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R1314-R1320.

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J. E. Larkin, J. Jones and I. Zucker

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M. R. Gorman

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Environmental induction of photononresponsiveness in the Siberian hamster, *Phodopus sungorus*

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Gorman, Michael R., and Irving Zucker. Environmental induction of photononresponsiveness in the Siberian hamster, *Phodopus sungorus*. *Am. J. Physiol.* 272 (*Regulatory Integrative Comp. Physiol.* 41): R887–R895, 1997.—In seasonally breeding rodent species, a fraction of the population is unresponsive to short day lengths (DL) and remains reproductively competent during winter. We previously observed that incidence of nonresponsiveness to short days was affected by photoperiodic history. Here we tested whether exposure to long DL (18 h light/day; 18L) renders animals unresponsive to short DL (10L). Hamsters, maintained from birth in 10L, were transferred at week 6 to 18L or 14L. Ten weeks later (week 16), groups were transferred to 10L for 10 wk. All hamsters maintained in short DL from birth had undeveloped testes at week 6. At week 26, however, 92% of hamsters previously kept in 18L failed to undergo complete gonadal regression in 10L, compared with only 10% of hamsters previously in 14L. Entrainment of locomotor activity in 10L in nonresponsive hamsters resembled that typically observed under long DL. Exposure to 18L may induce nonresponsiveness by altering interactions of component circadian oscillators that mediate gonadal regression in short DL.

testes; photoperiodism; circadian rhythm; nonresponders; melatonin

THE SIBERIAN HAMSTER (*Phodopus sungorus*, sometimes also known as the Djungarian hamster) is a cricetid rodent that inhabits the steppes and semi-arid deserts of Siberia, Mongolia, and central Asia and breeds in the field from April through September at 56° latitude (30). A similarly restricted breeding season can be reproduced in the laboratory by simulating the natural annual change in day length (DL) of 50° latitude (30). DL is represented physiologically as the duration of elevated pineal melatonin (Mel) secretion, a proximate mechanism that induces photoperiodic responses (9). Exposure to short DL or to long Mel signals that mimic winter DL induces gonadal regression, body weight loss, molt to a winter pelage, and thermoregulatory adaptations such as daily torpor (1, 16). Exposure to long DL or to short Mel signals reverses or prevents these changes (4).

Among many small, seasonally breeding rodents, a fraction of natural populations breeds during the winter (5). These individuals presumably correspond to laboratory animals that sustain reproductive activity despite exposure to short DL for several months (18, 21). Rodents (e.g., voles) born near the end of the normal breeding season (e.g., September) commonly delay somatic and reproductive maturation until the following spring, at which time reproduction commences (5, 20). Conspecifics born in spring typically

grow more rapidly and breed in the season of their birth; overwinter survival rates are low in these animals, and few survive to breed in the following spring (20). For late summer- or autumn-born animals likely to survive to breed in the following spring, the fitness benefits of winter breeding are likely outweighed by its intrinsic risks (3). In contrast, for spring-born animals the potential benefits of winter breeding may balance or outweigh the negligible reproductive costs associated with failure simply because these animals are unlikely to survive to breed in the following spring.

In several species (white-footed mice, Syrian hamsters, meadow voles, deer mice), the maintenance of reproductive competence in short DL reflects insensitivity of the neuroendocrine axis to long-duration Mel signals (2, 7, 15). Nonresponsiveness to Mel is trait specific, as gonadally nonresponsive voles nevertheless exhibit typical short-day pelage and behavioral traits (11, 27). Nonresponsiveness has a strong genetic component in several rodent species, including Siberian hamsters (6, 19). In the Siberian hamster, however, nonresponsiveness results from a failure to produce a long-duration Mel pulse in short DL, rather than insensitivity to long Mel signals. Nonresponsive Siberian hamsters transferred from long to short DL do not increase the duration of the nighttime Mel signal or locomotor activity rhythm (expansion of activity duration), nor do they exhibit any other short-day traits (22). The circadian systems of nonresponders differ from those of responders in having longer free-running periods, different phase response curves to light, and a decreased likelihood of splitting in constant light (23, 25). Expansion of Mel secretion and activity duration is thought to result from changing phase relations of two functionally distinct circadian oscillators (17). The evening (E) oscillator is proposed to drive both onset of locomotor activity and elevated nocturnal Mel secretion, whereas the morning (M) oscillator is believed to terminate both processes (8). Nonresponsiveness may result either from a lengthened free-running rhythm of the E oscillator (12) or from increased asymmetric coupling of the E and M oscillators (23), either of which prevents decomposition of E and M oscillators in short DL.

During an examination of photoperiodic responses of Siberian hamsters held under simulated natural photoperiods (SNP), we observed that almost one-half (16/35) of the hamsters born into a vernal equinox DL of a 60° latitudinal SNP (SNP60) (12L on March 22) failed to undergo gonadal regression when DL eventually decreased to 5L in the autumn. In contrast, virtually all

hamsters (30/31) in the 40° latitude SNP (SNP40) responded with gonadal regression to DL that decreased to 9L in the fall (13). Such wide variations in the incidence of gonadal regression as a function of photoperiodic history among animals of a common genetic stock raise the question as to whether nonresponsiveness observed in SNP60 is a manifestation of the same highly heritable circadian phenomenon reported by others (23). Alternatively, it may reflect an environmentally induced loss of responsiveness to long Mel signals (15). *Experiment 1* examined the circadian locomotor activity patterns of responsive and nonresponsive hamsters from SNP60 and demonstrated that nonresponders failed to manifest the typical short-day pattern of entrainment. *Experiment 2* demonstrated an increased incidence of nonresponsiveness to short DL in hamsters that previously were exposed to long DL. We show that nonresponsive hamsters in our colony are intrinsically photoresponsive but that exposure to very long DL prevents expansion of the phase relation of the E and M circadian oscillators believed to control the timing of nocturnal Mel secretion.

GENERAL METHODS

Siberian hamsters from our colony (derived from stock provided in 1985 by Bruce Goldman of the University of Connecticut, Storrs) were maintained from birth in 16 h light and 8 h dark/day (16L; lights on 0200 PST) in polypropylene cages (27 × 16 × 13 cm; 1–3 hamsters/cage) on pine shavings. Food (mouse chow no. 5015; Purina Mills, St. Louis, MO) and tap water were provided ad libitum. Female hamsters at least 10 wk old were paired and transferred to 12L (*experiment 1*; time of lights off was held constant for all static photoperiod conditions) or transferred and housed singly in 10L (*experiment 2B*) for 10–14 days, after which they were paired with colony males (from 16L) and monitored daily for litters. Male offspring, weaned at 18 days of age and subsequently housed with same-sex littermates (1–3 hamsters/cage), were used in experiments.

Measures

Testis measurement. At predetermined intervals, hamsters were lightly anesthetized with methoxyflurane vapors (Metofane; Pittman Moore, St. Louis, MO), and length and width of the left testis were measured externally (± 0.1 mm) with calipers. The product of testis width squared times length is linearly correlated with testis weight ($r = 0.97$, $df = 87$, $P < 0.001$; data from *experiment 2B*) and was used as a measure of estimated testis volume (ETV).

Locomotor activity. General locomotor activity was measured at intervals throughout the experiment. Passive infrared motion detectors were mounted on plastic hoods set on top of wire cage lids. Movement in the cage across 3 or more of 27 zones activated a closed-contact relay to Dataquest III software (Mini-Mitter, Sunriver, OR). From these data, activity duration was determined as follows: activity counts for 10-min intervals were averaged over 7–14 days to generate a 24-h histogram. Mean number of counts per 10 min was calculated for each animal. Activity onset and offset were defined as the first and last points, respectively, at which activity levels were 150% of the 10-min average and sustained at that level for at least three of the next six (or last six) 10-min intervals. Activity duration was obtained by subtracting time of activity onset from time of activity offset.

Photoresponsiveness. The criterion used to define responsiveness to short DL was derived in a separate study con-

ducted under similar conditions (13). A decrease of 48% in testis volume from any previous value defined a photoperiodic testis response. A decrease of 12% in body weight defined a photoperiodic body weight response. These values exceed the maximum decrease in testis volume and body weight among hamsters maintained in stimulatory DL (16L) attributable to repeated measurement, aging, illness, etc. and not to photoperiodic inhibition (see Ref. 13 for details). Nonresponders and responders identified by this criterion have been shown to exhibit typical long- and short-day locomotor activity patterns, respectively, thereby independently validating its use (12).

Experiment 1

Hamsters were exposed to simulated natural photoperiods for SNP60 from the day of birth, set to correspond to the vernal equinox (Fig. 1A). In SNP60, DL varies sinusoidally increasing to 19L on the summer solstice (*week 13*) before decreasing to 12L on the autumnal equinox (*week 26*) and 5L on the winter solstice (*week 39*). At the winter solstice, the photoperiod was clamped at 5L. Responsive ($n = 7$) and nonresponsive ($n = 8$) male hamsters remained in this photoperiod for an additional 13 wk, during the last two of which general locomotor activity was monitored. The testis and body weight patterns of these hamsters have been described previously (13).

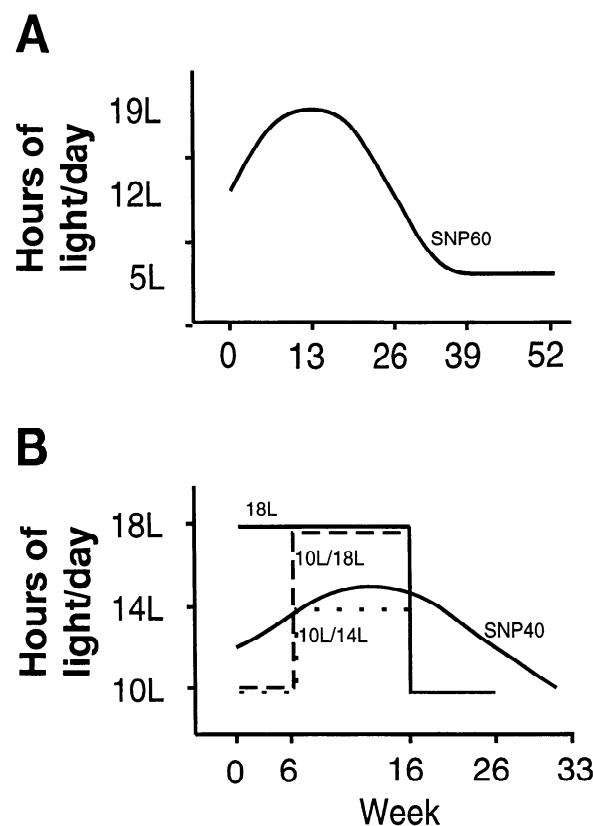


Fig. 1. Schematic representation of day lengths (DL) in *experiments 1* (A) and *2B* (B). A: hamsters were born into a 12-h light/day (12L) photoperiod, which increased gradually over 3 mo to a solstice value of 19L before decreasing until the winter solstice value of 5L was reached, at which it was clamped for the next 3 mo. B: hamsters were gestated in 10L and transferred at birth to 18L, 10L (2 groups), or 12L (SNP40). Hamsters in 18L remained in this DL for 16 wk; those in 10L were transferred at *week 6* to either 14L or 18L for 10 wk. These three groups were transferred at *week 16* to 10L for 10 wk. Hamsters placed in 12L at birth were maintained in a simulated natural photoperiod of 40°N latitude for 33 wk (SNP40).

Experiment 2A: Post Hoc Analysis

Because photoperiodic history affected the incidence of nonresponsiveness to short DL, we reexamined data from several other experiments in an attempt to correlate incidence of nonresponsiveness with some aspect of photoperiodic history. Specifically, we assessed whether the maximum DL hamsters experienced before they were challenged with short DL influenced the incidence of nonresponsiveness in three studies (12–14) (Table 1). Hamsters in each of these experiments had been treated as described in GENERAL METHODS, with similar criteria used for defining photoresponsiveness. Minor differences between experiments not described here can be found in the original reports. The results of this reanalysis led us to test formally the hypothesis that long DL induce nonresponsiveness by fixing the phase relations of the E and M oscillators in a long-day state.

Experiment 2B

On the day of birth (day 0), litters were assigned to one of four experimental groups. One group (group 18L; $n = 30$; Fig. 1B) was transferred from 10L to 18L and remained in 18L for 16 wk. Other hamsters remained in 10L until week 6, whereupon one group (group 10L/14L; $n = 31$; Fig. 1B) was transferred to 14L and the other (group 10L/18L; $n = 29$; Fig. 1B) to 18L, where both remained until week 16. At week 16, all three groups were moved to 10L for 10 wk to assess the incidence of gonadal regression. A fourth group (SNP40; $n = 15$; Fig. 1B) was transferred at birth to an SNP for 40°N latitude, with DL on the day of birth set to the vernal equinox (12L, March 22); DL increased gradually over 13 wk to reach a maximum of 15L on the summer solstice and then decreased until animals were killed at week 33 when the DL was 10L.

Body weights were measured weekly, and ETV was determined at weeks 6, 12, 16, and 26 for all groups. Hamsters in the three fixed photoperiods were killed at week 26, those in SNP40 at week 33, and paired testis weight (PTW) was determined. General locomotor activity was assessed in a subset of animals from each group (except SNP40) between

Table 1. Photoperiodic conditions in the weeks preceding exposure to short days for groups described in experiment 2A: post hoc analysis

Group	Natal DL	Max DL	SD	Week in SD	<i>n</i>	%NR	Ref.
SNP60	12L	19L	12L	26	35	46	13
10L	16L	16L	10L	40	14	29	14
10L/8L	16L	16L	10L, 8L	12, 28	17	29	14
14L/10L-1	16L	16L	10L	28–32	14	50	14
14L/10L-2	16L	16L	10L	16–20	15	27	14
SNP	16L	16L	12L	8	16	31	12
SNP-E	16L	16L	12L	8	20	50	12
SNP-M	16L	16L	12L	8	22	41	12
SQ-E	16L	16L	8L	16	21	38	12
SQ-M	16L	16L	8L	16	21	52	12
SNP40	12L	15L	12L	26	31	3	13
SNP40-2	10L	13L	12L	32	35	3	13
12L	12L	12L	12L	30	23	0	13
10L	10L	10L	10L	30	24	0	13

Natal day length (DL) and maximum (max) DL are the DL on the day of birth and the longest DL prior to short-day (SD) treatment, respectively. Sample size (*n*) and percentage of nonresponsive hamsters (%NR) are shown. Transfers to shorter DLs were achieved using simulated natural photoperiods (SNP) or abrupt square-wave (SQ) transitions. SNP60, SNP40, and SNP, 60, 40, and 55° latitude, respectively. In some instances, only the time of the evening (E) or morning (M) light/dark transition was altered. In another case, SNP40-2, the light phase was altered by 2 h daily. L, hours of light/day.

weeks 4 and 6 and weeks 12 and 16, and in all animals except those in SNP40 between weeks 24 and 26.

Body weights and ETV were analyzed separately by repeated-measures analysis of variance (Statview 4.01; Abacus Systems, Berkeley, CA) and by *t*-tests where appropriate.

RESULTS

Experiment 1

Activity duration was significantly longer in responsive (14.6 ± 0.6 h; mean \pm SE) than in nonresponsive hamsters (7.0 ± 0.7 h) from SNP60 ($P < 0.001$). Activity onset in responders was nearly coincident with lights off (Fig. 2A) and delayed by 11 h in nonresponders (Fig. 2B), as indicated in the representative actograms.

Experiment 2A

Reanalysis of earlier studies. Incidence of nonresponsiveness was high among hamsters that had been exposed to DL ≥ 16 L before exposure to short DL. Among these groups, nonresponsiveness varied from 27 to 52% (Table 1). In contrast, nonresponsiveness was nearly absent (0–3%) among hamsters whose longest prior DL was ≤ 15 L. In two groups (12L and 10L), only initial nonresponsiveness from birth was assessed, as opposed to nonresponsiveness to short DL after exposure to stimulatory DL.

Experiment 2B

Incidence of nonresponsiveness to short days from birth. In the current study, gonads were completely regressed at week 6 in all hamsters exposed to 10L from birth. ETV values in 10L ranged from 97 to 142 (Fig. 3A), which corresponds to a PTW < 75 mg (ETV-PTW correlation presented below). In contrast, the gonads were stimulated in the majority of hamsters maintained in 18L or exposed to increasing photoperiods in SNP40. In the former group, only one hamster had an ETV within the range observed in 10L, and most hamsters had ETV corresponding to PTW > 300 mg (Fig. 3A). Hamsters in SNP40 had more modest testicular growth (Fig. 3A). ETV were lower in 10L than in either of the other groups ($P < 0.001$) and were greater in 18L than in SNP40 ($P < 0.001$).

Activity duration at week 6 was longer among hamsters in 10L than in 18L ($P < 0.001$; Fig. 3B), with no overlapping values between groups. One outlying data point among the 18L hamsters (long activity duration) probably reflected an artifact of the algorithm used to determine activity onset and offset; visual inspection of the record suggested a shorter activity duration.

Body weights between weeks 3 and 6 differed between treatment groups ($F = 48.4$; $df = 3$; $P < 0.001$) and over time ($F = 1,872$; $df = 3$; $P < 0.001$), with a significant interaction of these factors ($F = 70.9$; $df = 9$; $P < 0.001$). Hamsters gained weight more rapidly in 18L and SNP40 than in 10L (data not shown).

Stimulation by longer DL. Transfer from 10L to longer DL stimulated gonadal growth. ETV differed between groups ($F = 50.9$; $df = 3$; $P < 0.001$) and increased over time ($F = 327$; $df = 2$; $P < 0.001$; Fig. 4A). Testis volume increased more rapidly in hamsters

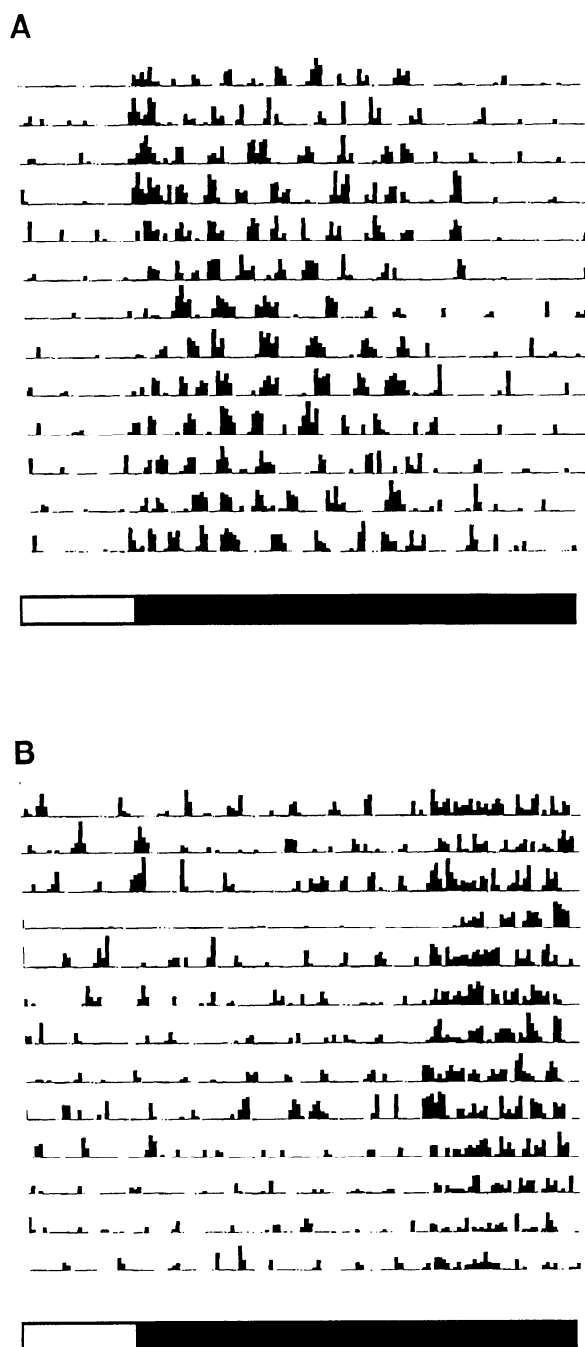


Fig. 2. Representative activity rhythms from weeks 50-52 of photoreponsive (A) and nonresponsive (B) hamsters exposed to SNP60 from birth until week 39 and to 5L during weeks 39-52. Black bar indicates darkness. Values below mean activity level were filtered to enhance the clarity of the actogram.

previously in 10L compared with those that were in 18L throughout ($F = 49.6$; $df = 6$; $P < 0.001$; Fig. 4A). After 10 wk in 14L (week 16), ETV was still smaller than in animals in either 18L group ($P < 0.05$) or in SNP40 ($P < 0.01$). Almost all hamsters in each group, however, had fully mature testes (Fig. 4C), and the magnitude of the difference between group means was not great (9.7% lower in 14L than 18L).

Similarly, body weights differed among groups ($F = 15.3$; $df = 3$; $P < 0.001$) and increased over time ($F = 1,028$; $df = 10$; $P < 0.001$; Fig. 4B), increasing more

rapidly in the groups previously housed in 10L ($F = 50.5$; $df = 30$; $P < 0.001$; Fig. 4B). By week 16, body weights were comparable among groups, except that hamsters in group 18L weighed significantly less than those in SNP40 ($P < 0.05$) and 10L/18L ($P < 0.001$; Fig. 4B).

Activity durations were longer in hamsters in group 10L/14L than in groups 10L/18L or 18L ($P < 0.001$; Fig. 4D); the latter groups did not differ from each other ($P > 0.20$; Fig. 4D).

Short-day challenge in fixed DL groups. After 10 wk of short days (10L), PTW of hamsters from group 10L/14L was lower than those of hamsters from groups 10L/18L or 18L ($P < 0.001$; Fig. 5A); the latter two groups did not differ on this measure ($P > 0.35$). Testes of hamsters in 14L were nearly uniformly regressed (28 of 31 < 180 mg), whereas only one hamster in group 10L/18L and two in group 18L had PTW < 200 mg. When the criterion used to differentiate responders from nonresponders was applied to ETV values, only 2 of 29 hamsters from 10L/18L and 3 of 30 from 18L were classified as responders in contrast with 29 of 31 hamsters from 10L/14L ($P < 0.001$; Table 2).

Body weights likewise differed among groups ($F = 22.2$; $df = 2$; $P < 0.001$; Fig. 5B) and decreased over time ($F = 22.7$; $df = 10$; $P < 0.001$; Fig. 5B). The interaction of group and time was significant ($F = 33.3$; $df = 20$; $P < 0.001$), with body weights decreasing in group 10L/14L but not in groups 10L/18L and 18L (Fig. 5B). Significantly more hamsters in 10L/14L met the criterion for photoperiodic body weight loss than in groups 10L/18L or 18L ($P < 0.001$; Table 2).

Activity duration was longer in hamsters from group 10L/14L ($P < 0.001$; Fig. 5C) than in those from groups 10L/18L or 18L. The latter two groups did not differ on this measure ($P > 0.65$). Activity duration was negatively correlated with PTW ($r = 0.81$; $df = 84$; $P < 0.001$; Fig. 5D), although a few of the animals in 18L had PTW larger than would have been predicted on the basis of activity duration. One hamster from group 10L/14L had regressed gonads and a relatively short activity duration. Despite the exposure to 10L for 10 wk, many hamsters from groups 10L/18L and 18L exhibited stable patterns of entrainment that corresponded to patterns expected from hamsters housed in very long day DL (Fig. 6, A and B). Finally, four hamsters from 18L exhibited arrhythmic activity patterns that could not be analyzed for activity duration with criteria used herein. No other group contained arrhythmic animals.

PTW and ETV were correlated as in previous studies ($r = 0.97$; $df = 87$; $P < 0.001$; $PTW = -0.12 + 0.00139 \times ETV$).

SNP40. Most hamsters in SNP40 (12 of 14; Table 2) underwent complete gonadal regression by week 33 (PTW < 60 mg), whereas two animals were clearly nonresponsive to decreasing DL (PTW > 600 mg). Mean body weight, moreover, decreased from a maximum of 45.5 ± 0.7 g at week 16 to 37.1 ± 2.2 g at week 33 (not shown). The incidence of testicular nonresponsiveness in SNP40 differed from that observed in groups 10L/18L and 18L but not from that in group

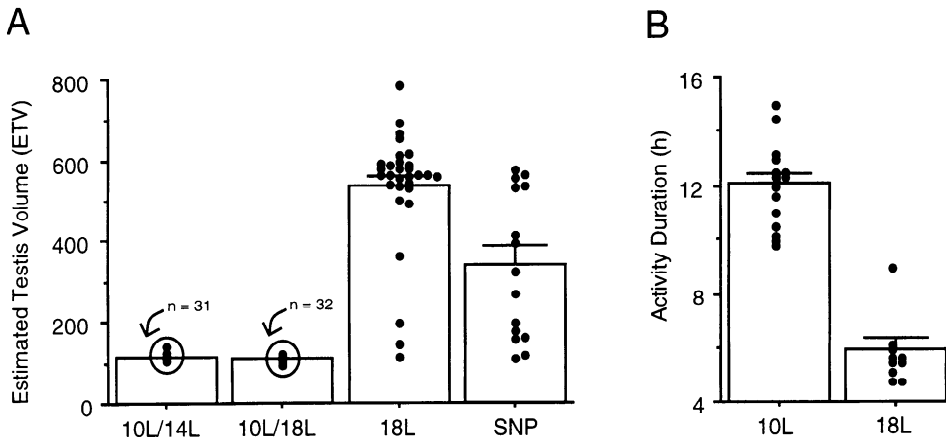


Fig. 3. A: mean \pm SE estimated testis volume (ETV) at 6 wk of age of hamsters maintained from birth in 10L (groups 10L/14L and 10L/18L), 18L ($n = 29$), or SNP40 ($n = 15$). B: mean \pm SE activity duration in a subset of hamsters in 10L ($n = 15$) and 18L ($n = 10$). Dots are individual data points.

10L/14L (Table 2). Similar results were obtained when body weight responsiveness was considered (Table 2).

DISCUSSION

Most hamsters exposed from birth to DL ≥ 16 L did not undergo gonadal regression and weight loss when subsequently maintained for 10 wk in short DL. Nonresponsiveness in short DL was accompanied by a shortened locomotor activity duration relative to that of responsive hamsters and more similar to that of hamsters held in long DL (22). All hamsters are capable of typical short-day responses at birth; this capacity was retained in adulthood when the maximum DL experienced during development was 14L or reached 15L as part of a simulated natural photoperiod. DL in excess of 15L compromised the ability of the circadian system to respond in the normal fashion to short DL. Within a given genetic pool, photoperiodic history can determine

whether a majority or only a small minority of hamsters will manifest typical short-day photoperiodic responses of gonadal involution and body weight loss.

Separate E and M oscillators are considered to initiate and terminate, respectively, locomotor activity and pineal Mel secretion (8, 17). In photoresponsive hamsters, the phase relations of the E and M oscillators, reflected in either the locomotor activity or Mel secretory pattern, are a function of DL: behavioral activity and Mel secretion are compressed or expanded in long and short days, respectively (8). Among nonresponsive Siberian hamsters, expansion (decompression) fails to occur either because of altered coupling between oscillators (23, 25) or changes in the free-running rhythms of the E and M oscillators (12). Under T-cycles or after entraining injections of Mel, formerly nonresponsive hamsters exhibited typical short-day responses and remained responsive after cessation of

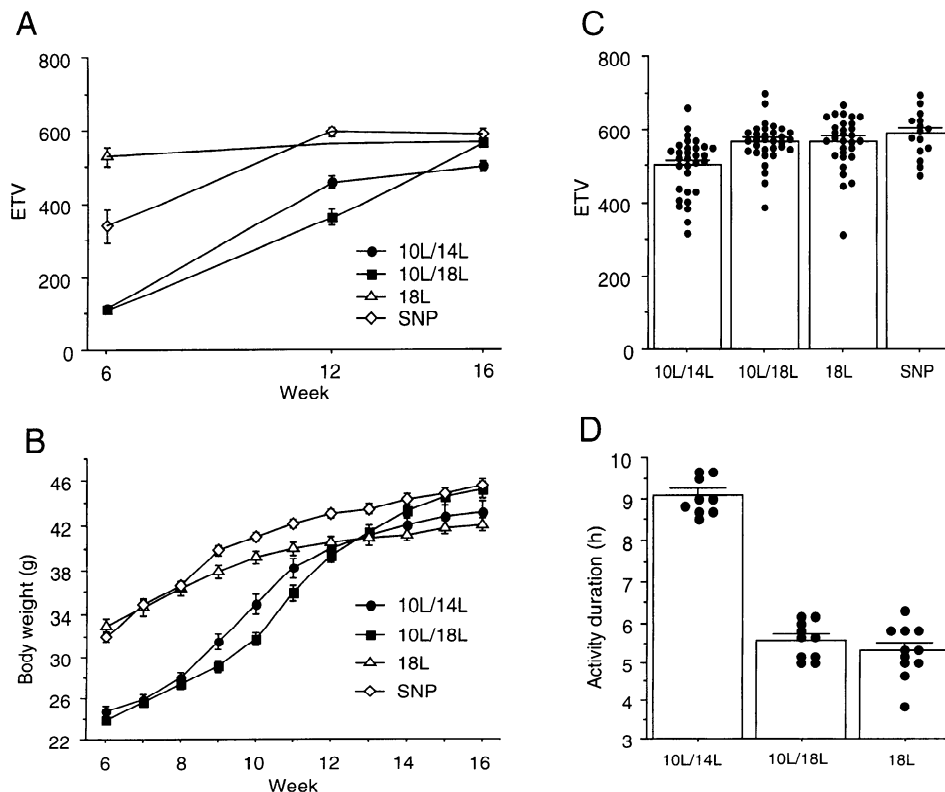
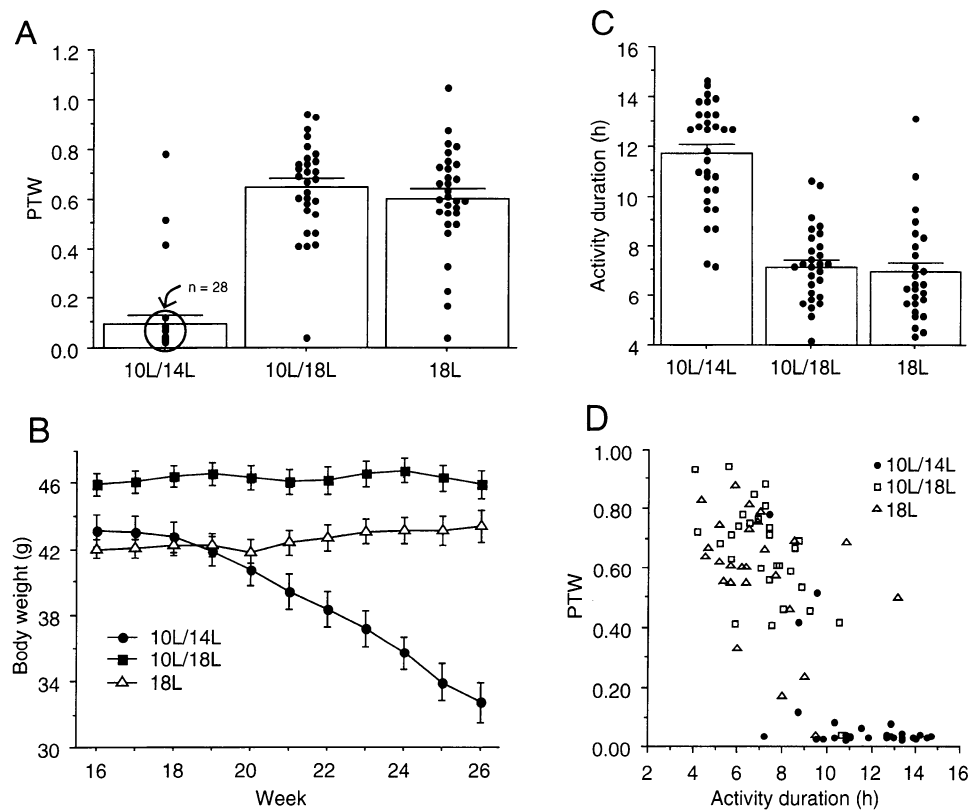


Fig. 4. Mean \pm SE ETV (A) and body weight (B) of hamsters maintained in photoperiods of experiment 2B. C: mean \pm SE and individual ETV values at week 16. D: mean \pm SE and individual activity durations of a subset of hamsters from each fixed photoperiod group monitored during weeks 14-16.

Fig. 5. A: mean + SE and individual paired testis weights (PTW) of hamsters in the experimental groups at week 26 after 10 wk of exposure to 10L. B: mean ± SE body weight of hamsters during exposure to 10L. C: mean + SE and individual activity durations during weeks 24–26. D: regression analysis of activity duration and PTW at week 26.



treatment; this suggests that the decompressed state is stable but that oscillator coupling prevents it from occurring under normal light-dark conditions (24, 26). We observed in a separate study, however, that nonresponsive hamsters showed a transient lengthening of activity duration after transfer from long to short DL with an extension of darkness into the morning but not evening hours (12). These results support the hypothesis that the E oscillator of nonresponders has an unusually long period >24 h. The present results suggest that very long DL lengthen the period of the E oscillator or increase coupling between E and M oscillators. Selection experiments that demonstrated considerable heritability of nonresponsiveness in Siberian hamsters may have increased its incidence by decreasing the minimum DL at which long DL exert either one of these effects (19). Although differences in experimental procedure preclude comparison, the much higher incidence of nonresponsiveness after treatment with

static 18L than static 16L photoperiods (92 vs. 39%; Table 1) is consistent with this idea.

The present results corroborate the recent report of uniform juvenile short-day responsiveness among offspring of selected photoresponsive and nonresponsive lineages (28) but fail to support the conclusion of these authors that increased incidence of nonresponsiveness among adults is age dependent. Our results from animals in groups 10L/14L and SNP40 suggest that adult nonresponsiveness does not increase in older animals maintained in shorter DL, but rather that exposure to standard housing conditions (16L in most laboratories) may increase nonresponsiveness.

We did not determine the minimum duration of long DL exposure sufficient to render a large proportion of hamsters nonresponsive to short DL. Exposure to 18L for 10 and 16 wk yielded similar results. Moreover, the age at first exposure did not appear to be critical; rates of nonresponsiveness were similar whether animals experienced 18L from birth or from 6 wk of age. Correlational data in Table 1 suggest an abrupt discontinuity in the effects of DL between 15L and 16L. However, 16L DL were static and in effect for several months, whereas 15L DL were part of an SNP that was only at the maximal DL for a few weeks. Whether static long-term exposure to 15L would render hamsters unresponsive to short DL is unclear; prolonged exposure to 14L, however, is consistent with nearly uniform photoresponsiveness to short DL (experiment 2B). The incidence of nonresponsiveness under static 18L was markedly higher than previously seen under SNP60 (Table 1) in which DL were ≥18L for ~8 wk. It is

Table 2. Number of hamsters manifesting photoperiodic testis or body weight responses

	10L/14L	10L/18L	18L	SNP40
Photoperiodic testis response*				
Responders	29	2	3	12
Nonresponders	2	27	27	2
Photoperiodic body weight response†				
Responders	29	3	3	12
Nonresponders	2	26	27	2

* $\chi^2 = 71.0$, $df = 3$, $P < 0.001$; † $\chi^2 = 67.8$, $df = 3$, $P < 0.001$.

unclear whether this difference in incidence reflects between-experiment variance or qualitative differences between abrupt and gradual changes in DL.

Can it be that photoresponsiveness is delayed after exposure to 18L and that the incidence of nonresponsiveness would be much lower if monitoring were extended

beyond 10 wk; i.e., did we underestimate the number of responsive hamsters in *groups 10L/18L* and *18L*? We believe not. In previous studies in which darkness was extended by 8 h into morning to generate an 8L DL (from 16L, not 18L as in the present case), the gonads underwent maximal regression within 8 wk and decompressed maximally within 6 wk (12). Furthermore, in *experiment 1*, in which DL decreased gradually from 19L, the majority of photoresponsive hamsters (12 of 19, 63%) could be correctly identified as such by applying the criteria for photoresponsiveness as early as 11 wk after initial exposure to 18L, the longest DL used in *experiment 2B* (post hoc analysis). The abrupt changes in DL employed in *experiment 2B* should have produced more rapid entrainment and gonadal regression than the gradual transitions used in *experiment 1* (12). Nonetheless, even if we underestimated the number of responders by 37%, as would have occurred if the response criteria were applied prematurely in *experiment 1*, we would still have found markedly increased incidences of nonresponsiveness in *groups 18L* and *10L/18L*.

Slight differences in gonadal size at the start of the short-day challenge could have contributed to the more complete regression observed in *group 10L/14L* relative to other groups. Differences in ETV between this group and others, however, were not large, and no differences in ETV at *week 16* existed between responders and nonresponders from *groups 18L* and *10L/18L* ($P > 0.9$) as would be expected if smaller gonads facilitated responsiveness to short DL. Furthermore, incidence of nonresponsiveness was defined in terms of percent decrease in, rather than absolute, testis volume. The different types of long-day stimulation between *weeks 6* and *16* also led to differences in body weight at *week 16*. The higher body weights among *groups 10L/18L* and *SNP40* compared with *group 18L* are consistent with past studies that demonstrated more rapid somatic growth in shorter but increasing DL than after unchanging long DL (10).

In several small rodent species, the adaptiveness of short-day nonresponsiveness may derive from the following considerations: animals that are unlikely to survive to breed again in spring attempt winter breeding even as they retain other seasonally appropriate photoperiodic traits (e.g., molt to winter pelage) (5, 21, 27). Successful winter breeding greatly enhances their reproductive fitness, whereas failed breeding may not reduce much further their already extremely low probability of surviving to breed again in spring (3). The advantage of nonresponsiveness in Siberian hamsters is less apparent: because nonresponsiveness reflects a failure to produce a typical short-day Mel profile and is global rather than trait specific, Siberian hamsters do not exhibit the pineal-dependent decreases in body weight; pelage thickness and coloration and locomotor activity patterns, moreover, resemble those of long-day animals in terms of activity duration (22, 23). If locomotor activity in the laboratory reflects behavior in the field, it is difficult to comprehend how retention of an above-ground activity pattern typical of long days

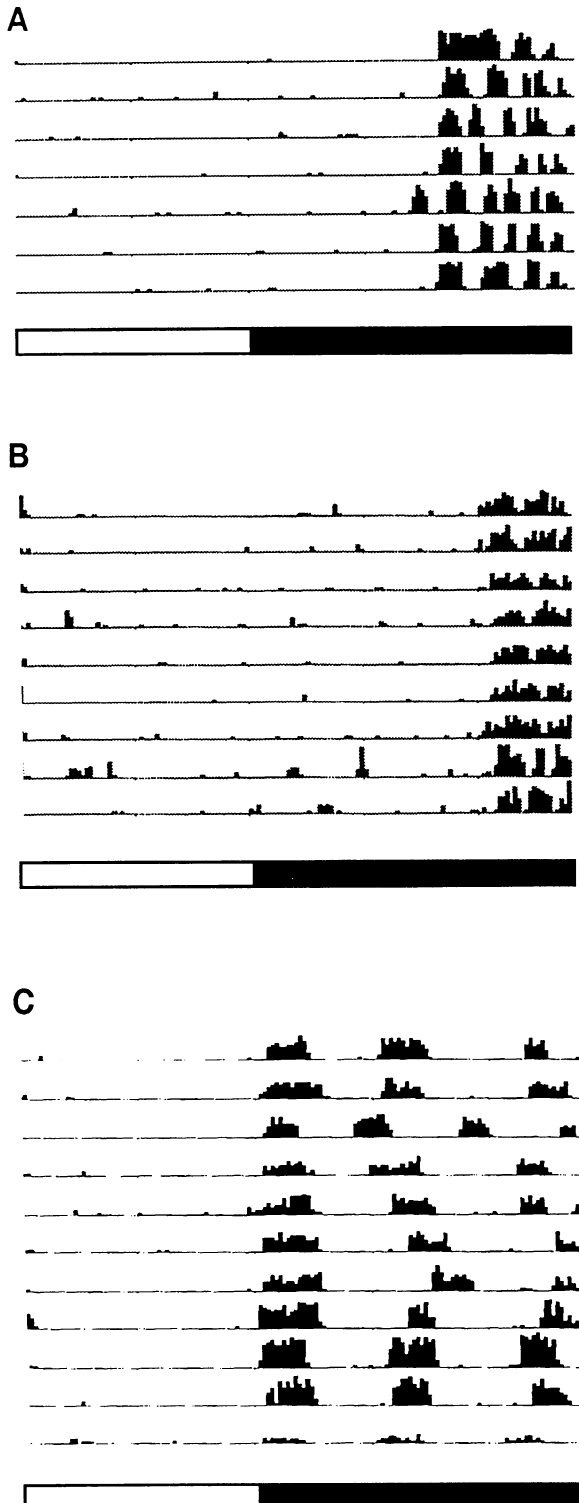


Fig. 6. Representative activity rhythms from *weeks 24-26* of nonresponsive (*A* and *B*) and responsive (*C*) hamsters beginning after 8–9 wk in 10L. Hamsters are from *groups 18L*, *10L/18L*, and *10L/14L* in *A*, *B*, and *C*, respectively. Black bar indicates time of darkness.

would be beneficial in the short DL of winter. It remains to be validated whether locomotor activity patterns in the laboratory predict behavior in the field. Moreover, factors such as low ambient temperature, prevalent in the field during winter (30) may promote decreases in prolactin secretion (29) and changes in pelage characteristics (16) through pineal-independent mechanisms and mitigate nonresponsiveness to DL.

Any mechanism that favors winter breeding ought to operate preferentially on animals unlikely to survive to breed in the following spring; only such animals have low expected future reproductive fitness to risk by attempting winter breeding. A genetic mechanism that rendered hamsters nonresponsive at birth would compromise the reproductive success of animals born near the end of the breeding season, which by all accounts benefit from deferring breeding until spring. In voles, Mel insensitivity is age dependent (7). Reliance on long DL by Siberian hamsters to induce nonresponsiveness achieves the same result: animals born before May 7 at 56°N latitude, where this stock originated, will have been exposed to long DL \geq 16L for 13 wk. In contrast, hamsters born after the solstice (e.g., on August 3) will be exposed to DL decreasing from 15L beginning when hamsters are first postnatally sensitive to DL. The parameters of long DL exposure required for inducing nonresponsiveness must be established before it will be possible to model more fully the seasonal pattern of nonresponsiveness in this species.

We are grateful to Christiana Tuthill for excellent technical assistance and Brian Prendergast for comments on the manuscript.

This research was supported by National Institute of Child Health and Human Development Grant HD-02982 and the Michigan Society of Fellows.

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Received 27 June 1996; accepted in final form 26 August 1996.

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