively, were measured with the assay. The intra-assay and inter-assay coefficients of variation were 10.1% and 12.7%, respectively (estimated from 10 assays).

Concentrations of PRL in porcine serum were quantified by a homologous double-antibody radioimmunoassay. The assay was similar to that described by Kraeling et al. (1982) except that USDA-pPRL-I-1 and USDA-pPRL-B-1 were used for iodination and standard, respectively. Quantities of standard PRL ranging from .1 to 12 ng/500  $\mu\text{l}$  were prepared in 50 ml volumes then divided into aliquots of approximately 3 ml and frozen. Standards were prepared in PBS with 1% bovine serum albumin added (1% BSA-PBS). The antiserum (goat anti-pPRL, RPI 10333) was purchased from Research Products International Corporation (Elk Grove Village, IL) and was diluted 1:80,000 in .05 M ethylenedinitrilo-tetra-acetic-acid-PBS (PBS-EDTA, pH 7.0), to which normal goat serum had been added (1:400, NGS-PBS-EDTA).

Duplicates (200 and 300  $\mu\text{l}$ ) of each serum sample were assayed in tubes containing 1% BSA-PBS (300 and 200  $\mu\text{l}$ , respectively). Total binding tubes (500  $\mu\text{l}$  1% BSA-PBS), standard tubes and tubes containing serum samples all received 200  $\mu\text{l}$  of antisera. Nonspecific binding

tubes (500  $\mu$ l 1% BSA-PBS) received 200  $\mu$ l NGS-PBS-EDTA. All tubes were incubated for 24 h at 4 C. Then, 100  $\mu$ l  $^{125}$ I-pPRL ( $\sim$  10,000 cpm) were added to all assay tubes and the assay was incubated for 24 h at 4 C. Then, rabbit anti-goat gamma globulin (Research Products International Corp., Elk Grove, IL) diluted in PBS-EDTA (1:20) was added to all tubes (200  $\mu$ l) and the tubes were incubated for 72 h at 4 C. Then, cold PBS (3 ml) was added to each tube and the tubes were centrifuged at 2000 x g. The supernatant was decanted and the radioactivity in the precipitate was quantified.

Quantities of USDA-pFSH-B-1, USDA-pGH-B-1 and USDA-pLH-B-1 up to 1000 ng did not cross react with the antisera to pPRL. Increasing volumes of boar serum and a porcine pituitary homogenate were parallel to the standard curve between .8 and 6.4 ng of USDA-pPRL-B-1 per tube (figure 3). One, five and 10 ng pPRL were added to 1 ml samples of gilt serum (n = 7) and  $1.5 \pm .1$ ,  $6.8 \pm .2$ , and  $10.6 \pm .5$  ng were measured in the assay (corrected for concentration of PRL in gilt serum to which 0 ng pPRL were added). The intra- and inter-assay coefficients of variation were 6.8% and 15.5%, respectively.

All boars were castrated the day following blood sampling. Weights of the testes and epididymides were recorded. Sperm numbers were determined hemocytometrically from homogenates (Amann and Lambiase, 1969) of testicular parenchymae and C-C and caudae (C) epididymides.

The data obtained for body weights, testicular characteristics and concentrations of hormones before GnRH are described by:

$$Y_{ij} = \mu + P_i + C_j + (PC)_{ij} + e_{ij}$$

where  $Y_{ij}$  is either body weight, a testicular characteristic or LH, PRL



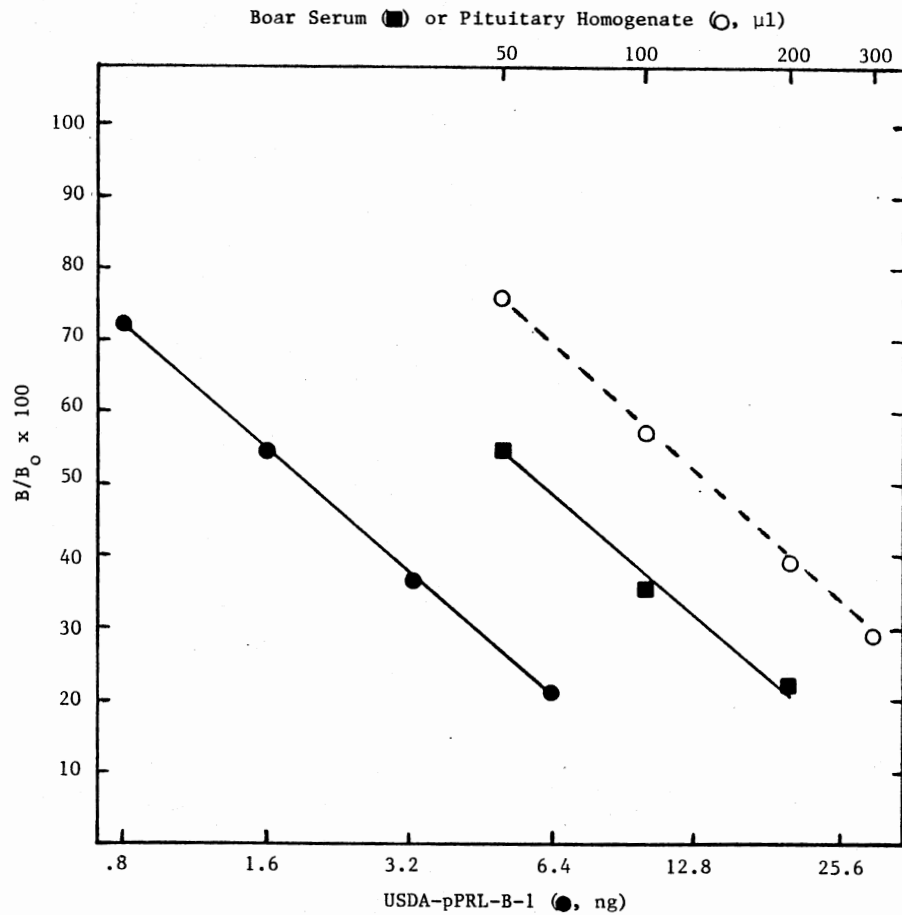


Figure 3. Displacement of  $^{125}$ I-USDA-pPRL-B-1 by USDA-pPRL-B-1, Barrow Serum and Porcine Pituitary Homogenate in the Prolactin Assay

or testosterone, P is photoperiod, C is castration status (I or HC) and PC is the interaction of these effects. The components  $\mu$ ,  $P_i$ , and  $C_j$  were treated as fixed effects of all records of photoperiod i and castration status j. Random error  $e_{ij}$  was specific to each observation.

Polynomial equations were fit to LH and testosterone data following GnRH to compare the responses over time. Time was a continuous independent variable and LH and testosterone concentration were dependent variables. The order of best fit was identified as the highest order equation with statistical significance ( $P < .05$ ). However, if increasing the order of equation by one degree resulted in a significant fit but did not increase  $R^2$  by at least 2%, the lower order equation was used. Table 1 illustrates  $R^2$  values and probability levels associated with each order of fit.

The LH data obtained from the regressions are explained by:

$$Y_{ijkl} = \mu + P_i + C_j + (PC)_{ij} + B(PC)_{kij} + T_L + T_L^2 + T_L^3 + e_{ijkl}$$

and that for testosterone by:

$$Y_{ijkl} = \mu + P_i + C_j + (PC)_{ij} + B(PC)_{kij} + T_1 + T_1^2 + e_{ijkl}$$

where  $Y_{ijkl}$  is either LH or testosterone response to GnRH and P is photoperiod, C is castration status (HC or I), PC is the interaction of these effects, B(PC) is boar within photoperiod-castration status and T is time. The components  $\mu$ ,  $P_i$ ,  $C_j$ , and  $T_L$  were treated as fixed effects of all records of photoperiod i, castration status j, boar k within photoperiod i and castration status j and time 1. Orthogonal comparisons (table 2) were used to determine differences in LH and testosterone following GnRH treatment. Tests of treatment effects were

TABLE 1  
 $R^2$  VALUES AND LEVELS OF SIGNIFICANCE FOR POLYNOMIAL EQUATIONS  
 CONTAINING INCREASING ORDERS OF TIME AFTER GnRH TREATMENT

Item	Hormone	
	LH	Testosterone
Time		
$R^2$	.4529	.3627
Prob > F	.3915	.0001
Time <sup>2</sup>		
$R^2$	.7217	.5575 <sup>a</sup>
Prob > F	.0001	.0001
Time <sup>3</sup>		
$R^2$	.7527 <sup>a</sup>	.5594
Prob > F	.0001	.4578
Time <sup>4</sup>		
$R^2$	.7527	.5617
Prob > F	.0001	.4142

<sup>a</sup>Equation that was used in the analyses.

made by comparing residual sums of squares obtained from combined analysis of treatments under consideration against the sum of residual sums of squares for treatment comparisons analyzed individually (tables in Appendix).

TABLE 2  
ORTHOGONAL COMPARISONS OF TREATMENT EFFECTS FOR LH  
AND TESTOSTERONE CONCENTRATIONS AFTER GnRH

Comparison	Duration of Photoperiod			
	8h <sup>a</sup>		16h <sup>a</sup>	
	I <sup>b</sup>	HC <sup>b</sup>	I	HC
8I, 8HC vs 16I, 16HC	1	1	-1	-1
8I vs 8HC	1	-1	0	0
16I vs 16HC	0	0	1	-1

<sup>a</sup>Exposure to 8 or 16 h of light daily.

<sup>b</sup>Intact (I) or hemicastrate (HC).

### Experiment 2

This experiment utilized boars from in Exp. 1 after castration. At the time of castration, 16 cm of Silastic<sup>®</sup> tubing (3.35 mm ID x 4.65 mm OD, Dow Corning Corporation, Midland, MI) containing crystalline testosterone were subdermally implanted in the neck of all boars. Testosterone was packed into 8 cm lengths of tubing and the ends of the tubing were plugged with silicone elastomer (Eli Lilly and Company, Indianapolis, IN). The implants were washed in dilute soap and water

solution, then rinsed with tap water before two, 8 cm implants were placed in each castrated boar. The boars were returned to their respective photoperiod treatments for 2 wk to recover from castration, then venous cannulae were placed in all barrows.

The following morning, blood samples were obtained at 15-min intervals from 0800 to 1000 h. At 1200 h a blood sample was taken, then 50 mg of testosterone in corn oil (10 mg/ml) were injected intramuscularly. Blood samples were obtained at 15-min intervals until 1500 h, then at 30-min intervals from 1500 h to 1800 h (6 h after testosterone injection). Thereafter, blood samples were obtained every 3 h until 1200 h the following day (24 h after testosterone injection). Serum was obtained and LH and testosterone were quantified as described for Exp. 1.

Concentrations of LH in serum were generally below the sensitivity of the assay, so, these data are reported as means  $< .5$  ng/ml. Concentrations of testosterone in serum after testosterone injection were regressed on time and effects of photoperiod treatment and number of testes before castration were determined by orthogonal comparisons (table 12) as described for Exp. 1. Concentrations of testosterone in serum before testosterone injection were averaged within barrows and analyzed by analysis of variance with effects of photoperiodic treatment, previous number of testes and the interaction of these effects included in the model. Least-squares means for concentrations of testosterone before and after testosterone injection are presented.

## Results and Discussion

### Experiment 1

Body Weight. Body weights of boars are illustrated in figure 4. Hemicastration did not significantly affect growth of boars, so these data were pooled across HC and I boars within each photoperiod. Body weights were similar for boars exposed to 8 and 16 h of light daily.

These results demonstrate that duration of photoperiod does not significantly affect body weight gain of boars from 10 to 24 wk of age and concur with other studies (Berger et al., 1980; Hoagland and Diekman, 1982). Similar to our results, it has been reported that hemicastration does not alter growth of bulls (Barnes et al., 1980) or boars (Sundby et al., 1981).

Testicular Characteristics. There was a tendency for an interaction ( $P < .10$ ) between duration of photoperiod and number of testes for testicular sperm cell concentration (table 3). The reason for this tendency is not clear, but when total sperm/testis are considered, no interaction was evident. Duration of photoperiod did not influence testicular weight, total testicular sperm, epididymal weight or sperm numbers in the epididymides (table 3). Similarly, in a previous study, we observed that duration of photoperiod did not influence weight of the testes and epididymides (Minton et al., 1980).

There was a significant effect of HC on testicular characteristics. Since there was no effect of photoperiod on testicular characteristics, the data were pooled across photoperiods within I and HC boars (table 4). Clearly, HC increase ( $P < .01$ ) the weight of the testes (472 vs 309 g for HC and I boars, respectively). Testicular sperm concentrations were

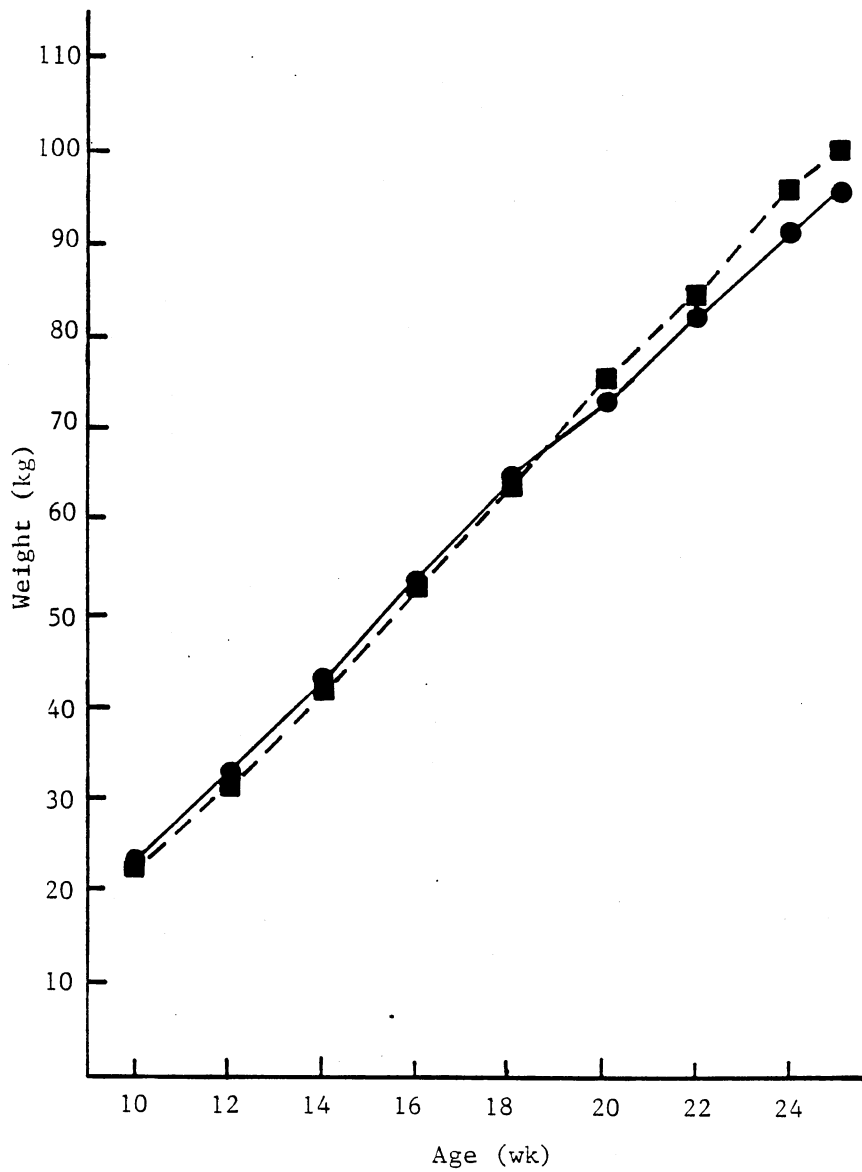


Figure 4. Body Weights of Boars Exposed to 8 (■) or 16 (●) Hours of Light Daily

TABLE 3

TESTICULAR AND EPIDIDYMAL CHARACTERISTICS (MEAN  $\pm$  SEM) OF INTACT (I) AND HEMICAstrate (HC) BOARS EXPOSED TO 8 OR 16 HOURS OF LIGHT DAILY

Item	Treatment			
	8I	8HC	16I	16HC
No. boars	4	5	5	4
Testicular wt. (g)	293.9 $\pm$ 34.2	512.0 $\pm$ 30.6	324.0 $\pm$ 30.6	432.5 $\pm$ 34.2
Testicular sperm ( $\times 10^6$ /g)	95.5 $\pm$ 12.0	78.9 $\pm$ 10.7	67.8 $\pm$ 10.7	92.2 $\pm$ 12.0
Testicular sperm ( $\times 10^9$ /testis)	28.4 $\pm$ 5.3	39.6 $\pm$ 4.8	22.1 $\pm$ 4.8	40.7 $\pm$ 5.3
C-C <sup>a</sup> wt. (g)	26.4 $\pm$ 2.9	35.4 $\pm$ 2.6	28.4 $\pm$ 2.6	33.1 $\pm$ 2.9
C-C sperm ( $\times 10^9$ /g)	.8 $\pm$ .1	1.3 $\pm$ .1	.6 $\pm$ .1	.9 $\pm$ .1
C-C sperm ( $\times 10^9$ /side)	20.4 $\pm$ 6.2	46.9 $\pm$ 5.6	18.0 $\pm$ 5.6	30.7 $\pm$ 6.2
C <sup>b</sup> wt. (g)	35.0 $\pm$ 3.0	37.9 $\pm$ 2.7	33.8 $\pm$ 2.7	35.6 $\pm$ 3.0
C sperm ( $\times 10^9$ /g)	1.6 $\pm$ .2	2.0 $\pm$ .2	1.6 $\pm$ .2	1.9 $\pm$ .2
C sperm ( $\times 10^9$ /side)	58.7 $\pm$ 10.5	75.2 $\pm$ 9.4	54.5 $\pm$ 9.4	68.0 $\pm$ 10.5

<sup>a</sup>Capita-corpora epididymides.

<sup>b</sup>Caudae epididymides.



TABLE 4  
 TESTICULAR AND EPIDIDYMAL CHARACTERISTICS (MEAN  $\pm$  SEM)  
 OF INTACT (I) AND HEMICAstrate (HC) BOARS

Item	Treatment	
	I	HC
No. boars	9	9
Testicular wt. (g)	308.9 $\pm$ 22.9 <sup>c</sup>	472.2 $\pm$ 22.9 <sup>d</sup>
Testicular sperm (X10 <sup>6</sup> /g)	81.7 $\pm$ 8.0	85.6 $\pm$ 8.0
Testicular sperm (X10 <sup>9</sup> /testis)	25.2 $\pm$ 3.6 <sup>c</sup>	40.2 $\pm$ 3.6 <sup>d</sup>
C-C <sup>a</sup> wt. (g)	27.4 $\pm$ 1.9 <sup>e</sup>	34.2 $\pm$ 1.9 <sup>f</sup>
C-C sperm (X10 <sup>9</sup> /g)	.7 $\pm$ .1 <sup>c</sup>	1.1 $\pm$ .1 <sup>d</sup>
C-C sperm (X10 <sup>9</sup> /side)	19.2 $\pm$ 4.2 <sup>c</sup>	38.8 $\pm$ 4.2 <sup>d</sup>
C <sup>b</sup> wt. (g)	34.4 $\pm$ 2.0	36.7 $\pm$ 2.0
C sperm (X10 <sup>9</sup> /g)	1.6 $\pm$ .1	2.0 $\pm$ .1
C sperm (X10 <sup>9</sup> /side)	56.6 $\pm$ 7.1	71.6 $\pm$ 7.1

<sup>a</sup>Capita-Corpora epididymides.

<sup>b</sup>Caudae epididymides.

<sup>c,d</sup>Significant effect of number of testes (P < .01).

<sup>e,f</sup>Significant effect of number of testes (P < .05).

similar for I and HC boars but HC boars, with larger testes, had more total testicular sperm ( $P < .01$ ) per testis than I boars. The weight of C-C epididymides was also increased ( $P < .05$ ) for HC compared with I boars. Although the weight and sperm content of C epididymides were greater for HC boars than I boars, this difference was not significant ( $P < .10$ ).

In agreement with our data, increased testicular weight following HC has been previously observed for boars (Sundby et al., 1981) as well as bulls (Johnson, 1978; Barnes et al., 1980a; Leidl et al., 1980; Barnes et al., 1981; Sundby et al., 1981; Barnes et al., 1983), rams (Voglmayr and Mattner, 1968; Johnson et al., 1971; Land and Carr, 1975; Hochereau-de Reviers et al., 1976; Walton et al., 1978; Land et al., 1979) and rats (Liang and Liang, 1970; Ojeda and Ramirez, 1972; Ramirez and Sawyer, 1974; Cunningham et al., 1978). We observed a 53% increase in testicular weight which is less than that previously observed (98%) for boars castrated after 7 mo of age (Sundby et al., 1981). Hemicastration of bulls also results in increased weight of the remaining epididymis (Barnes et al., 1980a; Barnes et al., 1983) and we found that HC boars had heavier C-C epididymides than I boars. Perhaps increased epididymal weight following HC is the result of increased length and diameter of tubular elements within the epididymis as has been demonstrated for seminiferous tubules in the testes of HC bulls (Barnes et al., 1980b; Leidl et al., 1980).

The failure of duration of photoperiod to alter the number of sperm in the testes and epididymis of boars is consistent with our previous findings (Minton et al., 1980) and is supported by observations that 15 h of light supplied to boars of similar ages as

those in this experiment did not significantly alter the quantity of sperm in ejaculates (Mahone et al., 1979; Berger et al., 1980).

Increased total testicular and epididymal sperm were found in HC rams (Johnson et al., 1971) and bulls (Barnes et al., 1980a). Similarly, we found more total sperm in the testes and C-C epididymides of HC than I boars. In addition, concentrations of sperm in C-C epididymides were significantly increased and small, non-significant increases in sperm concentrations in the testes and C epididymides of HC boars were observed in this study. Thus, our results, together with the observation that HC bulls had increased relative numbers of each germinal cell type in stage VII seminiferous tubules (Johnson, 1978), indicates that the testes of HC males produce more sperm per gram of tissue than tissue from intact males.

Endocrine Function. Average concentrations of LH in the serum of boars in each treatment group were usually below the sensitivity ( $< .5$  ng/ml) of our assay (table 5). Consequently, these data are skewed and preclude the use of analysis of variance. Relatively low concentrations of LH probably reflect the high purity of the standard (USDA-pLH-B-1) we used, however low concentrations of LH in serum have also been observed in other studies utilizing pubertal boars and different preparations of LH standards (FlorCruz and Lapwood, 1978; Lapwood and FlorCruz, 1978). Nonetheless, based on these and other data (Minton et al., 1980; Hoagland and Diekman, 1982), we suggest that duration of photoperiod did not dramatically alter concentrations of LH in the serum of pubertal boars.

TABLE 5

AVERAGE CONCENTRATIONS (MEAN  $\pm$  SEM) OF LUTEINIZING HORMONE (LH), PROLACTIN AND TESTOSTERONE IN INTACT (I) AND HEMICAstrate (HC) BOARS EXPOSED TO 8 OR 16 HOURS OF LIGHT DAILY

Item	8I	8HC	Treatment		16HC	$\overline{16}$
			$\overline{8}$	16I		
No. boars	4	5		5	4	
LH (ng/ml)	<.5	<.5		<.5	<.5	
Prolactin <sup>a</sup> (ng/ml)	2.7 $\pm$ .3	2.6 $\pm$ .3	2.6 $\pm$ .2 <sup>b</sup>	2.8 $\pm$ .3	3.5 $\pm$ .3	3.1 $\pm$ .2 <sup>c</sup>
Testosterone (ng/ml)	4.7 $\pm$ .8	4.0 $\pm$ .7	4.3 $\pm$ .5	3.2 $\pm$ .7	3.6 $\pm$ .8	3.4 $\pm$ .5

<sup>a</sup>Mean for entire 16 h sampling period.

<sup>b,c</sup>Mean for boars in 8 h versus 16 h (P < .13).

Average concentrations of PRL in the serum were not significantly affected by HC of boars (table 5). Similarly, PRL was not significantly different in HC and I bulls at 6 and 12 wk after hemicastration (Barnes et al., 1983). Boars exposed to the longer photoperiod tended ( $P < .13$ ) to have increased concentration of PRL in serum ( $3.1 \pm .2$  vs  $2.6 \pm .2$  ng/ml for boars exposed to 16 and 8 h of light daily, respectively). Increases in PRL in serum occur when bulls (Bourne and Tucker, 1975; Leining et al., 1979) and rams (Pelletier, 1973; Lincoln, 1979; Lincoln et al., 1982; Almeida and Lincoln, 1982) are exposed to longer photoperiods. In contrast, concentrations of PRL were similar when samples of serum were collected infrequently from boars in extended and natural photoperiods (Hoagland et al., 1981). European wild boars had greatest concentrations of PRL during the summer months but no clear seasonal trend was observed for domestic boars (Ravault et al., 1982). Taken together, these data suggest that variations in duration of photoperiod may have marginal effects on PRL secretion in the pubertal domestic boar.

Average concentrations of testosterone in serum were similar for HC and I boars, regardless of photoperiod treatment (table 5). Our data are in agreement with data for HC bulls (Johnson, 1978; Barnes et al., 1980c; Barnes et al., 1981; Barnes et al., 1983) and boars (Sundby et al., 1981) and suggests that the testes of HC males secretes sufficient testosterone to maintain peripheral concentrations that are similar to those found in intact males. Duration of photoperiod did not significantly influence average concentrations of testosterone in the serum of boars (table 5). Boars exposed to 16 h of light daily tended to have increased testosterone in serum compared with boars

exposed to 8 h of light (Minton et al., 1980). Hoagland and Diekman (1982) observed increases in testosterone in the serum of boars exposed to increased photoperiods at 24 and 25 wk of age in one experiment but the effect was not observed in a follow-up experiment. Perhaps unknown environmental variables are responsible for the inconsistent results which have been reported for testosterone in boars exposed to long versus short photoperiods.

Concentrations of LH and testosterone following treatment with GnRH were similar ( $P > .10$ ) for boars exposed to 8 and 16 h of light daily (figure 5). This observation is consistent with our previous findings (Minton et al., 1980). The pattern of LH release was different over time ( $P < .05$ ) for HC and I boars. Hemicastrate boars responded to GnRH treatment with greater LH secretion than I boars (figure 6), but testosterone secretion after GnRH was similar ( $P > .10$ ) for I and HC boars (figure 6). Increased LH secretion following GnRH treatment has also been observed in HC bulls (Barnes et al., 1981). Thus increased LH secretion following GnRH treatment may reflect a greater pituitary content of releasable LH in HC males. This conclusion is supported by the observation that pituitary content of LH is increased in HC bulls (Barnes et al., 1980c).

### Experiment 2

Concentrations of LH before and after testosterone injection were generally below the sensitivity of the LH assay ( $< .5$  ng/ml) and are represented in figure 7. Concentrations of testosterone in the serum of boars with 16 cm of testosterone filled Silastic implants averaged .6 ng/ml for all treatment groups. After injection of testosterone,

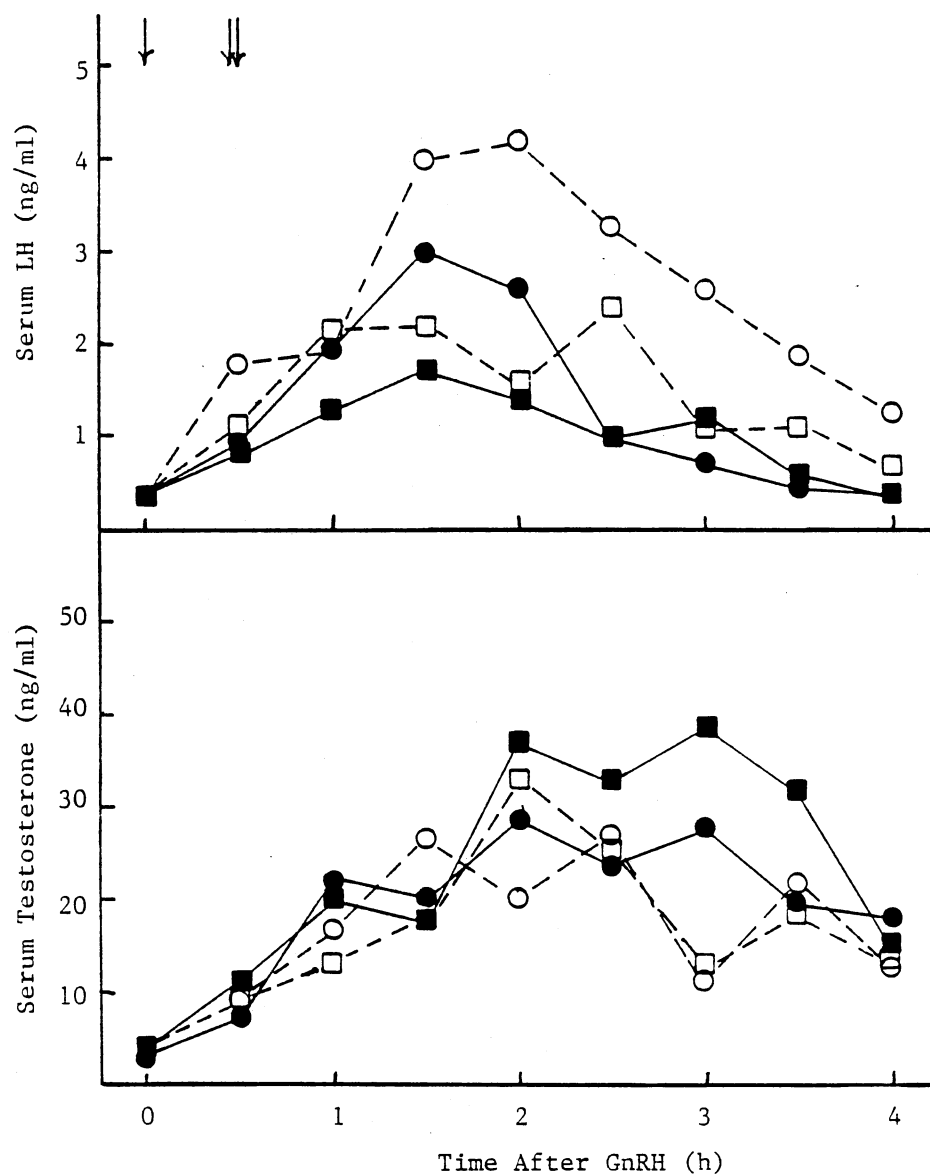


Figure 5. Concentrations of LH and Testosterone in Serum After Infusion of 50  $\mu\text{g}$  ( $\downarrow$ ), Then 250  $\mu\text{g}$  ( $\downarrow\downarrow$ ) of GnRH in Intact (Closed Symbols) and Hemicastrate (Open Symbols) Boars Exposed to 8 (Squares) or 16 (Circles) Hours of Light Daily

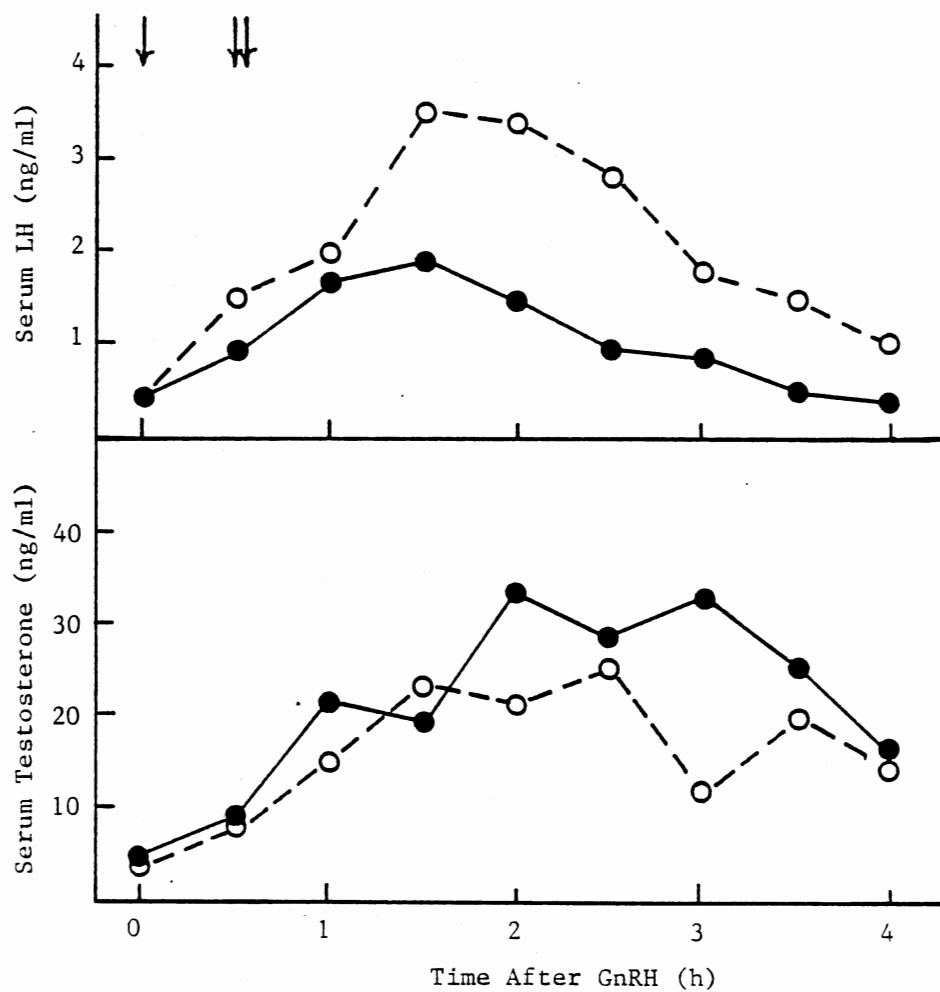


Figure 6. Concentrations of LH and Testosterone in Serum After Infusion of 50  $\mu$ g ( $\downarrow$ ), Then 250  $\mu$ g ( $\downarrow\downarrow$ ) of GnRH in Intact ( $\bullet\text{---}\bullet$ ) and Hemicastrate ( $\circ\text{---}\circ$ ) Boars



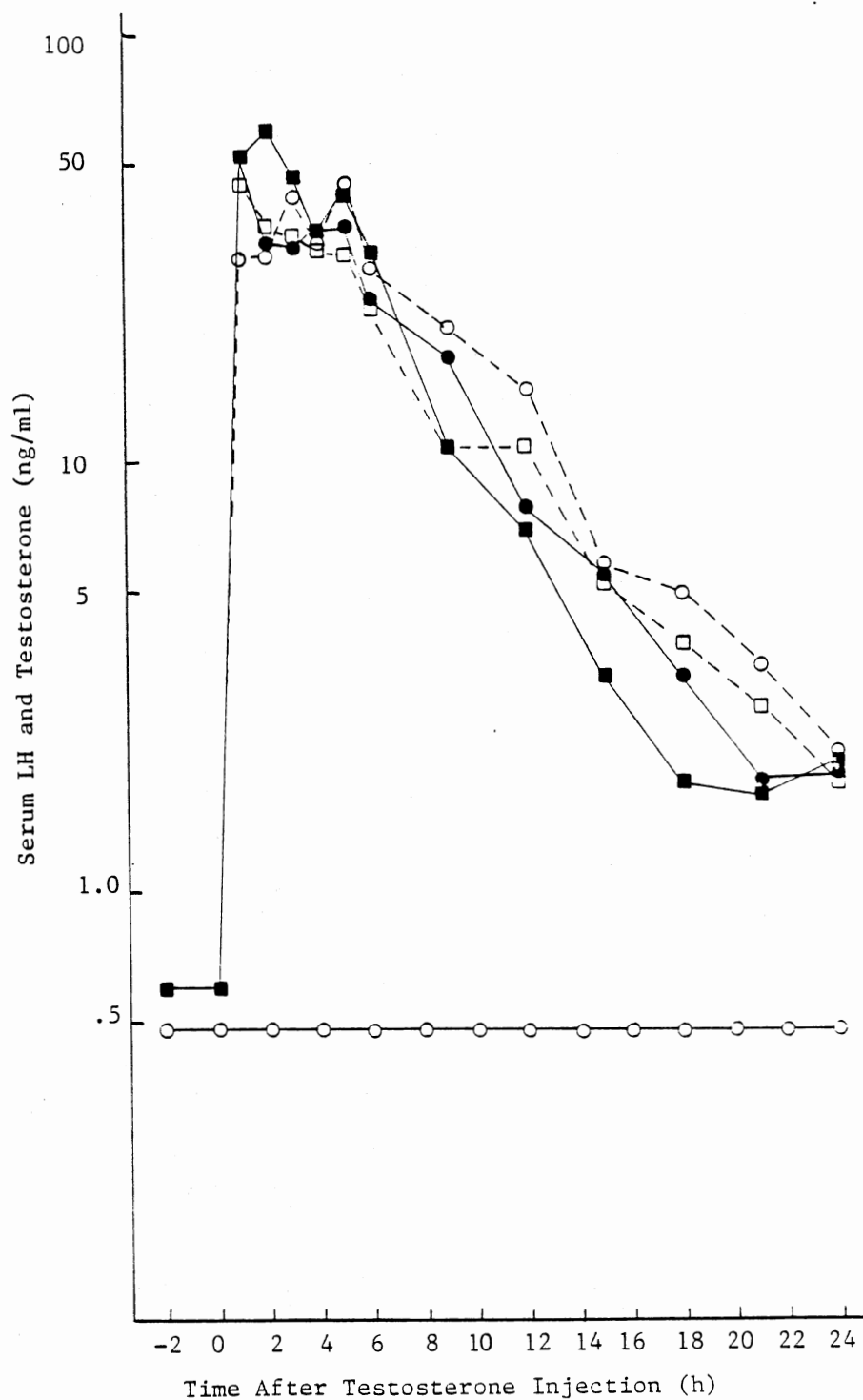


Figure 7. Concentrations of LH (o—o, All Treatments) and Testosterone in Serum Before and After Injection with Testosterone (50 mg) in Intact (Closed Symbols) and Hemicastrate (Open Symbols) Boars Exposed to 8 (Squares) or 16 (Circles) Hours of Light Daily

concentrations of testosterone in serum increased rapidly and had not returned to pre-injection concentrations within 24 h. The testosterone response curves following testosterone injection were similar ( $P > .10$ ) over time for I and HC boars exposed to 8 and 16 h of light daily. Even with the limitation of extremely low concentrations of LH in this experiment, it is evident that low, but continuous concentrations of testosterone in the serum effectively suppress LH secretion independently of duration of photoperiod. However, we can not unequivocally conclude that duration of photoperiod does not affect testosterone feedback on gonadotropin secretion in boars since concentrations of LH in serum do not normally increase after castration of boars at similar ages (Allrich et al., 1982).

## CHAPTER IV

### THE INFLUENCE OF EXPOSURE OF BOARS TO 8, 16 OR 24 HOURS OF LIGHT DAILY ON GROWTH, TESTICULAR AND ENDOCRINE FUNCTION

#### Summary

Sixty purebred boars of Yorkshire breeding were used in two replicates to evaluate the influence of duration of photoperiod on growth, testicular and endocrine function. At 8 wk of age, the boars were exposed to either 8, 16 or 24 h of fluorescent light (200 lx) daily and maintained on these treatments until 8 mo of age. Body weights were obtained at 2-wk intervals. At 4, 6, and 8 mo of age, venous cannulae were placed into 5 boars from each treatment and samples of serum were collected at 30-min intervals from 0800 to 2000 h. Gonadotropin releasing hormone (GnRH) was infused at 2000 h (50 µg) and at 2030 h (250 µg) and samples of serum were collected until 2400 h. The day following blood sampling at 6 and 8 mo of age, samples of boars from each treatment were castrated and weights and sperm content of the testes and epididymides were determined. Body weights of boars were similar for all treatments throughout the experiment. Duration of photoperiod did not affect weight of the testes or epididymides or total numbers of sperm within these tissues at either 6 or 8 mo of age. Concentrations of LH in the serum and the

LH response to GnRH were not affected by duration of photoperiod at 4, 6, or 8 mo of age. Concentrations of testosterone in serum were greater for boars exposed to 16 and 24 h of light at 4 and 8 mo of age, but this difference was not significant. Testosterone secretion in response to GnRH mediated LH release was similar among treatments at all ages.

### Introduction

Swine are considered to be relatively insensitive to changes in the length of the daily light period since most non-pregnant sows have regular estrous cycles throughout the year. However, some seasonal variations in fertility may exist in sows which is independent of temperature (Hurtgen et al., 1980) and indicates that photoperiod may have a role in regulating reproductive performance. Photic influences on reproductive function of boars may also exist. Boars exposed to increased daily light during the prepubertal period have increased sexual activity and can ejaculate at younger ages than boars exposed to fewer hours of light daily (Mahone et al., 1979; Berger et al., 1980; Hoagland and Diekman, 1982). Increased reproductive function of pubertal boars exposed to long days may be related, in part, to increased testosterone secretion (Minton et al., 1980). However, photic influences on endocrine function of boars during early and late pubertal development have not been rigorously tested. In addition, the influence of continuous exposure to light on growth and reproductive function of boars has not been evaluated. Therefore, this experiment was designed to evaluate the influence of exposure of boars to 8, 16, or 24 h of light daily on growth, testicular and endocrine function.

## Materials and Methods

Experiment 3

Sixty purebred boars of Yorkshire breeding were used in this experiment. Thirty boars from 7 litters farrowed from May 14, 1980 to May 26, 1980 were used in the first replicate and 30 boars from 11 litters farrowed from July 14, 1981 to August 2, 1981 were used in the second replicate. From weaning at 4 wk of age until about 7 wk of age, the boars were exposed to ambient photoperiod and temperature. At an average age of  $61.0 \pm .3$  d, the boars were allotted to one of three treatments and, where possible, full-sib boars were distributed across treatments. The boars were exposed to 8, 16, or 24 h of fluorescent light (200 lx) daily in pens with solid concrete floors that were similar in size (4 m x 5 m, 4 m x 5 m and 8 m x 3 m for 8 h, 16 h and 24 h pens, respectively). Lights were controlled by automatic timers and were turned on at 0800 h every morning. Supplemental heating and cooling were provided to insure that ambient temperatures were similar for boars on all treatments. Average daily temperatures reflected seasonal changes and ranged from 13 to 27 C. A pelleted, 18% crude protein ration (.98% lysine) and water were supplied ad libitum.

Boars were maintained on their photoperiodic treatments until 34 wk of age and body weights were obtained at biweekly intervals throughout the experiment. At 4 ( $128.8 \pm .6$  days of age), 6 ( $186.9 \pm .9$  days of age) and 8 ( $244.8 \pm .6$  days of age) mo of age, venous cannulae were surgically placed (similar to Exp. 1) in 4 or 5 boars selected at random from each treatment. The following day, blood samples

were obtained at 30-min intervals for 12 h beginning at 0800 h. Following sampling at 2000 h, 50  $\mu$ g of GnRH (Abbott Laboratories, North Chicago, IL, first replicate; National Institute of Arthritis, Metabolism and Digestive Diseases, second replicate) were infused into the cannulae, and the cannulae were flushed with 10 ml of sterile .85% NaCl followed by 3 ml of sterile 2.9% sodium citrate. At 2030 h, a blood sample was obtained, then 250  $\mu$ g of GnRH were infused and the cannulae were flushed with NaCl and sodium citrate. Blood samples were taken at 30-min intervals until 2400 h.

Serum was obtained and frozen as described for Exp. 1. Concentrations of LH (Hallford et al., 1975, with revisions described in Exp. 1) and testosterone (Wettemann and Desjardins, 1979) were determined in all samples.

Boars from each treatment were castrated the day following blood sampling at 6 and 8 mo of age. Weights of the testis and epididymides were recorded and samples of testicular parenchymae and capita-corpora and caudae epididymides were homogenized (Amann and Lambiase, 1969) and numbers of sperm in these tissues were estimated by hemocytometric counts.

The data obtained for body weights, testicular characteristics and endocrine data before GnRH treatment are described by:

$$Y_{ij} = \mu + P_i + R_j + PR_{ij} + e_{ij}$$

where  $Y_{ij}$  is body weight, a testicular characteristic or an average hormone concentration, P is photoperiod, R is replicate and PR is the photoperiod by replicate interaction. The components  $\mu$ ,  $P_i$ , and  $R_j$  were treated as fixed effects of all records of photoperiod i and replicate j. Random error  $e_{ij}$  was specific to each observation.

Testosterone and LH data after treatment with GnRH were analyzed by split-plot analysis of variance for repeated measurements of animals (Gill and Hafs, 1971). The data are described by:

$$Y_{ijk} = \mu + P_i + T_j + B(P)_{ki} + PT_{ij} + e_{ijk}$$

where  $Y_{ijk}$  is average LH or testosterone concentration and P is photoperiod, T is time after GnRH, B(P) is boar within photoperiod and PT is the photoperiod by time interaction. The components  $\mu$ ,  $P_i$ ,  $T_j$  and  $PT_{ij}$  were treated as fixed effects of all records of photoperiod i, time j, boar k within photoperiod i. Random error  $e_{ijk}$  was specific to each observation. Mean hormone concentrations after GnRH treatment used in figures are least-squares means obtained by analysis at each time after GnRH. These data can be described by:

$$Y_{ij} = \mu + P_i + R_j + e_{ij}$$

where  $Y_{ij}$  is an average LH or testosterone concentration and P is photoperiod and R is replicate. The components  $\mu$ ,  $P_i$  and  $R_j$  were treated as fixed effects of all records of photoperiod i and replicate j. Random error  $e_{ij}$  was specific to each observation

## Results

### Body Weights and Testicular Characteristics

Body weight gains for boars exposed to 8, 16 or 24 h of light daily between 8 and 34 wks of age were not significantly affected by duration of photoperiod (figure 8). Average growth rate of boars on all treatments was  $.65 \pm .11$  kg/d.

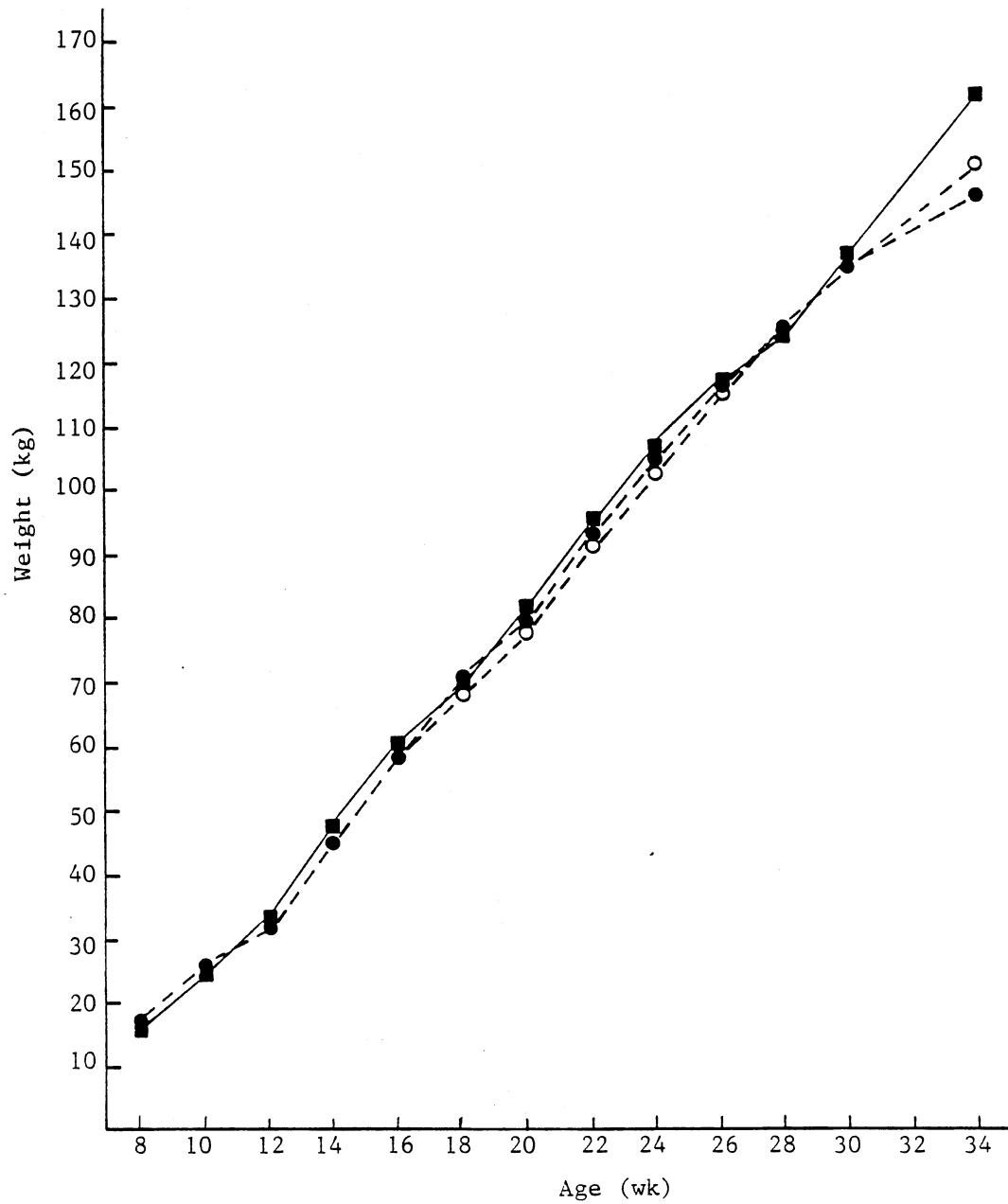


Figure 8. Body Weights of Boars Exposed to 8 (■-■), 16 (o-o) and 24 (●-●) Hours of Light Daily



Testicular characteristics of boars castrated at 6 and 8 mo of age are illustrated in tables 6 and 7, respectively. Neither testicular or epididymal weights nor total sperm numbers in these tissues were affected ( $P > .10$ ) by the duration of photoperiod that boars were exposed to during growth. Although a statistical comparison can not be made, testicular weights increased from 303.8 g at 6 mo to 331.4 g at 8 mo of age. Total weights of epididymides increased from 65.4 to 83.7 g between 6 and 8 mo of age. Total testicular and epididymal sperm content were 24.2 and  $80.5 \times 10^9$ /side and 39.5 and  $114.4 \times 10^9$ /side at 6 and 8 mo of age respectively.

#### Basal LH and Testosterone

Concentrations of LH in serum were similar for boars on all treatments and averaged .6 ng/ml when boars were evaluated at 4 mo of age (table 8). Although boars exposed to 16 and 24 h of light daily had greater average concentrations of testosterone in serum than boars exposed to 8 h of light at 4 mo of age (table 8), these differences were not significant (5.0 and 4.0 vs 2.7 ng/ml, respectively). Concentrations of LH in serum were low, but measurable for boars evaluated at 6 mo of age (table 8) but, for the most part, LH concentrations were non-detectable in the serum of boars evaluated at 8 mo (table 8). In either case, duration of photoperiod did not influence average LH concentrations. Concentrations of testosterone at 6 mo of age (table 8) were similar for boars exposed to 8, 16 or 24 h of light daily. A nonsignificant increase in average testosterone concentrations in the serum at 8 mo of age (table 8) was observed for boars exposed to longer photoperiods (5.5 and 7.6 ng/ml for boars in

TABLE 6  
 TESTICULAR CHARACTERISTICS (MEAN  $\pm$  SEM) AT 6 MONTHS OF AGE FOR BOARS  
 EXPOSED TO 8, 16 OR 24 HOURS OF LIGHT DAILY

Item	Treatment		
	8	16	24
No. boars	5	7	4
Testicular wt. (g)	313.3 $\pm$ 44.7	292.7 $\pm$ 33.4	305.4 $\pm$ 46.1
Testicular sperm ( $\times 10^9$ /testis)	23.4 $\pm$ 6.3	21.3 $\pm$ 4.7	27.9 $\pm$ 6.5
C-C <sup>a</sup> wt. (g)	31.2 $\pm$ 4.0	27.0 $\pm$ 3.0	32.9 $\pm$ 4.2
C-C sperm ( $\times 10^9$ /side)	34.6 $\pm$ 10.5	16.9 $\pm$ 7.8	24.9 $\pm$ 10.8
C <sup>b</sup> wt. (g)	38.5 $\pm$ 4.4	30.6 $\pm$ 3.3	36.0 $\pm$ 4.5
C sperm ( $\times 10^9$ /side)	67.9 $\pm$ 15.0	32.4 $\pm$ 11.2	64.7 $\pm$ 15.5

<sup>a</sup>Capita-corpora epididymides.

<sup>b</sup>Caudae epididymides.

TABLE 7

TESTICULAR CHARACTERISTICS (MEAN  $\pm$  SEM) AT 8 MONTHS OF AGE FOR BOARS  
EXPOSED TO 8, 16 OR 24 HOURS OF LIGHT DAILY

Item	Treatment		
	8	16	24
No. boars	5	8	7
Testicular wt. (g)	228.0 $\pm$ 28.2	358.9 $\pm$ 22.5	347.3 $\pm$ 23.6
Testicular sperm ( $\times 10^9$ /testis)	32.9 $\pm$ 5.2	44.8 $\pm$ 4.2	40.8 $\pm$ 4.4
C-C <sup>a</sup> wt. (g)	37.9 $\pm$ 4.1	41.7 $\pm$ 3.3	37.5 $\pm$ 3.4
C-C sperm ( $\times 10^9$ /side)	23.4 $\pm$ 5.6	33.1 $\pm$ 4.5	35.8 $\pm$ 4.7
C <sup>b</sup> wt. (g)	41.5 $\pm$ 4.5	46.8 $\pm$ 3.6	45.7 $\pm$ 3.8
C sperm ( $\times 10^9$ /side)	73.1 $\pm$ 10.8	78.7 $\pm$ 8.6	99.1 $\pm$ 9.0

<sup>a</sup>Capita-corpora epididymides.

<sup>b</sup>Caudae epididymides.

TABLE 8

AVERAGE CONCENTRATIONS OF LUTEINIZING HORMONE (LH) AND TESTOSTERONE (MEAN  $\pm$  SEM)  
 IN THE SERUM OF BOARS AT 4, 6 AND 8 MONTHS OF AGE  
 EXPOSED TO 8, 16 OR 24 HOURS OF LIGHT DAILY

Age, mo	Treatment		
	8	16	24
4			
No. boars	5	5	5
LH (ng/ml)	.6 $\pm$ .1	.7 $\pm$ .1	.6 $\pm$ .1
Testosterone (ng/ml)	2.7 $\pm$ 1.2	5.0 $\pm$ 1.2	4.0 $\pm$ 1.2
6			
No. boars	4	4	4
LH (ng/ml)	.5 $\pm$ .1	.5 $\pm$ .1	.6 $\pm$ .1
Testosterone (ng/ml)	4.7 $\pm$ 1.4	5.1 $\pm$ 1.5	4.9 $\pm$ 1.5
8			
No. boars	4	4	4
LH (ng/ml)	<.5	<.5	<.5
Testosterone (ng/ml)	1.5 $\pm$ 2.5	5.5 $\pm$ 2.5	7.6 $\pm$ 2.3

16 and 24 h light daily, respectively) compared with boars exposed to 8 h of light daily (1.5 ng/ml).

### Luteinizing Hormone and Testosterone

#### Response to GnRH

Concentrations of LH in the serum of boars at 4, 6, and 8 mo of age after treatment with GnRH are illustrated in figure 9. At all ages, the LH response to GnRH was not influenced ( $p > .10$ ) by the duration of photoperiod that boars were exposed to during growth. In general, concentrations of LH after GnRH were maximum at 1 h after treatment and returned to pre-injection concentrations by 4 h after treatment. Although the design of this experiment precludes statistical comparisons among ages, the response of LH to GnRH treatment appeared to decrease with age.

At 4 and 6 mo of age, concentrations of testosterone in serum after GnRH treatment were not significantly affected by duration of photoperiod (figure 10). At 8 mo of age, a treatment by time interaction ( $P < .05$ ) was noted for testosterone response to GnRH treatment. However, when the data were evaluated at each time after GnRH, no significant treatment effects were observed.

### Discussion

Body weight gains were similar from 8 to 34 wk of age for boars exposed to 8, 16, and 24 h of light daily. These findings support conclusions from Exp. 1 and those previously reported (Berger et al., 1980; Minton et al., 1980; Hoagland and Diekman, 1982) and indicate that duration of photoperiod does not significantly alter growth rate

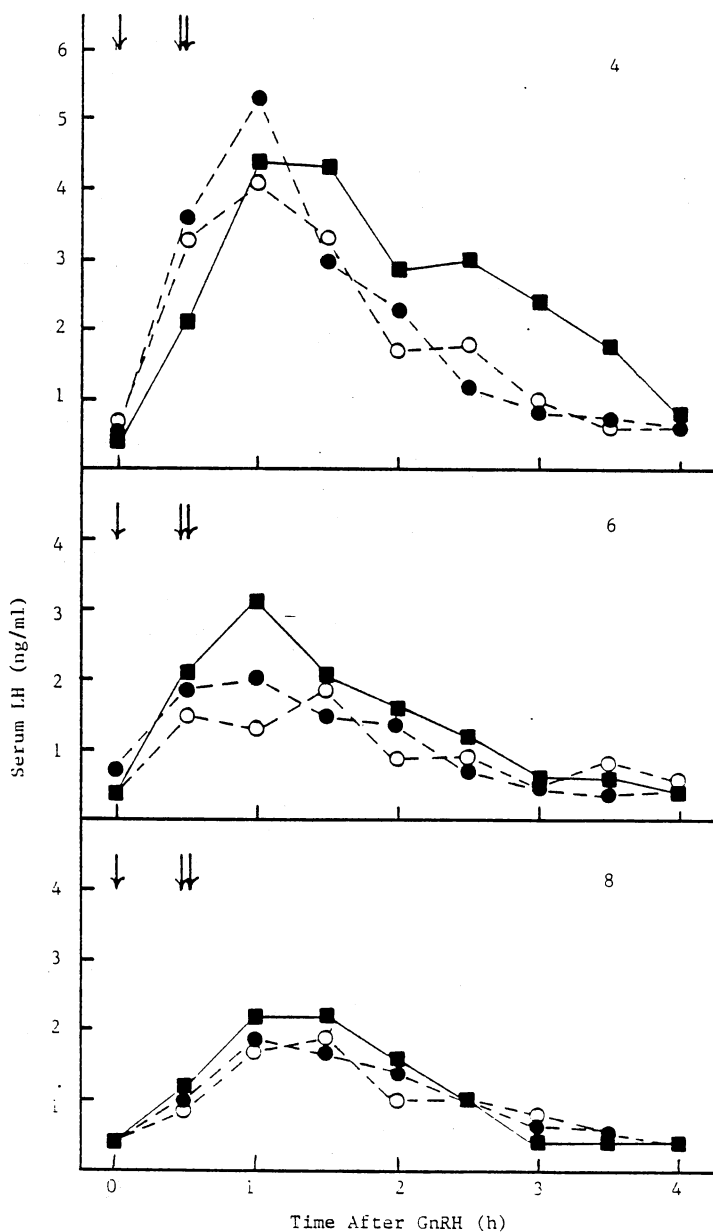


Figure 9. Concentrations of LH in the Serum of Boars After Infusion of 50  $\mu\text{g}$  ( $\downarrow$ ), Then 250  $\mu\text{g}$  ( $\downarrow\downarrow$ ) of GnRH During Exposure to 8 (■-■), 16 (○-○) and 24 (●-●) Hours of Light Daily at 4, 6 or 8 Months of Age

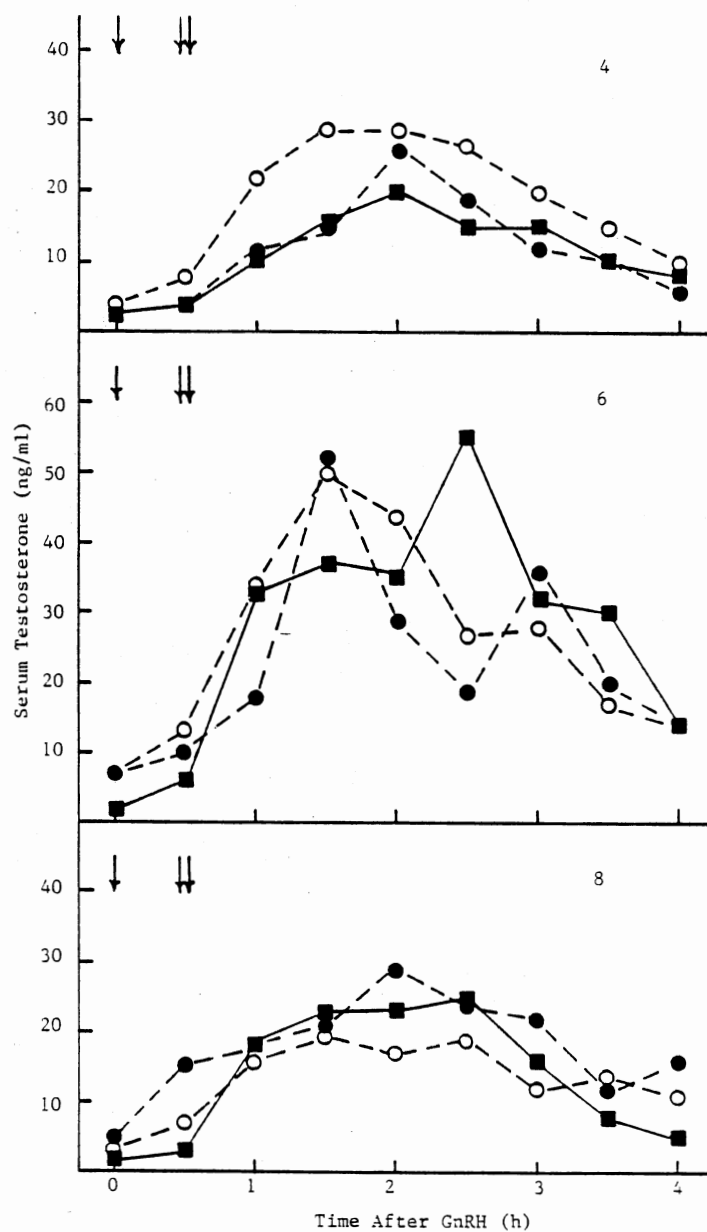


Figure 10. Concentrations of Testosterone in the Serum of Boars After Infusion of 50  $\mu\text{g}$  ( $\downarrow$ ), Then 250  $\mu\text{g}$  ( $\downarrow\downarrow$ ) of GnRH During Exposure to 8 (■-■), 16 (○-○) and 24 (●-●) Hours of Light Daily at 4, 6 or 8 Months of Age

of boars. This conclusion is in agreement with the observation that duration of photoperiod does not influence growth rate of gilts (Braude et al., 1958; Dufour and Bernard, 1968; Ntunde et al., 1979; Berger et al., 1980; Wheelhouse and Hacker, 1982).

Similar testicular and epididymal weights were observed for boars exposed to all photoperiods that were castrated at 6 or 8 mo of age. Total sperm content in these tissues was also similar for boars at both castration ages regardless of photoperiodic treatment. These results are in agreement with our previous finding that testicular and epididymal weights and sperm content were not influenced by duration of photoperiod when boars were evaluated at 6 mo of age (Minton et al., 1980). The data from the present experiment also support the conclusion that total sperm in ejaculates were not affected when boars were exposed to increased photoperiods (Mahone et al., 1979; Berger et al., 1980). Although the effect age could not be tested statistically, testicular and epididymal weights and sperm numbers increased from 6 to 8 mo of age. These increases in testicular and epididymal weights with age are similar in magnitude to those reported previously (Allrich et al., 1983).

We reported that exposure of boars to 8 or 16 h of light daily during growth did not significantly alter concentrations of LH in the serum at 6 mo of age (Minton et al., 1980). Our present findings support and extend our previous conclusion and indicate that LH concentrations are similar for boars exposed to 8, 16 and 24 h of light daily when evaluated at 4 or 6 mo of age. Admittedly, LH concentrations in serum at 8 mo of age were generally below the sensitivity of our assay, so we do not have a good estimate of the



effects of photoperiod at that age. Boars exposed to 15 h of light daily from December to April or March to August had similar LH and FSH concentrations at 31 wk of age as boars exposed to natural photoperiods (Hoagland and Diekman, 1982). Secretion of LH in response to GnRH treatment was not significantly affected by duration of photoperiod at any age. Although we could not statistically test an age effect, the LH response to GnRH tended to decrease with age. FlorCruz and Lapwood (1978) observed that concentrations of LH in the plasma of boars generally decreased from 110 to 240 d of age.

Average concentrations of testosterone at all ages were consistently greater for boars exposed to 16 and 24 h of light daily. However, with limited numbers of boars evaluated at each age and the variability in average testosterone between boars, we did not demonstrate a significant influence of duration of photoperiod on average concentrations of testosterone. At 6 mo of age, concentrations of testosterone were elevated in serum of boars exposed to 16 vs 8 h of light daily (Minton et al., 1980). Increased concentrations of testosterone in serum of boars exposed to longer photoperiods were observed at 23 and 25 wk of age in one of two experiments reported by Hoagland and Diekman (1982). Perhaps unidentified environmental variables can account for inconsistencies among experiments evaluating photic influences on testicular endocrine function of boars.

Increases in testosterone in serum after treatment of boars at 4, 6 and 8 mo of age with GnRH were similar for all treatments. Although we could not statistically compare boars at different ages, the testosterone response at 6 mo of age appeared to be greater than at 4 or 8 mo of age. This apparent increase in testosterone response

may reflect increased sensitivity of the testes to LH. Testicular tissue of boars at 130 and 160 d of age secrete more testosterone in vitro in response to hCG stimulation than at earlier and later periods of sexual development (Allrich et al., 1983).

The results of this experiment indicate that growth rate, testicular characteristics and LH are not significantly influenced by duration of photoperiod in prepubertal and pubertal boars. Photoperiod effects on testosterone in the serum of boars may exist but other factors (e.g., season of birth, geographic location, etc.) may interact with the response. We conclude that altering the duration of photoperiod does not influence development of boars, although differences in testicular endocrine function may occur.

## CHAPTER V

### SUMMARY AND CONCLUSIONS

#### Summary

Previous research indicated that exposure of boars to 16 h of light daily from 2 to 6 mo of age increased testosterone concentrations in the serum at 6 mo of age (Minton et al., 1980). These results suggested that duration of photoperiod may influence pubertal development and reproductive endocrine function of boars and encouraged us to design the experiments for this dissertation.

In the first set of experiments, which were conducted in tandem, we sought to develop a sensitive model to evaluate photoperiodic influences on testicular function. We approached these experiments with this objective in mind because the large variations in concentrations of LH and testosterone in the serum of boars makes assessment of treatment effects difficult. Therefore, we used the hemicastrate (HC) boar to evaluate the influence of duration of photoperiod on reproductive function because we theorized that testicular hypertrophy associated with HC would exploit any effects of photoperiod on testicular function. In a companion study, the boars from this experiment were castrated and implanted with testosterone to evaluate the influence of duration of photoperiod on gonadotropin sensitivity to testosterone negative feedback. The third experiment was designed to evaluate reproductive

function of boars at 4, 6 and 8 mo of age when exposed to 8, 16 or 24 h of light daily during growth.

It was anticipated that these experiments would allow us to determine the presence and magnitude of photoperiodic effects on pubertal development of boars.

### Experiments 1 and 2

Neither duration of photoperiod nor HC altered growth of boars. In general duration of photoperiod did not influence any testicular characteristic that was evaluated or concentrations of LH or testosterone in the serum. There was a trend for concentrations of PRL in the serum to be increased in boars exposed to 16 h of light daily. Serum concentrations of PRL averaged 2.6 and 3.5 ng/ml for boars exposed to 8 and 16 h of light daily, respectively. Hemicastrated boars had heavier testes (472 vs 309 g) and epididymides (70.9 vs 61.8 g) than I boars and sperm content in these tissues was increased. Intact and HC boars had similar basal concentrations of LH and testosterone in serum but HC boars released more LH (but not testosterone) than I boars after treatment with GnRH. Castrated boars from this experiment that received testosterone filled implants and testosterone injections had concentrations of LH in serum which were generally below the sensitivity of our assay.

### Experiment 3

Similar to the results of Exp. 1, there were no significant effects of duration of photoperiod on growth of boars. Testicular and epididymal weights and sperm content were similar for boars castrated

at 6 or 8 mo of age that had been exposed to 8, 16 or 24 h of light daily. No statistical comparisons could be made, but from 6 to 8 mo of age, testicular weights and sperm content increased (304 to 332 g and 24 to  $40 \times 10^9$  sperm/side, respectively). Concentrations of LH in the serum at 4, 6 and 8 mo of age were not affected by duration of photoperiod. However, LH responses to GnRH treatment appeared to decrease with age. From 4 to 8 mo of age, maximum LH response decreased from 4 ng/ml to about 2 ng/ml. Concentrations of testosterone in the serum were not significantly different for boars exposed to 8, 16 or 24 h of light daily at any age evaluated. However, average testosterone concentrations were consistently greater for boars in the longer photoperiods than boars exposed to 8 h of light daily at 4, 6 and 8 mo of age.

#### Conclusions

Based on the results of these experiments, it appears that duration of photoperiod does not greatly influence reproductive development of boars. Photoperiods of longer duration may stimulate testicular endocrine secretions as was suggested by our previous research. Apparently, evaluation of larger numbers of animals per treatment would be necessary to resolve this question. In addition, such factors as season of birth and preweaning environment may influence the responses of boars to duration of photoperiod during the prepubertal and pubertal periods and may be factors to consider for future experiments.

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TABLE 9

ORTHOGONAL COMPARISONS OF RESIDUAL SUMS OF SQUARES OF POLYNOMIAL  
 RESPONSE CURVES FOR LUTEINIZING HORMONE (LH) CONCENTRATIONS  
 AFTER INFUSION OF GnRH IN THE SERUM OF INTACT (I)  
 AND HEMICAstrate (HC) BOARS EXPOSED TO 8 OR  
 16 HOURS OF LIGHT DAILY

Remainder	df	SS	MS	F	P
8I, 8HC	66	18.8368			
16I, 16HC	68	47.4648			
Total	134	66.3016	.4948		
Combined	137	67.2842			
Difference	3	.9826	.3275	.66	>.10
8I	27	4.2354			
8HC	36	11.9293			
Total	63	16.1647	.2566		
Combined	66	18.8368			
Difference	3	2.6721	.8907	3.47	<.05
16I	37	5.6488			
16HC	28	30.8235			
Total	65	36.4723	.5611		
Combined	68	47.4648			
Difference	3	10.9925	3.6642	6.53	<.01

TABLE 10

ORTHOGONAL COMPARISONS OF RESIDUAL SUMS OF SQUARES OF POLYNOMIAL  
 RESPONSE CURVES FOR PROLACTIN CONCENTRATIONS AFTER INFUSION  
 OF GnRH IN THE SERUM OF INTACT (I) AND HEMICAstrate (HC)  
 BOARS EXPOSED TO 8 OR 16 HOURS OF LIGHT DAILY

Remainder	df	SS	MS	F	P
8I, 8HC	66	63.4139			
16I, 16HC	66	63.5178			
Total	132	126.9317	.9616		
Combined	135	129.4517			
Difference	3	2.5200	.8400	.87	>.10
8I	28	26.8125			
8HC	35	32.0811			
Total	63	58.8936	.9348		
Combined	66	63.4139			
Difference	3	4.5203	1.5068	1.61	>.10
16I	35	18.7073			
16HC	28	41.0212			
Total	63	59.7285	.9481		
Combined	66	63.5178			
Difference	3	3.7893	1.2631	1.33	>.10

TABLE 11

ORTHOGONAL COMPARISONS OF RESIDUAL SUMS OF SQUARES OF POLYNOMIAL  
RESPONSE CURVES FOR TESTOSTERONE CONCENTRATIONS AFTER INFUSION  
OF GnRH IN THE SERUM OF INTACT (I) AND HEMICAstrate (HC)  
BOARS EXPOSED TO 8 OR 16 HOURS OF LIGHT DAILY

Remainder	df	SS	MS	F	P
8I, 8HC	62	5496.6171			
16I, 16HC	66	7773.6887			
Total	128	13270.3058	103.6743		
Combined	130	13298.0786			
Difference	2	27.7728	13.8864	.13	>.10
8I	24	2788.4420			
8HC	26	2439.9304			
Total	60	5228.3724	87.1395		
Combined	62	5496.6171			
Difference	2	268.2448	134.1224	1.54	>.10
16I	36	4404.0611			
16HC	28	3359.6863			
Total	64	7763.7474	121.3086		
Combined	66	7773.6887			
Difference	2	9.9413	4.9706	.04	>.10

TABLE 12

ORTHOGONAL COMPARISONS OF RESIDUAL SUMS OF SQUARES OF POLYNOMIAL  
 RESPONSE CURVES FOR TESTOSTERONE AFTER TESTOSTERONE INJECTION  
 IN THE SERUM OF BARROWS WHICH HAD PREVIOUSLY BEEN  
 INTACT (I) OR HEMICASTRATED (HC) AND EXPOSED  
 TO 8 OR 16 HOURS OF LIGHT DAILY

Remainder	df	SS	MS	F	P
8I, 8HC	80	10697.5850			
16I, 16HC	86	8557.7803			
Total	166	19255.3653	115.9962		
Combined	172	19757.7247			
Difference	6	502.3594	83.7266	.72	>.10
8I	24	2898.4420			
8HC	50	6455.1534			
Total	74	9353.5954	126.3999		
Combined	80	10697.5850			
Difference	6	1343.9896	223.9998	1.77	>.10
16I	47	5566.9657			
16HC	33	2307.1513			
Total	80	7874.1170	98.4265		
Combined	86	8557.7803			
Difference	6	683.6633	113.9439	1.16	>.10

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