

Photoperiod Control of Reproductive Development in the Male Djungarian Hamster (*Phodopus sungorus*)*

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ABSTRACT. The Djungarian or Siberian hamster (*Phodopus sungorus*) is a seasonally breeding rodent in which maturation of gonadal function depends upon the photoperiod during rearing. It was hypothesized that the ability of short days to block testicular growth resulted from insufficient gonadotropin secretion during critical stages of development. This question was studied by measurement of serum concentrations of FSH, LH, PRL, and androgens by RIA systems validated for use in this species. Males reared from birth in long (16 h of light, 8 h of darkness) or short (10 h of light, 14 h of darkness) photoperiods were killed at 5- to 10-day intervals between 5 and 60 days of age. Regardless of photoperiod before 15 days of age, body and testes weights similarly increased. Serum concentrations of FSH and PRL gradually increased during this age period, although PRL concentrations were statistically higher in males under long days compared to those under short days. Circulating serum LH and androgen levels were high before 10 days of age, but decreased by 15–20 days of age in both photoperiods. Under long

days, the period between 15 and 30 days of age was characterized by rapid body (1 g/day) and testicular (10–38 mg/day) growth, peak serum FSH concentrations (20–25 days), sustained elevation in serum LH and androgen concentrations, and further increases in serum PRL values. After 30 days of age, a reduced growth rate for body and testes occurred; serum FSH levels declined, while adult serum concentrations of LH, PRL, and androgens were attained. In contrast, hamsters exposed to short days from birth exhibited a slower rate of body and testicular growth by 20 days of age. Short days blocked peak FSH secretion and suppressed serum concentrations of LH and androgens after 20 days of age. PRL titers were significantly lower in short day compared to those in long day housed hamsters at all ages. These results support the hypothesis that the short day-induced suppression of gonadotropins and PRL secretion during development blocked gonadal maturation. (*Endocrinology* 114: 664, 1984)

SEXUAL maturation in a variety of rodent species is known to depend upon the season of the year at which birth occurred. Development may be influenced by such diverse environmental factors as nutritional availability, temperature, pheromonal cues, and population density (1, 2). In many species, the seasonal change in the daily photoperiod appears to play a major role in determining the transition into adulthood. Short natural or artificial daylengths delay gonadal development in several species of mice (3), the cotton rat (4), and the field vole (5). By contrast, in the collared lemming (6) and Syrian hamster (7, 8), puberty is apparently unaffected by the photoperiod.

The effect of photoperiod on testicular weight has been studied in the Djungarian hamster (9). At the earliest age examined, 31 days, testes weights in hamsters exposed to long days approximated those in the adult.

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When reared under short days, the testes remained immature at this age. The purpose of the present study was to evaluate the influence of photoperiod on the developmental patterns of reproductive hormones in serum and their relation to maturation of gonadal function in the male Djungarian hamster (*Phodopus sungorus*). It was hypothesized that short day-induced suppression of circulating gonadotropins blocked gonadal maturation.

Materials and Methods

Djungarian hamsters were born in our laboratory breeding colony, which was illuminated for 16 h each day (lights on from 0200–1800 h). This colony was derived from an original stock provided by Dr. Klaus Hoffmann (Max Plank Institut für Verhaltensphysiologie, Ehrling-Andechs, West Germany). Purina F-6 laboratory chow and water were available *ad libitum* along with a weekly sunflower seed supplement. On the day of birth (day 0), each cage containing both parents and litter (usually 4–8 pups) was transferred to a separate experimental room under either long (16 h of light, 8 h of dark; lights on from 0200–1800 h) or short (10 h of light, 14 h of dark; lights on from 0500–1500 h) photoperiods. Pups were weaned at 18 days of age and group housed (4–6/plastic cage) until the appropriate age. Male progeny, between 5 and 60 days of age, were killed by decapitation between 2 and 4 h before lights-off, and the body trunk was exsanguinated. Body weight and paired

testes weights were measured with a triple beam or torsion bar balance, respectively. At the younger ages, the small amount of blood collected from each animal necessitated pooling of blood from 2–8 individuals. Five to 11 replicate samples (blood pools) were obtained for each age group in a method similar to previous reports (10, 11). After collection, blood was allowed to clot for 24 h at 4 C, then centrifuged at 2500 rpm for 30 min. Serum was stored at –20 C for later assays. Serum volumes used for hormone quantification were 125–150 μ l for FSH and LH, 50 μ l for PRL, and 100 μ l for androgens.

Protein hormone assays

The procedures for the RIA of serum FSH, LH, and PRL concentrations have been previously described and validated for use in the Syrian hamster (12–14). Validation of these assay systems for the Djungarian hamster was based upon determination of parallelism between the linear portion of appropriate reference curves and evaluation of nonspecific interference in serum. Specific antibodies used in the assays were provided by NIAMDDK RIA kits (antirat FSH S-7 and antirat PRL S-5) and by Dr. Gordon Niswender (antiovine LH-15). Reference preparations were the RP-1 standards for FSH, LH, and PRL as well as a pool of sera obtained from lactating Syrian hamster (LHS-3). A stock pituitary homogenate preparation consisted of two pituitary glands excised from adult Djungarian hamsters and dispersed in 1 ml PBS. One milliliter of supernatant from this stock was assigned a value of two pituitary equivalents. In addition, three pools of Djungarian hamster sera were collected for the validation procedure and for quality control analysis: intact adults (denoted as no. 2300), postpartum lactating females, and long term castrated adult males. Hormone concentrations in serum were calculated after linear regression analysis of a log-dose and logit-response transformation of raw standard curve data (15).

In Fig. 1, the dose-response displacement curves are illustrated for various reference standards, dilutions of the pituitary homogenate preparation, and pooled sera. In the FSH and LH assays, the slopes of the regression lines generated by the RP-1 standards were similar to the slopes observed for serial dilutions of pooled sera (no. 2300) and pituitary homogenate preparation ($P > 0.05$). The absence of nonspecific interference was suggested by the parallelism between the RP-1 standards and the various serum and pituitary reference curves. Furthermore, serial dilutions of pooled sera to which known amounts of hormone were added (extrapolated from pituitary equivalent data) demonstrated proportional concentration changes within the limits of assay variation (16).

In the PRL assays, our validation was similar to results in the Syrian hamster (17); slopes of the displacement curves for hamster serum and pituitary extracts were different from those of the RP-1 standard curve [$P < 0.01$ (18)]. Serial dilutions of the various Djungarian hamster serum pools, though, exhibited slopes parallel to the curve for the hamster serum standard (LHS-3). Therefore, the reference standard in the PRL assay consisted of serial dilutions of LHS 3, where 1 μ l LHS 3 was assigned a value of 1 U hamster PRL.

The results of the validation procedure, as indicated in Fig. 1, suggest that heterologous RIA systems can be used to mea-

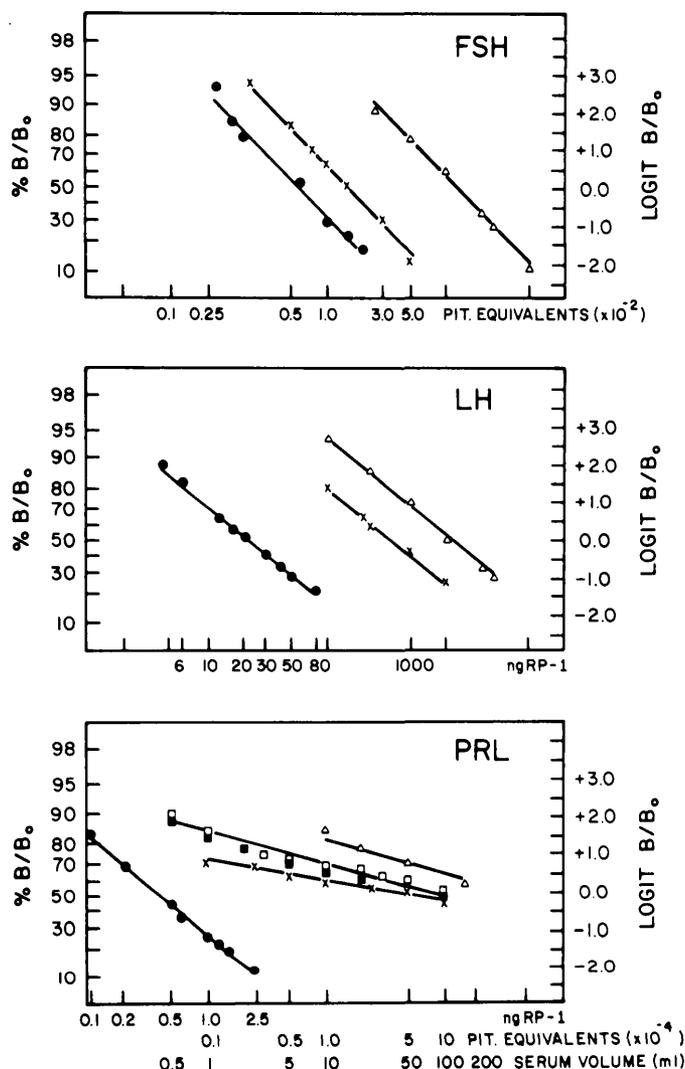


FIG. 1. Tests for parallelism among the various NIAMDDK reference preparations and Djungarian hamster pituitary preparations and serum. The following standards were employed: the NIAMDD rat RP-1 standard (●), dilutions of a pituitary homogenate preparation where 1 ml was designated a value of 2 pituitary equivalents (X), serial aliquots of pooled serum standard 2300 (Δ), and serial aliquots of two serum pools from lactating female Djungarian (□) or Syrian (■) hamsters. A log-dose and logit-response ($\text{LOGIT } B/B_0 = \ln(B/B_0)/(1 - B/B_0)$) transformation was made of the raw data, where B_0 was a blank buffer control (0% displacement), and B was the competitive displacement dose response for each standard. For the *abscissa*, the log scale at the *bottom of the figure* applies to all curves except where noted and as subsequently described. The scale for pituitary equivalents represented *below the FSH panel* was 100-fold less sensitive than that for LH or PRL. The rat RP-1 standard scale *under the LH panel* applies to both FSH and LH. The rat RP-1 PRL standard was moved one log cycle to the right for illustrative purposes. The *left ordinate* is scaled as the percentage of counts bound (% B/Bo). On the *right ordinate*, the corresponding logit scale for % B/Bo is presented. Parallelism occurred among all reference curves in the FSH and LH RIA systems (no significant differences, $P > 0.01$). However, for PRL, Parallel curves only occurred among the various hamster sera pools. Therefore, the LHS-3 was designated an appropriate standard where 1 μ l LHS-3 was arbitrarily assigned a value of 1 U hamster PRL.

sure serum concentrations of FSH, LH, and PRL. More extensive verification of assay specificity would be facilitated by the use of homologous RIA reagents and availability of serum from hypophysectomized Djungarian hamsters. The relation of immunoactive and bioactive hormone concentrations may further validate these assay procedures. In this regard, a pool of sera from long term castrated adult males (in 16-h light, 8-h dark photoperiod) contained 2248 ng FSH/ml and 369 ng LH/ml. This characteristic castration response to removal of gonadal steroid feedback is similar in kind and magnitude to that in the Syrian hamster (19).

These findings were comparable to previous reports for the Syrian hamster that employed heterologous RIA systems to measure FSH and LH (12, 13) and PRL (17). Sensitivities for the protein hormone assays were as follows: FSH, 96 ng RP-1/ml; LH, 12 ng RP-1/ml; and PRL, 10 U LHS-3/ml. The mean intra- and interassay coefficients of variation at the 50% displacement level (bound to free ratio) were: FSH, 5.2% and 7.7%; LH, 5.7% and 16.2%; and PRL, 9.3% and 19.6%, respectively.

Androgen assay

RIA procedures for the measurement of serum androgen concentrations have been described previously (20). The testosterone antiserum (no. 250, Dr. G. Niswender) cross-reacted with dihydrotestosterone (67%), 4-androstenedione (0.4%), and other androgens (<0.10%). Therefore, results were expressed in terms of the concentrations of serum androgens. Assay sensitivity was 0.1 ng/ml. The intra- and interassay coefficients of variation at the 50% displacement level were 4.5% and 6.7%, respectively.

Data analysis

The data for body weight, testicular weight, and various hormone measurements were analyzed by a two-way analysis of variance, which compared photoperiod *vs.* age effects. Individual comparisons were then made between selected means using a *t* test (21). Differences were considered significant when $P < 0.01$. Comparisons for similarity of slopes were made between the linear portions of the various hormone reference standards and serial dilutions of sera and pituitary homogenate preparations using previously described methods for linear regression analysis (18, 21).

Results

The developmental growth patterns for total body weight (grams) and paired testes weight (milligrams) depended upon the photoperiod of rearing (Fig. 2). Exposure to short days from birth retarded body weight gain and maturation of testes. Body weight gain was similar before 15 days of age in long and short day reared hamsters. After 20 days of age, however, the rate of growth changed, such that significantly lower body weights occurred in males maintained under short days compared to those under long days.

Before 15 days of age, testicular growth rates were

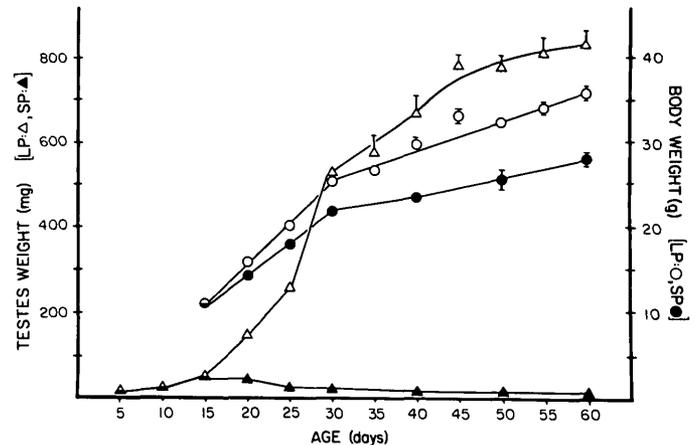


FIG. 2. Developmental changes in body (○ and ●) and testicular (Δ and ▲) weights in Djungarian hamsters reared under long (16 h of light, 8 h of darkness; ○ and Δ) or short (10 h of light, 14 h of darkness; ● and ▲) photoperiods. Body weights in males from 15–60 days of age have been plotted. Paired testes weights in males from 5–60 days of age are also illustrated. The data represent the mean \pm SE of as many as 27 individuals for the 5-day-old group and then along a continuum to as few as 8 individuals for 60-day-olds. Where SE bars are not present, the variance was encompassed by the area of the symbol.

similar in both long and short photoperiods. In long days, the testes attained adult size by about 45 days of age. By contrast, under short days the testes remained immature; significant differences between groups in long and short days became apparent by 20 days of age. At 60 days, testes weights were 10- to 15-fold greater in hamsters exposed to the long photoperiod than in comparably aged males that had been housed under short days from birth.

FSH

The patterns of serum FSH concentrations (Fig. 3) were similar in long and short day reared hamsters until 15 days of age. Thereafter, under long days, peak FSH levels occurred between 20 and 25 days of age. At 25 days, four of eight males exhibited FSH concentrations beyond the linear portion of the standard curve for that serum volume. The limited amount of serum precluded re-assay. By 45 days of age, FSH concentrations gradually declined to values similar to those found in mature adults (Yellon, S. M., unpublished results). In contrast, FSH levels in short day reared hamsters were significantly reduced by 20 days of age compared to those in males reared under long daylengths. Between 25 and 60 days of age, FSH concentrations in short day reared hamsters remained at or below the limits of assay sensitivity.

LH

Serum LH concentrations (Fig. 4) in male hamsters were generally higher before 15 days of age than in adulthood, regardless of the prevailing light/dark sched-

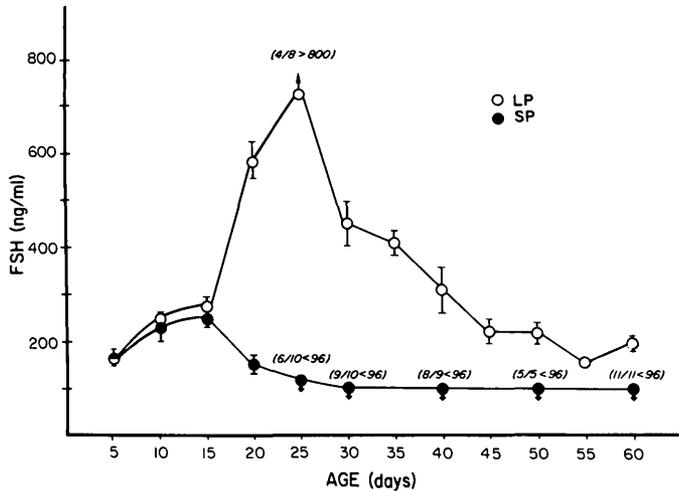


FIG. 3. Serum FSH concentrations from 5–60 days of age in males reared under long (O) or short (●) days. Each data point represents the mean ± SE of 5–11 individual pooled serum samples. Each sample consisted of a pool of sera derived from 1–10 males depending on age, i.e. 8–10 males/sample for 5-day-olds to 1–2 individuals for males older than 40 days of age. Where SE bars are not present, the variance was encompassed by the area of the symbol. In long days, 4 of 8 males at 25 days of age showed concentrations greater than 800 ng/ml. In short day reared males after 25 days of age, FSH concentrations below the limits of the linear portion of the standard curve consistently occurred (<96 ng/ml).

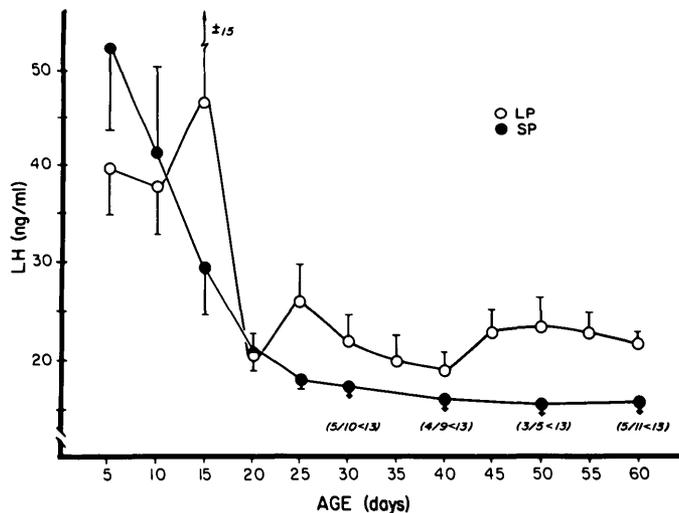


FIG. 4. Serum LH concentrations from 5–60 days of age in males reared under long (O) or short (●) days. Each data point represents the mean ± SE of 5–11 individual pooled serum samples. See Fig. 3 for details. LH titers in short day reared males after 30 days of age were frequently below the limits of the linear portion of the standard curve (<13 ng/ml).

ule. Photoperiod effects were apparent by 25 days of age. Beginning at 30 days, LH concentrations in animals raised under long days ranged between 15 and 30 ng/ml; short day reared males consistently exhibited values at or below the limits of assay sensitivity.

PRL

In long days reared animals, concentrations of serum PRL (Fig. 5) gradually attained adult levels by 25 days of age. At all ages, PRL values were higher in long day than short day reared males. Serum PRL concentrations in long day reared males before 20 days of age were significantly elevated above those exhibited by comparably aged short day housed hamsters.

Serum androgens

Serum androgen concentrations (Fig. 6) in both long and short day reared males were high at 5 and 10 days of age. In long day reared males, a nadir occurred between 15 and 20 days of age, followed by increased serum androgen concentrations to values (2–5 ng/ml) commonly found in the 60- to 90-day-old adult male hamster. Three of the seven males in the long day reared group at 60 days of age exhibited unusually high values, ranging from 5.8–11.6 ng/ml. In hamsters under short days, serum androgen concentrations remained low from 15–60 days of age. By 20 days of age and thereafter, values were lower in short day compared to long day reared hamsters.

Discussion

The results indicate that the photoperiod profoundly influences early stages of sexual maturation in the male Djungarian hamster. This confirms and extends other reports that focused upon testicular growth (after 30 days of age) as an index of maturation (9, 22). The ability

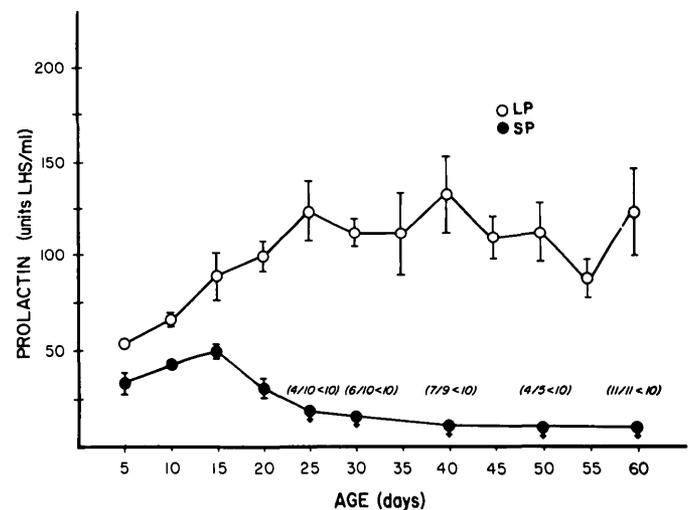


FIG. 5. Serum PRL concentrations from 5–60 days of age in males reared under long (O) or short (●) days. Each data point represents the mean ± SE of 5–11 individual pooled serum samples. See Fig. 3 for details. Where SE bars are not present, the variance was encompassed by the area of the symbol. After 25 days of age, PRL titers in short day reared males were below the limits of the linear portion of the standard curve (<10 U LHS-3/ml).

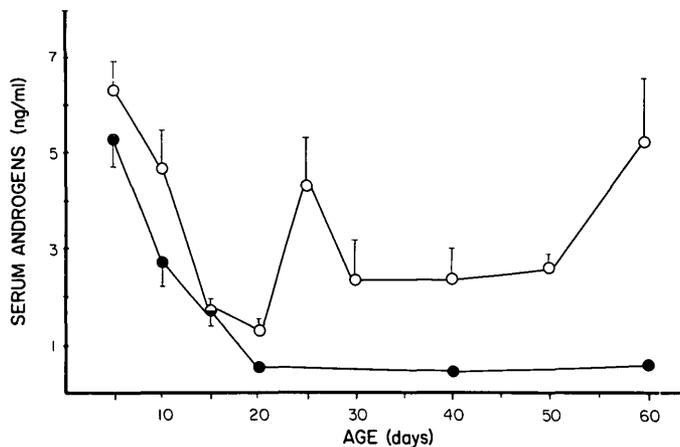


FIG. 6. Serum androgen concentrations from 5–60 days of age in males reared under long (O) or short (●) days. Each data point represents the mean \pm SE of 5–11 individual pooled serum samples. See Fig. 3 for details. Where SE bars are not present, the variance was encompassed by the area of the symbol.

of artificial short days to block testicular development resulted in a hamster which at 45 days of age resembled an adult in which short photoperiod had induced gonadal atrophy, *i.e.* reduced body and testicular weights and the appearance of a white winter pelage (23).

Based on the ability of short days to block gonadal maturation, it was hypothesized that the pattern of gonadotropin hormone secretion during development plays a deterministic role in the maturation of gonadal function. In long days, the rapid growth of testes between 15 and 30 days of age was correlated with peak FSH concentrations and somewhat higher concentrations of serum LH. These events coincided with the increased production of androgens after 20 days of age. In contrast, short day exposure (from birth) reduced FSH and LH concentrations to or below detectable limits by 25 days of age. Suppression of serum androgens in short day reared males correlated with marked testicular involution. These differences between long and short day reared males support the hypothesis that the patterns or amount of circulating gonadotropins are important to initiate or sustain the rapid phase of early testicular development.

In contrast to the Djungarian hamster, testicular maturation in the Syrian hamster is independent of photoperiod (8). Gonadal growth occurs up until 42 days of age whether Syrian hamsters are reared under short days or constant dark or are blinded. The Syrian hamster may simply have a longer response latency to short days than the Djungarian hamster. However, the period of most rapid testicular weight gain occurs between 25 and 49 days of age. Vomochka and Greenwald (10) found peak concentrations of FSH and high LH levels in serum at

40 days of age. Therefore, in both the Djungarian and Syrian hamsters, similar patterns of gonadotropins in the circulation coincide with the period of rapid testicular growth during pubertal development. It is possible that a common photoperiod-sensitive mechanism may be responsible for this rapid phase of sexual maturation in both hamster species.

In this regard, an inhibitory photoperiod during development may only block the mechanism controlling increasing or peak gonadotropin secretion. Therefore, the rapid phase of testicular growth might be blocked by short days because it actively blocks the required increase in FSH and LH secretion during development, *i.e.* 20–30 days in the Djungarian hamster or 35–50 days in the Syrian hamster. Alternatively, the forestalled gonadal growth may not result from an inhibition by short days, but rather, from the absence of a long day induced photostimulation of gonadotropin secretion. Long days may be required to drive peak secretion of FSH and sustain serum LH and PRL concentrations. Either hypothesis may represent a common photoperiodic mechanism underlying sexual development in these seasonally breeding hamsters.

Another commonality between these two hamster species is the phenomenon of spontaneous recrudescence. The testes of adult Djungarian hamsters maintained under a short photoperiod will not remain atrophic. Rather, a refractoriness to short days will restore gonadal function. Djungarian hamsters reared in short days attain full reproductive competence within 150 days of age; this is associated with a moult into the summer agouti coat color (9). In both time course and pattern, this delayed onset of fecundity resembles the spontaneous recrudescence of gonadal function in adult Djungarian (23) and Syrian (24) hamsters after prolonged exposure to short days.

The role of PRL in testicular development is not clear. However, the pattern of circulating PRL during development in the Djungarian hamster appears to have both age and photoperiod components. Under long days, the 2- to 3-fold increase in serum PRL concentrations between 5 and 15 days of age preceded both the rise in serum gonadotropins and the rapid phase of testicular growth. A similar relationship occurs in other rodent species. In the prepubertal male Syrian hamster, enhanced serum PRL concentrations precede increases in serum FSH (10) and the rapid increase in testicular weight (8). In the prepubertal rat, Dohler and Wuttke (11) reported that PRL concentrations increase before alterations in serum FSH.

These developmental changes in serum PRL may be important for the onset or support of gonadal function. Other studies have implicated PRL as potentiating the action of gonadotropins through enhancement of testic-

ular LH receptors (25, 26). In addition, PRL treatments substantially advanced the onset of puberty in the female rat (27). These data suggest a locus of PRL action at the gonadal level. An additional effect on the hypothalamo-pituitary axis is suggested by studies in immature and adult rodents in which increased concentrations of PRL stimulated endogenous FSH secretion (17, 28, 29). The Djungarian hamster may be a useful model for further study of the role of PRL in sexual maturation.

The ability of short days to inhibit testicular development in the Djungarian hamster is known to involve the pineal body. Pinealectomy at 2 days of age (30) or pineal denervation (superior cervical ganglionectomy) at 15 days of age (31) results in marked testicular growth. The circadian pineal melatonin rhythm has been hypothesized to transduce daylength information and mediate the effects of photoperiod on the hypothalamo-pituitary-gonadal axis (22, 32). Maturation of the pineal melatonin rhythm occurs between 15 and 20 days of age (33). The onset of this rhythm correlates with the ability of short days to block both the peak in serum FSH concentrations and gonadal growth by 20 days of age. Therefore, maturation of a pineal-dependent mechanism may be hypothesized as a requisite component to the photoperiodic mechanism controlling gonadal development in this hamster species.

The observation that serum PRL concentrations were lower in short day reared males before 15 days of age is potentially intriguing. This effect preceded the maturation of an adult-like pineal melatonin rhythm (31) and the photoperiod-induced decrease in both serum gonadotropins and testicular weight. More recent work using a homologous RIA for serum PRL (Goldman, B. D., unpublished data) has confirmed that serum PRL concentrations are lower in males reared under short compared to long photoperiods after 20 days of age. However, before 10 days of age, no significant differences in serum PRL levels were observed in males housed under short or long days. Thus, differences in PRL secretion before 15 days of age may be the result of an assay discrepancy between the rat PRL RIA and the new homologous hamster PRL RIA rather than some pineal independent photoperiod effect.

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American Diabetes Association

Please note that the American Diabetes Association will hold its Annual Meeting in Las Vegas, Nevada June 10–13, 1984.