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Effect of Different Photoperiods on Gonadal Maintenance and Development in Mongolian Gerbils (*Meriones unguiculatus)*

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ABSTRACT—The role of photoperiod in adult testicular maintenance and body weight and juvenile development was assessed in male Mongolian gerbils (*Meriones unguiculatus)*. Gerbils were raised on a 14L (14 hr of light) photoperiod. In the first study, adult gerbils with functional testes were transferred to thirteen different photoperiods (0L, 2L, 4L, 6L, 8L, 10L, 12L, 14L, 16L, 18L, 20L, 22L, or 24L) and body weights and testicular size were measured every week for 10 weeks. Body weights were similar in all groups. Testicular regression had occurred in animals housed on 0L, 2L, 4L, 6L, 8L, and 24L by week 10. In the second study, 14L-born prepubertal gerbils were transferred to thirteen different photoperiods as in the first study. Body weights and testicular development were examined for 10 weeks. At the end of 10 weeks the body weights of animals in all groups except 24L were similar to those of adults. Animals in 24L had a lower body weight gain. Exposure to 0L, 2L, and 24L inhibited testicular development and testes weights were significantly different from those of the other groups.

These results demonstrate that maintenance of body weight in adult gerbils appears to be independent of photoperiodic signal. Exposure to very long (24L) and short photoperiods (<10 hr) causes testicular regression in adult gerbils. Moreover, different photoperiods experienced in early life can influence prepubertal testis growth and body weight gain.

Key words: body weight, gerbil, photoperiod, reproduction, pineal melatonin

INTRODUCTION

Many mammalian species which live in the temperate zone show behavioral and physiological responses including seasonal cycles of body mass and sexual activity. Mammals rely on upon cues from the environment to time seasonal breeding and photoperiod is by far the most reliable predictor of season. In many rodents, exposure to short photoperiods causes regression of the gonads in adults and delays reproductive organ growth in prepubertal animals, while long photoperiods maintain gonadal function and stimulate reproductive growth (Gaston and Menaker, 1967; Johnson and Zucker, 1980; Horton, 1984; Stetson *et al*., 1986).

Responses to photoperiod are species-specific. Lack of responsiveness of reproductive system to photoperiodic changes has been reported for male laboratory rats (Wallen *et al*., 1987), prairie voles (Nelson, 1985) and Shaw's jirds (El-Bakry *et al*., 1999). Studies on hamster species (Hoffmann, 1981), deer mice (Nelson *et al*., 1992) and marsh rice rat (Edmonds and Stetson, 1994) revealed that short photoperiods reduced testicular mass. Tropical rodents have also been investigated for an influence of photoperiod on reproduction. Gonadal regression in short photoperiods has been reported for the Indian palm squirrel (Haldar and Pandey, 1988). It was demonstrated that in the Indian desert gerbil, constant light resulted in reproductive inhibition whereas constant darkness was stimulatory (Sinhasane and Joshi, 1997; Thomas *et al*., 2001)

Reproductive development in many photoperiodic species occurs only when the animal is exposed to photoperiods greater than threshold (critical photoperiod), while reproductive development is greatly prolonged by photoperiods less than critical. Critical photoperiods, often between 12 and 14 hr of light per day, have been characterized for several rodent species (Elliott, 1976; Hoffmann, 1982; Rhodes, 1989; Hong *et al*., 1986), but not for the Mongolian gerbil.

Photoperiodic control of pubertal development has been examined in a number of rodent species. In Montane vole, deer mice and Siberian hamster, short photoperiod exposure appears to be responsible for the prevention of pubertal development. However, short photoperiod exposure has no effect on pubertal development in Syrian ham-

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ster (Horton, 1984, 1985; Stetson, 1985; Gaston and Menaker, 1967; Darrow *et al*., 1980; Rollag *et al*., 1982; Stetson *et al*., 1986; Sisk and Turek, 1987; Lee and Zucker, 1988). In Turkish hamster, the response of prepubertal hamsters to photoperiods depends on the lactational photoperiod (Gündüz and Stetson, 1998).

Mongolian gerbils, native to northeastern China and Mongolia, are in Gerbillinae family. They are nocturnal and the extensive geographical distribution of this genus suggests that the gerbil may be a valuable wild species to study environmental regulation of seasonal reproductive cyclicity. To date, the reproductive responses of adult and prepubertal Mongolian gerbil to different photoperiods have been controversial or were reported with insufficient data and critical photoperiods for both adult and juveniles have not been thoroughly studied. It has been shown that adult female Mongolian gerbils are responsive to short photoperiod (LD8:16) exposure (Devries *et al*., 1989). In the wild, Mongolian gerbils reproduce from February to September and their testes, like those of other seasonal breeders, undergo regression during autumn, the period of sexual inactivity (Benimetskii, 1975). On the other hand, in some reports adult gerbils failed to respond to photoperiods or they responded very poorly (Reiter *et al*., 1980). The reproductive responses of adult or prepubertal male gerbils to photoperiods may be different from those of the adult and prepubertal females and sex/species dependent. The objective of the experiments reported here was to determine the threshold (critical) photoperiod(s), to assess the effects of various photoperiods on adult reproductive system and body weight and to determine if the photoperiod controlled the onset of puberty in a laboratory population of male Mongolian gerbils.

MATERIALS AND METHODS

Animals

Mongolian gerbils (*Meriones unguiculatus)* were obtained from our laboratory colony maintained at the Abant Izzet Baysal University. The procedures used in this study were carried out in accordance with the Animal Scientific Procedure, Act of 1986 and approved by the Institutional Animal Care and Use Committee. Animals were exposed from birth to 14L (14 hr of light, 10 hr of darkness; lights off at 2000 hr). Animals were maintained in plastic cages (16×31×42 cm) with pine shavings used as bedding. Food pellets (Purina Rodent Chow) and tap water were accessible ad libitum. Cool-white fluorescent tubes controlled by automatic programmable timers provided all lightning; light intensities at the animal's eye level exceeded 200 lux. Ambient temperatures in the animal facilities were held constant at 20±2°C in air-conditioned rooms. Testis measurements were performed under ketamine (60 mg/kg BW, i.m.) and pentobarbital (25 mg/kg BW, i.p.) anesthesia. Maximum testis length and width were measured with hand-held calipers to the nearest 0.1 mm through the transparent tunica vaginalis (Kenagy, 1979). After measurement, the testis was returned to the scrotum and the skin was closed with stainless steel sutures. Alternate testes were measured on each successive surgery. Repeated surgery did not result in testicular damage. Linear regression analysis was used to determine the relationship between testicular volume (determined from length and width measurements) and weights of paired testes (Watson-Whitmyre and Stetson, 1985). Data were recorded as testes weights.

Experiment 1

To examine whether various photoperiods exerts an effect on testis and body weights and to determine the critical photoperiod in inducing testicular evolution, a total of 130, adult male gerbils (3–4 months age) were weighed and exposed to photoperiods of 0L, 2L, 4L, 6L, 8L, 10L, 12L, 14L, 16L, 18L, 20L, 22L, or 24L in separate rooms. Body weights and testicular measurements were determined at 1-week intervals for ten weeks. Measurements in 0L photoperiod were done under a dim red light. Lights off occurred at 2000 hr in all photoperiods characterized by a light-dark cycle.

Experiment 2

To examine the response of body weight and testicular growth of prepubertal gerbils to different photoperiods, gerbils were gestated in 14L photoperiod and reared in thirteen different photoperiods as in experiment 1. Adult animals were paired in 14L and on the day of parturition, at least five females with their litters were transferred to experimental photoperiods. Therefore each photoperiod had at least five females with litters to obtain enough males (n=10). Pups were weaned at 26 days of age and males with a similar size were placed in plastic cages, three males in each cage. Body weights and testicular measurements were determined at 1-week intervals throughout 10 weeks. Measurements in 0L photoperiod were done under a dim red light. As in experiment 1, lights off occurred at 2000 hr. Several gerbils in different photoperiods died during the experiment and they were excluded from the final analysis.

Statistical analysis

Testes and body weights were analyzed using a repeated-measures two-way analysis of variance (ANOVA; SPSS for Windows, ver. 9.0) to see effects of photoperiod and time. Differences between means within a photoperiod or between photoperiods were determined by t tests or a Student-Newman-Keuls test where appropriate; values were considered statistically significant at $p<0.05$. Data are presented as mean±SEM.

RESULTS

Experiment 1

There was no significant difference between the body weight of animals at week 1 and week 10 in all photoperiods (Fig. 1; $p>0.05$ for comparison of week 1 and week 10 in each photoperiodic group).Photoperiods did affect testes weights in males maintained in 0L, 2L, 4L, 6L, 8L and 24L (Fig. 2; $p<0.01$). Data are given only at week 1 and week 10. In other photoperiods final testes weights (week 10) were not significantly different than their initial testes weights (week 1) ($p>0.05$). Testes of males in 0L group underwent significant regression from week 5 ($p<0.05$). Testes of 2L, 4L, 6L, 8L and 24L group underwent significant reduction from week 7 ($p<0.01$) (data not shown).

Experiment 2

Exposure to a 24L photoperiod after parturition caused significantly ($p<0.001$) less body weight gain in gerbils than those of gerbils in other photoperiods after 10 weeks of treatment (Fig. 3).

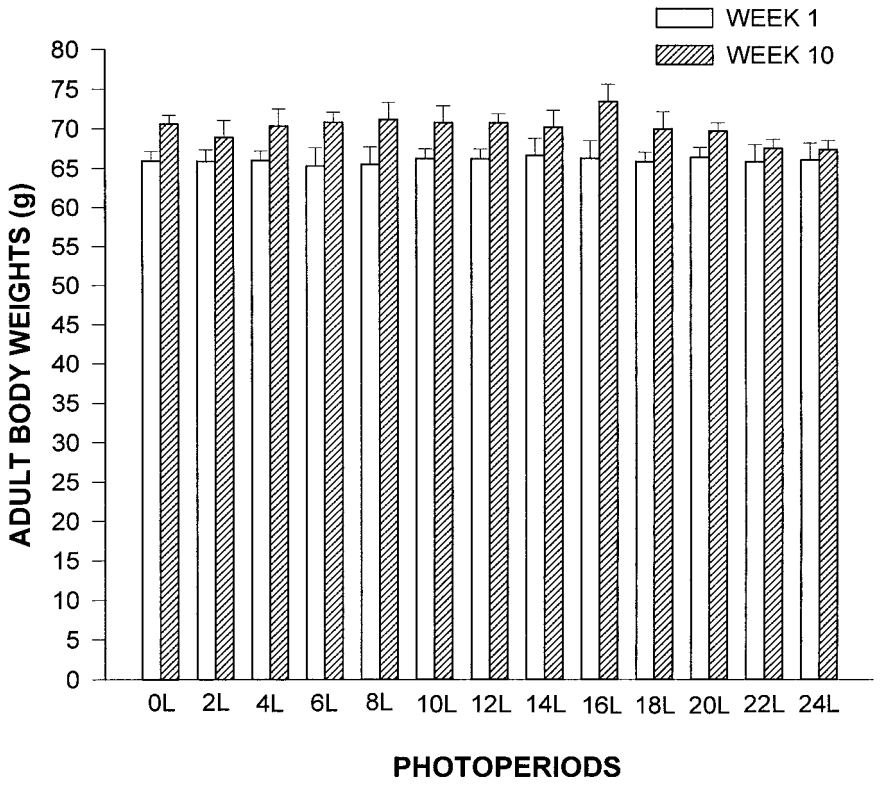

Fig. 1. Body weights of adult Mongolian gerbils raised in 14L and transferred to photoperiods ranging from 0–24 hr of light per day. Open bar represents body weight at week 1 and hatched bar represents body weights at week 10. Each bar represents mean±SEM of 10 male gerbils.

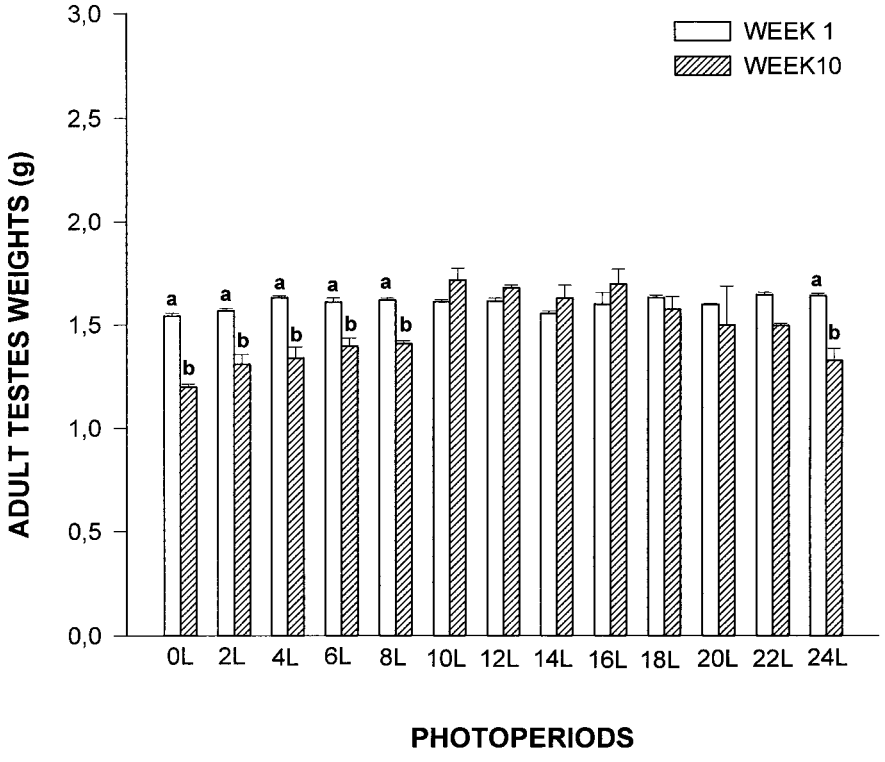

Fig. 2. Paired testes weights of adult Mongolian gerbils raised in 14L and transferred to photoperiods ranging from 0–24 hr of light per day. Open bar represents testes weights at week 1 and hatched bar represents testes weights at week 10. Each bar represents mean±SEM of 10 male gerbils. Groups with different letters in each photoperiod are significantly different from one another.

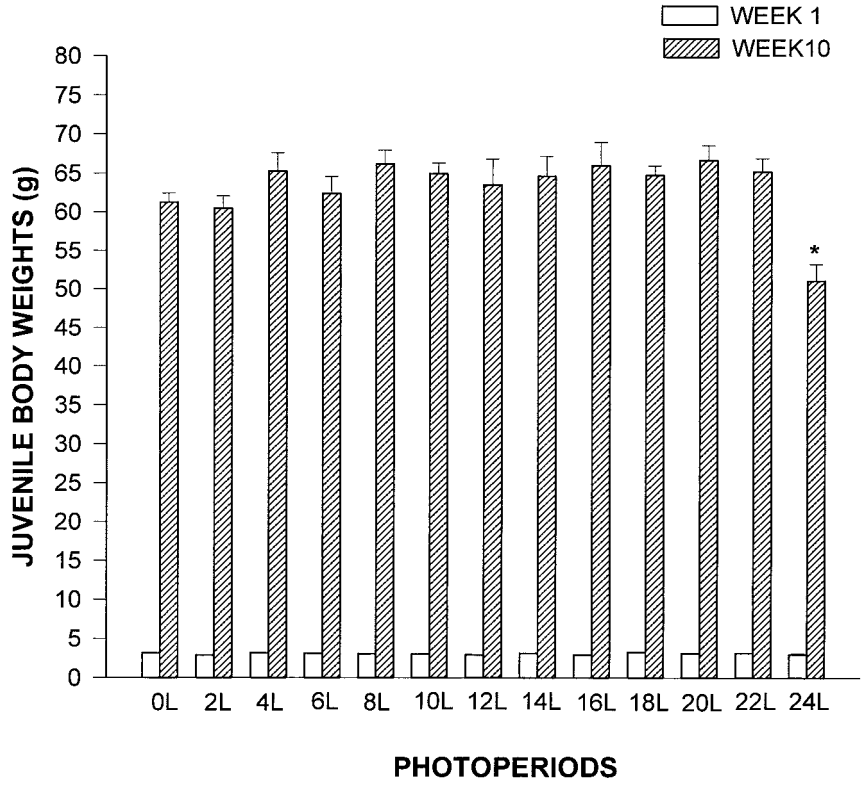

Fig. 3. Body weights of juvenile Mongolian gerbils gestated in 14L and reared on photoperiods ranging from 0–24 hr of light per day. Open bar represents body weight of newly born litters at week 1 and hatched bar represents body weights of male gerbils at week 10. Each bar represents mean±SEM of 8–10 male gerbils. * indicates statistical differences ($p<0.001$) among groups at week 10.

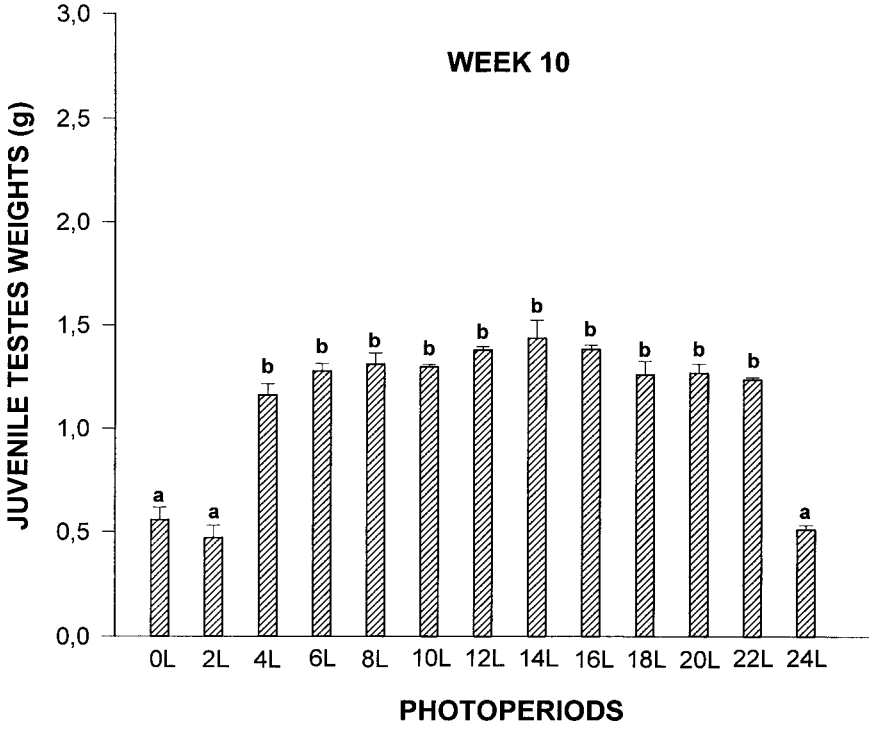

Fig. 4. Paired testes weights of juvenile Mongolian gerbils gestated in 14L and reared on photoperiods ranging from 0–24 hr of light per day. Each column represents mean±SEM of 8–10 male gerbils at week 10. Groups with different letters are significantly different from one another.

Testes weights of juveniles were significantly influenced by photoperiods (Fig. 4; $p<0.007$). Gerbils from 0L, 2L, and 24L photoperiods had paired testes weights that were significantly less ($p<0.001$) than those of animals in all other photoperiods, but were not significantly different from one another at week 10 ($p>0.05$). Paired testes weights of animals at other photoperiods (4L–22L) increased gradually from week 3 to week 5, and then increased rapidly between 6 and 10 weeks, when maximum weights were attained (data not shown).

DISCUSSION

This study provides evidence that both juvenile and adult male gerbils are sensitive to rapid changes in photoperiod. We examined the effects of photoperiod on both body weight and testicular regression by moving animals from 14L to one of 13 daylenghts with light exposure ranging from 0 to 24 hr per day for 10 week. Juvenile males required more extreme changes in photoperiod than did adult gerbils to prevent testicular development. There was little effect of photoperiod change on body weight changes in either adults or juveniles.

Our data show that prepubertal Mongolian gerbils are reproductively photoperiodic at an early age, that photoperiods present during specific stages of development determine the magnitude of testicular development. Testicular development was inhibited in male Mongolian gerbils gestated 14L and reared from birth on a single photoperiod of 0L, 2L and 24L hr of light per day (Fig. 4). The magnitude of testicular growth was more in animals maintained on photoperiods ranging from 4 hr to 22 hr of light per day. Although Mongolian gerbils would never be exposed to the extreme photoperiods used in this study, 6 to 18 hr of light per day represents the approximate range of day lengths that animals would encounter under natural conditions (Benimettskii, 1975). In addition, sensitivity to photoperiod decreases with decreasing latitude; small animals living around 30° latitude may stop using photoperiod as a proximate factor (Bronson and Heideman, 1994). Studies have demonstrated that many rodent species from this latitude are non-photoperiodic, although populations of the same species living at other latitudes are responsive to changes in photoperiod (Lynch *et al*., 1981; Dark *et al*., 1983). These juvenile results are in agreement with those from most photoperiodic rodents (excluding Syrian hamsters) in which short photoperiods retard testicular development, while long photoperiods promote rapid testicular development (Gaston and Menaker, 1967; Horton, 1985; Clark and Galef, 1980, 1981; Hong and Stetson, 1986; Stetson *et al*., 1986). The response of juveniles to 4L, 6L and 8L differed from that observed in adult gerbils. For instance, 4L, 6L, and 8L were inhibitory for adult testes, but prepubertal gerbils responded with rapid testes growth to those photoperiods at week 10. This point is remarkable because a different response of adults and juveniles to photoperiods is not common among rodents. It would be worthy to delve into this aspect through studies focused on the physiological role of light in each photoperiod especially in prepubertal Mongolian gerbils. The testicular responses of other prepubertal species, such as hamsters, to photoperiods may be different from those of the adult and are species dependent. Golden hamsters (*Mesocricetus auratus*) do not show a prepubertal response, in that all photoperiods applied failed to block gonadal maturation (Gaston and Menaker, 1967; Darrow *et al*., 1980; Rollag *et al*., 1982). In the Siberian hamster, short photoperiods (<13 hr) delay gonadal maturation (Hoffmann, 1978; Gündüz and Stetson, 1994).

In addition to demonstrating reproductive responsiveness, exposing Mongolian gerbils to photoperiods ranging from 0 to 24 hr of light per day identified two critical photoperiods for testicular development of between 2 and 4 hr of light and between 22 hr and 24 hr of light per day and two critical photoperiods for testicular maintenance of between 8 hr and 10 hr of light and 22 hr and 24 hr of light per day. Critical photoperiods, examined in several species, often demonstrate the relatively precise ability of different species to measure day length (Elliott, 1976; Hoffmann, 1982; Duncan *et al*., 1985). Photoperiods less than critical inhibit reproductive development, relative to that in animals reared on photoperiods longer than critical. The critical photoperiod determined here in the Mongolian gerbils is not in the range of critical photoperiods (12–14 hr of light per day) determined in most other photoperiodic rodent species. To date only the Turkish hamster has two critical daylenghts of 15 and 17 hr of light per day. Photoperiods less than 15 hr and greater than 17 hr promote testicular regression (Hong *et al*., 1986). But the response of prepubertal Turkish hamster to very long photoperiods (>17 hr) is different than that of adult Turkish hamster (Hong and Stetson, 1986). Greater than 17 h (20L or 24L) of light per day promotes testicular regression in adult Turkish hamster. In another study, juvenile Turkish hamsters respond to short (8L) or very long photoperiods (20L or 24L) in a similar way as the adult hamster did; i.e. small testes (Gündüz and Stetson, 1998). The major difference in those two studies was the different lactational photoperiods. Lee (1993) has shown effects of the lactational photoperiod on reproductive development in meadow voles. However, the mechanism(s) by which lactationally derived photoperiodic information influences reproductive development of the offspring is unknown. Either the dam could transfer photoperiodic information to the pup or the pup could respond directly to photoperiod. The present study in Mongolian gerbil does not distinguish between these two possibilities.

Exposure to all photoperiods did not affect body weight in adult male and juvenile Mongolian gerbils, but the body weight gain in 24L (constant light) was slower compared to other groups in male juvenile gerbils. Clark and Galef (1980, 1981, 1985) observed that both males and females pups reared either in 24L or on a 12L weighted significantly more than those reared in 0L or 6L. Champney (1988) found no

differences in body weight between long (14L) and short (10L) photoperiod-exposed gerbils. Our observations on body weights in juvenile gerbils are not consistent with Clark and Galef study; in our study body weight gain of prepubertal gerbils maintained from birth was significantly slower only in 24L. Neither in 0L nor in 6L animals exhibited slower growth rate. These results seem to be more complex than those associated with adult body weight. The cause of slower body weight gain in this group is presently not known. The fact that variation in photoperiod affected the body weight in juvenile gerbil may or may not indicate that Mongolian gerbils actually use photoperiod to regulate their body weights. On the other hand, the differences in body weight we observed in 14L-born and 24L-raised juvenile gerbils may simply reflect differences in hormone secretion (such as melatonin) and activity levels due to the duration of light. We know that in photoperiodic animals the pineal gland is a critical component of the system producing a response to photoperiod (Stetson and Watson-Whitmyre, 1984). The neuroendocrine pathway through which day-length regulates reproduction and body weight in mammals is well known (Reiter, 1991). This process involves the transduction of photic information to a neuroendocrine signal via production of melatonin by the pineal gland. Therefore continuous light will mask the release of melatonin and this might cause the animal to respond to 24L with slower body weight gain. That the photoperiodic body weight response of prepubertal Mongolian gerbils differs from that of the adult in 24L is apparent from the data presented here. In fact, we have not been able to demonstrate pineal involvement in the prepubertal response. Therefore, the body weight response of Mongolian gerbils does not seem to be governed by changes in the photoperiod and different mechanisms may regulate the body weight response to very long photoperiods (24L) in prepubertal vs. adult Mongolian gerbils, and prior photoperiodic history of the animal may be an important factor in body weight response to photoperiod.

The observation that juvenile and adult responded to short photoperiods (<10L) and very long photoperiods (24L) in a similar fashion suggests that the regulatory processes controlling delay of reproductive mechanism may be similar to those controlling reproductive regression in adult. In contrast, the neural mechanisms, which regulate the photoperiodic response to 4L, 6L, and 8L in adult gerbils, appear to be more sensitive than in juveniles. It is known that although there is testes regression, reproductive ability continuous in some species (Nelson, 1985). Recently published paper from our laboratory showed that short photoperiods (0L, 8L) and very long photoperiod (24L) caused inhibition of spermatozoon production in adult testes (Gündüz and Karakas, 2001). Given the existence of these reproductive differences between juvenile and adult gerbils in 4L, 6L, and 8L, we believe that comparison of pinealectomized juvenile and adult gerbils presents an ideal model for future investigations focusing on the melatonin effect.

In conclusion, the results reported here indicate that the reproductive organ of adult Mongolian gerbils are influenced by variations in photoperiod and suggest two critical photoperiods for reproductive maintenance of between 8 hr and 10 hr of light and 22 hr and 24 hr of light per day. In addition, reproductive development of prepubertal gerbils is also influenced by photoperiod. It appears from these laboratory data that Mongolian gerbil is a useful species for studies of environmental regulation of seasonal reproductive cyclicity.

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