

# Early Photoperiod History and Short-Day Responsiveness in Siberian Hamsters

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**ABSTRACT** Siberian hamsters exhibit seasonal, photoperiod influenced cycles of reproductive activity, body size, pelage characteristics, and thermoregulatory behavior. Laboratory populations generally exhibit inter-individual variability in expression of photoperiod responsiveness, with a subset of individuals that fail to show the species typical responses to short photoperiod. This variability is partly explained by a genetic component, as it has been possible to increase the number of short-day nonresponders by artificial selection. Responsiveness to short photoperiod is also substantially influenced by photoperiod history in this species; hamsters that have been raised under long (16L) or very long (18L) day lengths are less likely to exhibit winter-type responses to short days as compared to hamsters raised under an intermediate (14L) day length. In the present experiment, we examined effects of age and early photoperiod history in a strain of Siberian hamsters that had been selected for short-day nonresponsiveness. Hamsters transferred into short photoperiod on the day of birth were uniform in exhibiting winter-type responses. However, hamsters raised until 25 days of age in either continuous illumination or in 16L exhibited variation in responsiveness when subsequently moved into short photoperiod. We conclude that virtually all hamsters of the short-day nonresponsive strain are born responsive to short days. Subsequent development of resistance to potential short day effects is dependent on age and/or photoperiod history. *J. Exp. Zool.* 296A:38–45, 2003. © 2003 Wiley-Liss, Inc.

## INTRODUCTION

A wide variety of organisms use day length cues to time seasonal variations in physiology and behavior. These photoperiodic responses appear to have become established because they provide animals with an opportunity to better adapt to relatively predictable environmental changes that recur on an annual basis. Photoperiodic species sometimes exhibit inter-individual differences in response to day length cues (Nelson, '87; Blank and Freeman, '91; Kliman and Lynch, '91). These differences can be at least partly genetically based, and it has been possible to use artificial selection to develop breeding lines of photoperiod nonresponsive animals in species where most individuals are photoperiodic (Heideman and Bronson, '91; Kliman and Lynch, '92). Our laboratory has used artificial selection to develop a strain of short day nonresponsive (PNR, for photoperiod nonresponsive) Siberian hamsters. Most Siberian hamsters exhibit a constellation of winter responses—reproductive inhibition, loss of body weight, molt to winter pelage—when exposed to short day lengths (Hoffmann, '78). Most animals of our PNR line fail to exhibit these responses

when exposed to short photoperiod (Freeman and Goldman, '97a,b).

The basis for the failure of the PNR hamsters to respond to short days appears to lie in the properties of the circadian system of these animals. PNR hamsters have a longer freerunning period length (*tau*) as compared to the photoperiod responsive animals. In addition to their differences in *taus*, photoperiod responsive and short-day nonresponsive hamsters exhibit somewhat different phase response curves (Puchalski and Lynch, '86). These differences in *taus* and phase response curves are apparently responsible for a marked difference in the phase angle of entrainment to short photoperiods in the photoperiod responsive hamsters as compared to the PNR animals. The delayed phase angle of entrainment in PNR hamsters probably results in illumination of a portion of the photosensitive phase of the circadian cycle even in short days; hence, the failure of PNR animals to 'interpret' the

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photoperiod as a short day (Puchalski and Lynch, '86; Margraf et al., '91). Indeed, PNR hamsters did exhibit complete gonadal regression when housed in continuous darkness, indicating that light must be present at some part of the circadian cycle to prevent regression in these animals (Freeman and Goldman, '97a).

Recent studies in our laboratory revealed a strong effect of photoperiod history on responsiveness to short days in both our random-bred (UNS for random-bred or unselected) and PNR strains. This photoperiod history effect is similar to an effect that was previously reported in a random-bred line of Siberian hamsters (Gorman and Zucker, '97; Goldman et al., 2000). That is, hamsters exposed to a very long photoperiod (18L) for several weeks are more likely to be unresponsive to subsequent short day exposure as compared to hamsters that have never experienced such long day lengths. Hamsters of our PNR line were more responsive to this type of photoperiod history effect as compared to the UNS hamsters. The PNR animals were mostly nonresponsive to short days after being reared in 16L, whereas for the UNS animals a still longer day length was required to establish short-day nonresponsiveness in most of the population. Using hamsters derived from the PNR line, we determined that the percentage of animals that would exhibit the species-typical responses to short photoperiod could be increased by rearing the hamsters from birth to adulthood in 14L as compared to our standard long day photoperiod (16L). However, even when reared exclusively in this 'intermediate' day length, a significant proportion (44%) of male PNR hamsters failed to exhibit testicular regression following transfer to short days (Goldman et al., 2000).

What might be the significance of these effects of photoperiod history for hamsters living in the field? Hamsters born early in the breeding season (spring/early summer) would be exposed to the longest summer days, and many of these animals thus would be rendered insensitive to the reproductive inhibitory effects of short days. Most of the individuals remaining reproductively active through the winter would be members of this cohort. Animals born later in the summer would be exposed to fewer (and shorter) long days and would be more likely to undergo reproductive inhibition in the short days of autumn/winter. Finally, hamsters born at the very end of the breeding season, when day lengths are already short, would be uniformly responsive to short days. The same would be true for hamsters born

during the winter. Since Siberian hamsters are relatively short-lived rodents, it is likely that the large majority of the breeding population at any time is composed of animals less than one year old. In view of the considerations enumerated above, it would seem that the system of photoperiod history effects in Siberian hamsters would result in winter breeding mainly by the older members of the population (i.e., those animals born early, rather than late, in the previous spring/summer breeding season). This system would make sense as an evolved strategy to maximize lifetime reproductive potential; older animals should accept the greater risks of winter breeding because they are the individuals that are least likely to survive until the next main breeding season (Gorman and Zucker, '97).

Preliminary data in our laboratory indicated that PNR hamsters were uniformly responsive to short photoperiod provided they were exposed to short days beginning on the day of birth rather than waiting until later in life to test for responsiveness (Eric Anderson and David Freeman, unpublished data). This raised two possibilities: (a) There might be a major effect of age on short day responsiveness, with animals being responsive at birth but losing responsiveness as they mature. (b) Alternatively, it might be that hamsters are born responsive to short days, but lose responsiveness as a result of exposure to long (16L) or intermediate (14L) day lengths during rearing. This second hypothesis would not implicate age *per se* in the loss of responsiveness; rather, loss of responsiveness might be strictly a photoperiod history effect. We recognized that it would be difficult to distinguish experimentally between these alternative hypotheses. To support hypothesis "b" would require that we find a photoperiod of rearing that does not itself induce short day type responses, but which would not result in a loss of response potential during maturation. 14L is the shortest photoperiod that does not consistently evoke gonadal regression in this species (Carter and Goldman, '83a; Duncan et al., '85; Hoffmann et al., '86), and our earlier experiments revealed that when PNR hamsters are raised in 14L a substantial proportion of individuals become nonresponsive to short days, though the frequency of nonresponsiveness was less than for animals from the same population that had been raised in 16L.

In mammals, photoperiodic responses usually involve the rhythmic secretion of pineal melatonin, which appears to provide an internal 'signal'

that represents day length (Bartness et al., '93; Goldman, 2001). Exposure to continuous illumination (LL) is thought to result in the failure of melatonin secretion. Therefore, we reasoned that LL would be an 'ambiguous' photoperiod since it is not clear how the photoperiodic mechanism might 'interpret' day length when there is no melatonin signal. Thus, it seemed possible that rearing hamsters from birth in LL might result in the retention of responsiveness to short days, even though exposure to LL does not of itself result in testis regression in male Siberian hamsters (Carter and Goldman, '83b). Such a result would suggest that photoperiod history, and not age *per se*, is responsible for the loss of short day responsiveness during postnatal development in PNR Siberian hamsters. In the present study, we compared short day responsiveness of PNR hamsters under three conditions: (a) raised in 16L until postnatal day 25 (D<sub>25</sub>) and then transferred to 10L (LD-SD), (b) raised in LL until D<sub>25</sub> and then transferred to 10L (LL-SD), and (c) transferred to 10L at birth (SD-SD).

## MATERIALS AND METHODS

Animals used in this experiment were from a breeding line of photoperiod nonresponsive (PNR) Siberian hamsters that was developed through artificial selection in our laboratory. These animals were selected for their failure to exhibit the species-typical responses—body weight loss, reproductive inhibition, and pelage molt—when exposed to a short day photoperiod in adulthood (Freeman and Goldman, '97a,b).

Food (Agway Prolab 3500 RMH) and water were provided *ad libitum* at all times. Breeding pairs were established from adult (2–4 month old) hamsters raised in a long day photoperiod (16L; lights-on 0200–1800h). Pairs remained together in 16L during gestation, and cages were checked every morning for births. On the day of birth, the breeding pair and their litter were assigned to one of three treatment groups. Group 1 (16 male and 24 female pups) was left in 16L, Group 2 (25 male and 28 female pups) was transferred to continuous illumination, and Group 3 (24 male and 17 female pups) was transferred to 10L. Light intensities in all photoperiods were 200–500 lux. Beginning at 10–12 days after birth, the standard diet was supplemented with sunflower seeds to promote more rapid growth of the pups. Pups were weaned at 14 days of age (D<sub>14</sub>) and remained in the same photoperiod as during lactation. On D<sub>25</sub>, the

animals of Groups 1 (LD-SD) and 2 (LL-SD) were transferred to 10L; Group 3 (SD-SD) animals remained in 10L. Hamsters in all three groups were autopsied 60–64 days after their initial transfer to 10L. Thus, at the time of autopsy animals of LD-SD and LL-SD groups were 85–89 days old, whereas SD-SD animals were 60–64 days old. This experimental design was chosen because we considered the amount of time in short days to be a more important parameter to keep constant across groups rather than age. Testis weights were recorded for males and uterine weights were taken for females. Male hamsters raised in long days rarely exhibit paired testes weights <400 mg by 2 months of age (Shaw and Goldman, '95a). Therefore, paired testes weights <400 mg were considered to indicate partial or complete regression. Because the LD-SD and LL-SD animals were older than the SD-SD hamsters at autopsy it is important to note that for hamsters raised in long days, maximum testis size is achieved by about 6 weeks of age (Shaw and Goldman, '95a).

All experimental procedures received prior approval by the Institutional Animal Care and Use Committee of the University of Connecticut.

## Statistics

Body weights and organ weights were analyzed by two-way analysis of variance (ANOVA). Since this analysis indicated significant differences between groups, the data were further analyzed using Tukey's HSD test to evaluate the significance of differences between pairs of treatment groups. Data for percentages of animals failing to exhibit testicular regression were analyzed using Statistica's two-sided difference between two proportions test (based on chi-squared distribution).

## RESULTS

Hamsters of both sexes that were transferred to short photoperiod on the day of birth (Group 3) failed to show reproductive development. This was especially apparent in males, where all 24 subjects had paired testis weights <40 mg, indicating complete regression (Fig. 1). Animals in the other two groups exhibited significantly greater reproductive development. For males left in 16L until D<sub>25</sub> (LD-SD), 8 of 16 subjects had paired testis weights <400 mg, indicating regression ranging from partial to complete. For LL-SD males, 8 of 25 subjects had paired testis weights <400 mg. Neither mean testis weights, nor percentages of

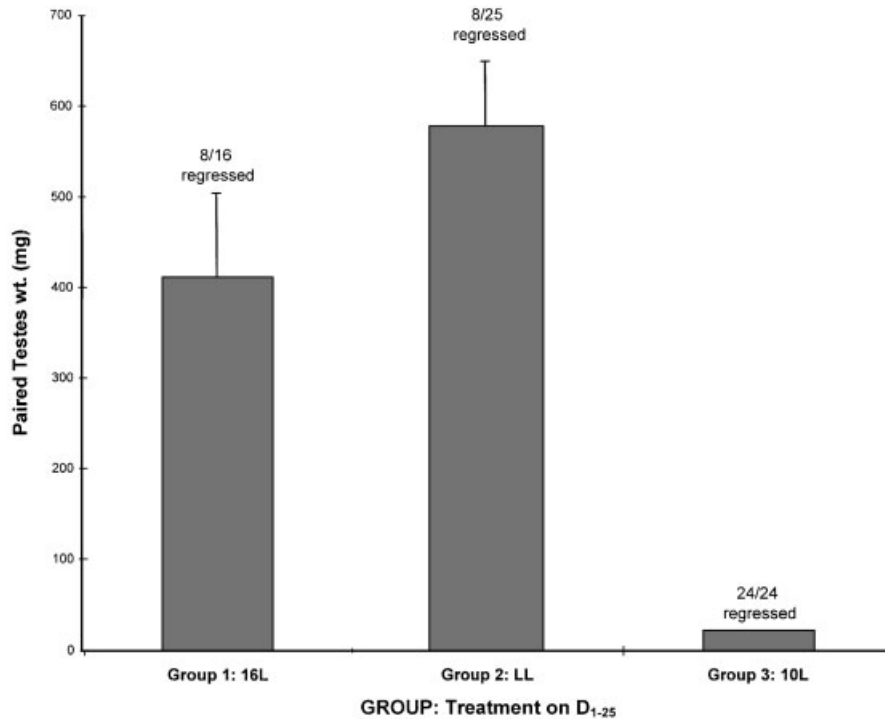


Fig. 1. Effects of photoperiod of rearing on testis development in male hamsters exposed to short days beginning at birth or at D<sub>25</sub>. Group 1 (LD-SD) was in 16L until D<sub>25</sub>, Group 2 (LL-SD) was in LL, and Group 3 (SD-SD) was in 10L. All animals were in 10L from D<sub>25</sub> until the time of autopsy. Height of each bar indicates mean paired testes weight for treatment group indicated beneath the bar. SEM and number of animals regressed (testes wts. <400 mg)/total N are indicated above each bar.

animals exhibiting testicular regression were significantly different between LD-SD and LL-SD males. However, mean testis weights and percent of animals regressed in both these groups were significantly different from Group 3 ( $P < 0.01$ ). Body weights of LD-SD males were less than those for LL-SD group ( $37.3 \pm 1.9$  vs.  $41.7 \pm 0.8$ g,  $P < 0.05$ ). Body weights for the SD-SD males were  $32.2 \pm 0.9$ g; however, since these hamsters were approximately 25 days younger than animals in the other two groups at autopsy, we did not include SD-SD group in the body weight comparison.

The uterine weights of SD-SD females were less than those for LL-SD ( $P < 0.01$ ), (Fig. 2). Mean uterine weights of the SD-SD females were also less than the mean for LD-SD, but the difference between these groups narrowly missed reaching statistical significance ( $P = 0.055$ ). Uterine weights of the LD-SD females were significantly less than those of Group 2 ( $P < 0.05$ ). Body weights of the LD-SD females were significantly less than those of LL-SD group ( $30.5 \pm 0.7$  vs.  $35.4 \pm 1.1$ g,  $P < 0.01$ ). The mean body weight for the SD-SD females was  $28.1 \pm 0.9$ g.

## DISCUSSION

The results of this study clearly demonstrate that hamsters of our PNR line, bred for non-responsiveness to short days when tested in adulthood, are fully responsive to short photoperiod when exposure begins on the day of birth. In an earlier study, male PNR hamsters that were transferred to short days at the time of weaning (17–19 days after birth) and allowed access to a running wheel exhibited testicular regression; animals similarly treated but without access to a wheel did not regress (Freeman and Goldman, '97a). A photoperiod history effect was also evident in PNR hamsters. Most (77–81%) male PNR hamsters failed to exhibit testicular regression when transferred to short days (10L) after having been raised to adulthood in long days (18L or 16L). However, only 44% of PNR males failed to regress in 10L after having been raised to adulthood in an 'intermediate' (14L) day length (Goldman et al., 2000). These earlier results underscored both genetic and experiential components of short day responsiveness.



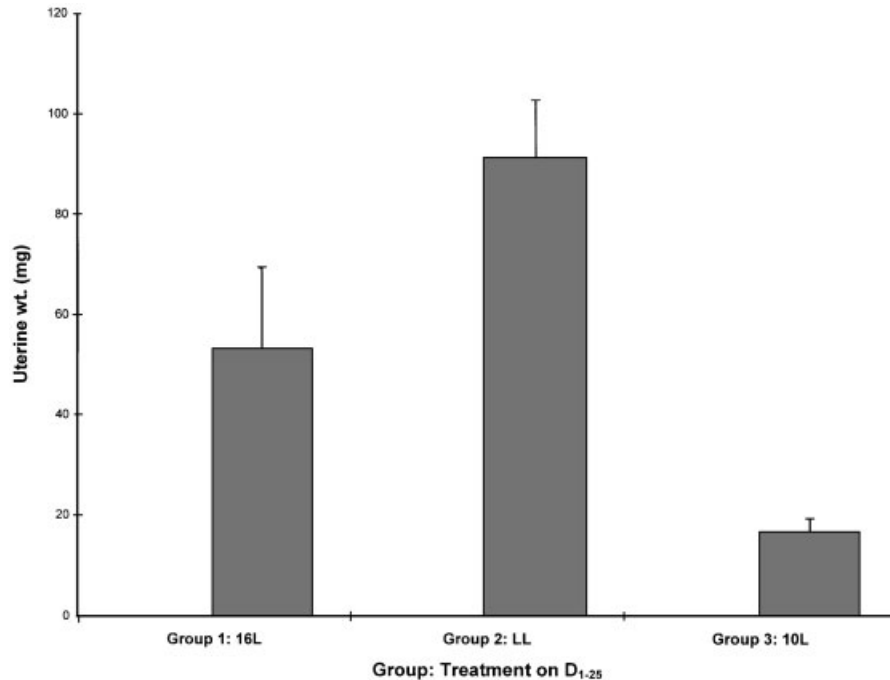


Fig. 2. Effects of photoperiod of rearing on uterine weight in female hamsters exposed to short days beginning at birth or at D<sub>25</sub>. Treatment groups are the same as in Figure 1. Height of each bar indicates mean uterine for treatment group indicated beneath the bar. SEM is indicated above each bar.

In the present study, all 24 males that were exposed to short days beginning on the day of birth exhibited a complete inhibition of testis development. In contrast, a substantial proportion of the hamsters exposed to 16L or LL from birth until short day exposure was initiated at D<sub>25</sub> were unresponsive to short days. In order to control for the amount of exposure to short days, the SD-SD hamsters were autopsied at 60–64 days of age, whereas the LL-SD and the LD-SD animals were sacrificed at 85–89 days. The difference in ages at autopsy is unlikely to have played a significant role in determining the differences between groups in reproductive status, however. Male Siberian hamsters reared in short days do not exhibit substantial testis growth until approximately 120–150 days of age (Hoffmann, '78). Thus, had we autopsied the SD-SD males at 85–89 days of age, as for the other treatment groups, we expect that their testes would have remained undeveloped at that time.

The failure of 64% of the animals reared in LL to respond to subsequent short days could be interpreted in at least two alternative ways: (a) LL is believed to result in complete inhibition of pineal melatonin secretion; therefore, there should be no

long day melatonin signal during exposure to LL. Nevertheless, it may be that LL exposure exerts an effect similar to long days and thereby acts to induce a state of short day nonresponsiveness in some PNR hamsters. (b) It may be that whereas virtually all hamsters are short-day responsive at birth, some of them become nonresponsive by D<sub>25</sub>, irrespective of photoperiod history effects. Thus, the results of the present study do not permit us to determine whether the uniform responsiveness to short days seen in PNR hamsters reared from birth in 10L is strictly related to the age at which short-day exposure began or whether it is a function of lack of any prior exposure to long days. However, the results do confirm our preliminary data indicating that all, or almost all, PNR hamsters are born with the potential to respond to short days, with this potential being lost later in life. Exposure to long or intermediate day lengths is clearly a factor in loss of short-day responsiveness (Goldman et al., 2000); age may also be a factor.

In the present study, we examined only hamsters from a breeding line that had been subjected to artificial selection for nonresponsiveness to short days because our objective was to determine whether at least some of these animals might be

constitutively nonresponsive regardless of photoperiod history. In an earlier study, we examined responsiveness to short photoperiod in young male hamsters of our random-bred line (UNS). Of 49 males born into a 16L photoperiod and transferred to 10L at 17–19 days of age, only one individual failed to exhibit inhibition of testis growth after 6 weeks (Freeman and Goldman, '97b). Therefore, it seems probable that virtually all male UNS hamsters, like the PNR males in the present study, would be fully responsive to short days at birth.

It should be noted that since the time our experiment was planned, another laboratory has reported that the regulation of short-day nonresponsiveness by photoperiod history is a pineal-independent phenomenon (Prendergast and Freeman, '99). It was not possible to test this hypothesis directly by assessing reproductive parameters, since regression of the gonads in short days is clearly pineal-dependent and cannot be observed in pinealectomized hamsters. However, the pattern of entrainment to a short photoperiod was clearly affected in the same way by prior exposure to a very long day (18L) in both intact and pinealectomized male hamsters. This observation suggests that the *circadian changes* that are induced in most individuals following exposure to very long day lengths are not pineal-dependent; these photoperiod history dependent changes appear to lead to the failure of the melatonin peak to expand in short days, precluding reproductive inhibition (Prendergast and Freeman, '99). Based on these findings, it would appear that the ability of LL to abolish the melatonin signal in the present experiment might have been irrelevant with respect to the photoperiod history effect. Nevertheless, it is still possible to conclude that the PNR hamsters are responsive to short photoperiod at birth and that this response is lost in many individuals housed in LL until D<sub>25</sub> — i.e., in the absence of any circadian entrainment cue.

The results for female hamsters paralleled those for males with respect to mean uterine weights for the different treatment groups. However, differences in reproductive organ weights between treatment groups were of lesser magnitude in females as compared to males. The differences in uterine weights between females exposed to short days from birth (SD-SD) and those first exposed to short days at D<sub>25</sub> reached statistical significance only in the comparison to the LL-SD animals (exposed to LL from birth until

D<sub>25</sub>). Differences between treatment groups were less clear among females as compared to males in earlier studies of this nature as well (Goldman et al., 2000), and this is probably related to (a) large variability in uterine weights among ovulating females depending on stage of the estrous cycle and (b) the failure of many female Siberian hamsters to reach ovulatory status by 2 months of age even when raised exclusively under long days.

The present results support conclusions drawn from earlier studies regarding effects of photoperiod history to modify the state of responsiveness to short day lengths in Siberian hamsters. It has been suggested that this photoperiod history effect leads to an increased likelihood of winter breeding among the older members of the population; an age-related strategy vis-à-vis winter breeding could be adaptive by allowing winter reproductive effort only by those individuals with minimal chances of survival until the next main breeding season (Gorman and Zucker, '97). If this is correct, one can ask why this species has evolved such an indirect system (via photoperiod history) for assigning different reproductive strategies based on age, rather than relying directly on age to determine the probability of winter breeding. Siberian hamsters exhibit a variety of photoperiod history effects. The species has been a model for examining the ability of the mother to transmit photoperiod cues to her offspring. In Siberian hamsters, this occurs during gestation, and the dam's rhythm of circulating melatonin appears to cue the fetus regarding the ambient day length (Weaver and Reppert, '86; Elliott and Goldman, '89), much as this endocrine rhythm serves as a day length 'code' in the adult animals (Bartness et al., '93). The photoperiod cues that hamsters receive during late fetal life can modify responses to intermediate day lengths ( $\approx 14L$ ) that are encountered shortly after birth (Stetson et al., '86; Shaw and Goldman, '95b). In adult Siberian hamsters, a 14L photoperiod can be either stimulatory or inhibitory to testicular function, depending on whether the previous day length was shorter or longer (Hoffmann et al., '86). For a species that makes extensive use of photoperiod history effects to refine its responses to the annual cycle of day length variation, it may have been a relatively easy step to evolve the use of photoperiod history to modify responsiveness to short days—even though the overall adaptive value of the pattern of response would appear to be related to age.

Until recently, all studies have suggested that short-day nonresponsiveness in Siberian hamsters is mediated by differences in the circadian system, specifically related to longer *taus* and modified phase response curves in the nonresponsive individuals. As a result of these circadian characteristics, nonresponsive hamsters exhibit a delay of several hours in phase angle of entrainment to short day photoperiods, and appear not to produce long duration melatonin peaks in short days (Puchalski and Lynch, '86; Margraf et al., '91; Freeman and Goldman, '97a; Prendergast and Freeman, '99). A recent study revealed that 43% of aged male Siberian hamsters failed to exhibit testicular regression or showed incomplete regression in short days. In this case, the nonresponsive hamsters did generate long duration melatonin peaks; their failure to undergo regression in short days was attributed to failure of responsiveness to melatonin (Horton and Yellon, 2001). The aged animals in this study were  $19 \pm 1.3$  months old, considerably older than the hamsters used in the earlier investigations of short-day nonresponsiveness. All the animals were raised under 16L, so it is not possible to determine whether photoperiod history had any role in the development of nonresponsiveness, or alternatively whether the effect was strictly linked to age. In any event, the combined findings of several studies now point to two mechanisms of short-day nonresponsiveness in Siberian hamsters: (a) a mechanism that involves specific characteristics of the circadian system that lead to a failure of extended melatonin peaks in short days and (b) a mechanism that may be seen only in aged hamsters that involves refractoriness to short day melatonin signals. It is not known whether a significant number of hamsters survive until 19 months of age in the field. If animals of this age constitute a sufficient proportion of the breeding population to provide a basis for selective forces to act, then it may be that a combination of photoperiod history and aging effects on short day responsiveness has been selected through evolution. This combination of effects would likely ensure that virtually all aged animals would attempt reproduction during the second winter of life, as they approach the maximum limit of life span.

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