

Temperature dependence of gonadal regression in Syrian hamsters exposed to short day lengths

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Larkin, Jennie E., Jennifer Jones, and Irving Zucker. Temperature dependence of gonadal regression in Syrian hamsters exposed to short day lengths. *Am J Physiol Regulatory Integrative Comp Physiol* 282: R744–R752, 2002; 10.1152/ajpregu.000299.2001.—We sought to determine whether ambient temperature (T_a) affects gonadal function by altering the rate at which circadian rhythms entrain to short day lengths. Syrian hamsters were housed in cages where they received 14 h of light per day (“long days,” 14L) at 22°C. Hamsters were then transferred to cages to receive 10 h of light per day (“short days,” 10L) and kept at 5, 22, or 28°C or were maintained in 14L at 22°C. Body mass and estimated testis volume as well as duration of nocturnal locomotor activity (α), previously established as a reliable indicator of the duration of nocturnal melatonin secretion, were determined over the course of 24 wk. Testicular regression in short days was accelerated by 4 wk at 5°C and delayed by 3 wk at 28°C relative to 22°C. The interval between α -expansion and initiation of testicular regression was markedly affected by T_a with delays of 0, 3, and 6 wk at 5, 22, and 28°C, respectively. All hamsters held at 5 and 22°C underwent testicular regression, but 25% of those maintained at 28°C failed to do so. We suggest that T_a modulates testicular regression primarily by affecting responsiveness of neuroendocrine target tissues to long melatonin signals.

melatonin; hibernation; body mass; refractoriness; photoperiodism; food hoarding

SYRIAN HAMSTERS SUSTAIN REPRODUCTION when day length exceeds 12.5 h/day and become reproductively quiescent in day lengths below this value (10). In short days, hamsters enter hibernation if kept at low ambient temperature (T_a) (23, 44). Day-length information is represented endogenously as the duration of the nocturnal melatonin signal produced by the pineal gland; long (>8 h) nightly melatonin signals trigger short-day responses (2). The long melatonin signal can be mimicked by daily melatonin injections given 1–3 h before the onset of darkness to hamsters kept in long days or by extended daily subcutaneous melatonin infusions delivered to pinealectomized animals; both treatments induce gonadal regression (2, 41). Hamsters maintained in short days do not sustain gonadal regression

indefinitely; instead, testes undergo recrudescence after ~15 wk of exposure to short days (34).

Although day length appears to be the primary environmental cue that Syrian hamsters use to initiate seasonally appropriate physiological and behavioral changes, T_a markedly affects the photoperiodic response (8, 22, 23, 26, 31, 33): low T_a (5°C) accelerates and high T_a (30–32°C) delays the onset of gonadal quiescence. A similar modulatory role of T_a on photoperiodic responses has been documented in other photoperiodic rodents (7, 25, 37–39). In Siberian hamsters, T_a affects the photoperiodic response by altering neuroendocrine responsiveness to long melatonin signals (25). A similar mechanism has been proposed but not demonstrated in Syrian hamsters (31, 33). T_a may also alter neuroendocrine responses by influencing generation of the melatonin signals (4, 39, 40, 45). Siberian hamsters transferred from long to short days entrain to the short photoperiod almost a week sooner when housed at 5°C rather than 22°C, and this is correlated with more rapid initiation of short-day responses (25). Cold may also affect reproduction independently of photoperiodic regulation via its effects on energy balance (5, 9, 23). Syrian hamsters do not always immediately increase food consumption when transferred into short days and cold (5°C), thus failing to fully compensate for increased energy demand (36). The resulting acute body mass loss may facilitate gonadal regression. In the absence of changes in day length, however, well-fed hamsters sustain the summer phenotype when challenged with low T_a values. Thus Syrian and Siberian hamsters kept in long days at 5°C do not undergo testicular regression or other behavioral and physiological responses that are typical of the winter phenotype (8, 30, 43, 42), although some investigators of male Syrian hamsters report partial gonadal involution under these conditions (22, 27).

The two goals of this study were to determine whether T_a modulates short-day photoperiodic responses in Syrian hamsters through changes in melatonin secretion and whether T_a exerts similar effects on both testicular regression and subsequent recrudescence. Because the duration of the nocturnal melatonin

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signal is highly correlated with the duration of nocturnal locomotor activity (α) in male Syrian hamsters housed at a T_a of 22°C (11), we presumed that the rate of α -expansion during entrainment to short days at both lower (5°C) and higher (28°C) T_a values remains a reliable indicator of the duration of melatonin secretion. Use of locomotor activity permits continuous albeit indirect assessment of melatonin signal duration in individual animals over the course of many weeks and is of value because direct repeated measurement of the hormone on a daily or hourly basis over long time spans is not feasible in a mammal of this size. Our conclusions regarding melatonin patterns must, however, remain tentative pending verification at low and high T_a values of the correspondence between melatonin secretory activity and locomotor activity.

MATERIALS AND METHODS

Seven-week-old male Syrian hamsters (Hsd:Han:AURA) obtained from Harlan Sprague Dawley (Madison, WI) were housed in groups of 3 or 4 individuals in polypropylene cages at $22 \pm 1^\circ\text{C}$ in a 14L photoperiod (14 h of light/day: lights on 0230–1630, Pacific standard time) for 3 wk after arrival at Berkeley, CA. Food (Simonsen rat chow) and tap water were available ad libitum. At 10 wk of age (*week 0*), body mass and estimated testes volume (ETV) were measured (19), and animals were randomly assigned to one of four experimental groups; thereafter, animals were housed individually. A long-day (LD) control group ($n = 13$ hamsters) remained in 14L at 22°C for 24 wk. The remaining three groups were transferred to the short-day (SD) 10L photoperiod (10 h of light/day: lights on at 0630) and kept at ambient temperatures of 5°C ($n = 13$), 22°C ($n = 13$), or 28°C ($n = 12$). Temperature control in the 28°C room failed for 3 days on *week 7*, and during this time T_a fell to 22°C.

Somatic, gonadal, and activity measurements. Body mass and ETV were measured weekly starting 2 wk before the temperature and photoperiod change (*week -2*), and presence or absence of food caches in the nest were noted. To measure ETV, each animal was anesthetized with isoflurane vapors (Fort Dodge Animal Health, Fort Dodge, IA), and the length and width of the left testis was measured externally. The product of testis width squared times length provides an ETV that is highly correlated with testis mass (19, 24, 46). From *week 0* until the end of the study, locomotor activity was monitored with passive infrared motion detectors 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 (Data Sciences, St. Paul, MN). From these data, nightly activity duration for each animal was determined using the Tau software package (Mini Mitter, Sunriver, OR). Activity counts for 10-min intervals were averaged over 1 wk to generate a 24-h histogram. Daily activity onset was defined as the time that activity levels first rose above the daily mean and remained above this value for ≥ 1 h. Activity offset was defined as the time that activity fell below the daily mean and stayed below this value for ≥ 1 h. Duration of the active phase (α) was calculated as the interval between activity onset and offset (17, 25). Weekly α -values are reported for the first 6 wk of the study to enable more detailed analyses during the entrainment period and biweekly for the remainder of the study. During *weeks 9–17*, hamsters kept at 5°C were monitored daily for hibernation using the noninvasive “sawdust technique” (29).

Hamsters were classified as photoresponsive (R) or non-photoresponsive (NR) on the basis of testis volume during *weeks 2–16*. The criterion for defining testicular regression and therefore photoresponsiveness was an ETV $< 48\%$ of the initial ETV value (*week 0*) maintained for at least two consecutive weeks. All R hamsters met and exceeded this standard for testicular regression; differences in the magnitude of testicular regression in R hamsters were quantified by calculating the minimum ETV and the timing of gonadal regression and recrudescence. Minimum ETV was the mean of the three lowest ETV values. Onset of gonadal recrudescence was defined as the date on which ETV increased by >300 mm³ above minimum ETV and was sustained at this value for two consecutive weeks. Testes were considered to have undergone recrudescence when ETV had recovered to $\geq 48\%$ of initial ETV. Latencies to gonadal regression and recrudescence were calculated as the intervals between α -expansion to >13 h and the ETV decline below and rise above 48% of the initial ETV, respectively.

Statistics. Differences in testis volume, body mass, and α -value as a function of treatment group were assessed with one-factor repeated-measures ANOVA (StatView 5.0, SAS Institute, Cary, NC). Where a significant effect or interaction was obtained in the overall ANOVA, Fisher’s protected least-significant difference test was used for pairwise post hoc comparisons. The χ^2 -test was used to compare the incidence of nonresponsiveness in hamsters housed in different T_a values. Observed differences were considered significant if $P < 0.05$. Data are presented as means \pm SE.

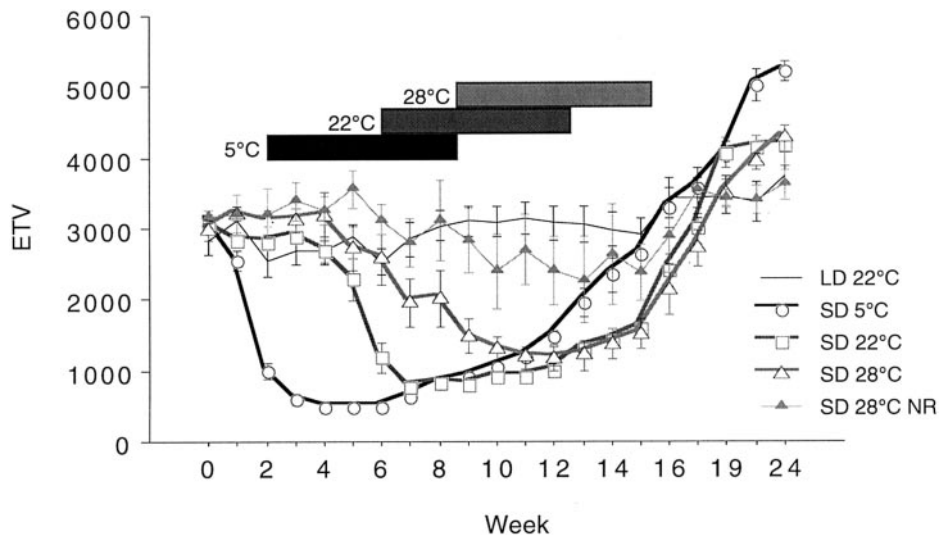
RESULTS

Neither body mass nor testis volume differed among the groups before transfer to SDs ($P > 0.38$ and $P > 0.50$, respectively). On *week 0*, ETV was $3,007 \pm 62$ mm³, and body mass was 95.9 ± 1.1 g.

Testis volume. Temperature had a significant impact on gonadal regression in SDs. All hamsters held in SDs at 5 and 22°C but only 75% of those at 28°C underwent gonadal regression (χ^2 , $P < 0.05$). Moreover, testis regression proceeded more slowly and was less complete at 28°C than at 22 or 5°C (Fig. 1). During the first 2 wk after initiation of testicular regression, testis volume decreased by $1,688 \pm 144$ mm³ at 5 and 22°C but decreased by only half that amount (708 ± 269 mm³) at 28°C ($P < 0.005$). Minimum testis volume achieved was inversely correlated with T_a (Fig. 1); it was 14% of initial testis volume at 5°C (424 ± 38 mm³), 24% at 22°C (733 ± 42 mm³), and 31% at 28°C (923 ± 60 mm³; $P < 0.001$, for comparisons among all T_a values). Minimum testis volume of NR hamsters at 28°C did not differ significantly from that of animals maintained in LDs ($2,167 \pm 424$ mm³ and $2,363 \pm 157$ mm³, respectively; $P > 0.60$) and never reached the criterion for gonadal regression.

Timing of gonadal regression and initiation of recrudescence were also temperature dependent, as both occurred earlier at lower temperatures. Regression was initiated on *week 1.9* \pm 0.1 at 5°C, *week 6.0* \pm 0.3 at 22°C, and *week 8.7* \pm 0.9 at 28°C ($P < 0.01$, significantly different at each T_a ; Fig. 1). At each T_a , gonadal involution was maintained for 6.3 ± 0.2 wk. Significant increases in gonadal size above minimal values, which signify the onset of testicular recrudescence, were re-

Fig. 1. Estimated testis volume (ETV, in mm³) of hamsters kept in long-day (LD) photoperiod (14 h of light/day) at ambient temperature (T_a) of 22°C or in short-day (SD) photoperiod (10 h of light/day) at 5, 22, or 28°C for 24 wk. Data of photoreponsive animals at 28°C that underwent testicular regression are plotted separately from those of nonphotoreponsive (NR) hamsters that maintained large testes throughout the experiment. Horizontal bars indicate the interval from onset of testicular regression to onset of testicular recrudescence at each T_a.

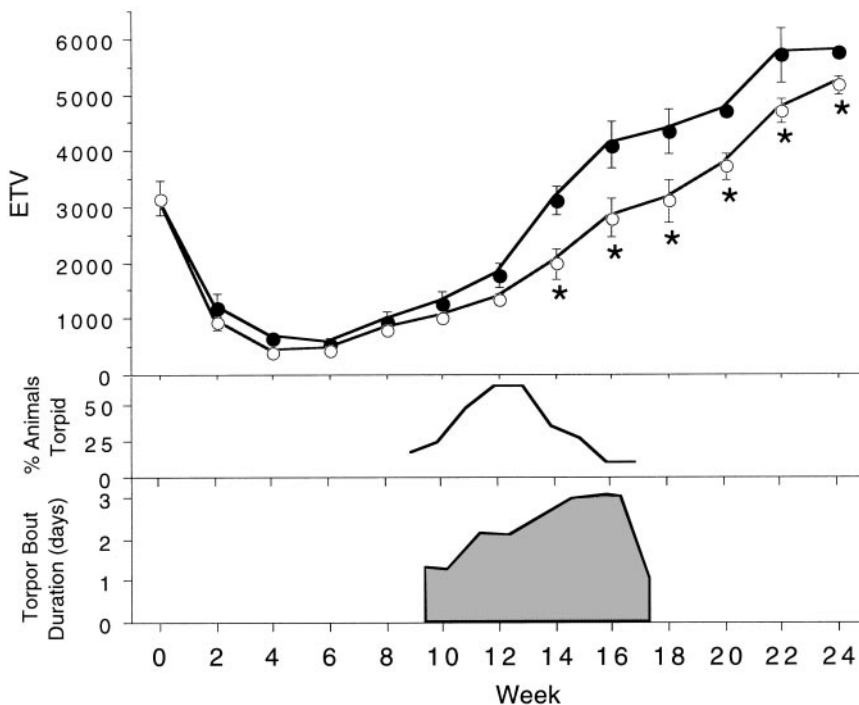


corded on *week* 8.1 ± 0.1 at 5°C, *week* 12.6 ± 0.3 at 22°C, and *week* 14.8 ± 0.7 at 28°C ($P < 0.05$, significantly different at each T_a). Because the rate of testicular recrudescence was substantially slower at 5°C than at the higher T_a values, the groups differed less with respect to when gonadal recrudescence was completed; this status was achieved 2 wk earlier in animals kept at 5°C than in those at 22 or 28°C (*weeks* 13.1 ± 0.4 vs. 15.1 ± 0.4 and 15.6 ± 0.6 , respectively; $P < 0.01$ for each comparison). During *weeks* 21–24, ETV values of hamsters at 5°C were higher than those of animals in the other groups ($5,210 \pm 146$ mm³ vs. $4,005 \pm 155$ mm³; $P < 0.01$).

Hibernation was recorded in 8 of the 13 animals kept in SDs at 5°C, and torpor-bout length ranged from 1 to 4

days (Fig. 2). Hibernation was initiated between *weeks* 9 and 12 after transfer to SDs as the testes were beginning to undergo recrudescence and was terminated between *weeks* 14 and 18 when substantial recrudescence was evident. Two of the most reliable hibernators died while torpid during *weeks* 14 and 16, respectively. Among hamsters held at 5°C, testicular recrudescence was slower in hamsters that entered torpor than those that did not ($P < 0.01$; Fig. 2). Testis volume increased at similar rates in both groups during *weeks* 8–12 but more rapidly in nontorpid animals during *weeks* 14 and 16. Testis dimensions remained greater for the remainder of the experiment in hamsters that were never detected in hibernation, but by *week* 24 the magnitude of the difference had decreased (Fig. 2).

Fig. 2. ETVs (in mm³) of hamsters kept in SD photoperiod at T_a of 5°C for 24 wk (top), percentage of animals found torpid at least once each week (middle), and average torpor-bout duration (bottom). ●, ETVs for hamsters never found torpid ($n = 5$); ○, ETVs for hamsters that entered torpor ($n = 8$). *Significant difference between the two groups, $P < 0.05$.



Food hoarding to the nest, which was observed during *weeks 10–21*, was not quantified but was observed only in hamsters that did not hibernate and was most prevalent during *weeks 10–14*. Four of the five hamsters never detected in torpor during *weeks 12–14* cached food in their nests throughout this interval of maximal hibernation. In contrast, none of the five hamsters that hibernated during *weeks 12–14* had food caches. Three hamsters hibernated during *weeks 12 and 13* but were euthermic on *week 14*; none of these hamsters had food caches during *weeks 12 and 13*, and only one stored food on *week 14* (after it had terminated hibernation).

Body mass. Temperature and photoperiod exerted less pronounced influences on body mass than on testis volume. In LD animals, body mass increased during the first 10 wk and was constant for the remainder of the experiment (Fig. 3). NR animals at 28°C weighed significantly more than all other groups throughout the experiment ($P < 0.005$). Body mass increased significantly during the first 6 wk in SD R animals at 22 and 28°C. In contrast, at 5°C there was a transient decline in body mass of 4.4 ± 2.3 g during the first 2 wk, which corresponds to an increase of 6.3 ± 0.9 g in other SD R groups ($P < 0.005$). During the first week of SDs, there was a significant relation between changes in body mass and testis size for the 5°C group and for all SD hamsters ($P < 0.05$ and $P < 0.0001$, respectively). During *week 1*, testis size increased $9 \pm 4\%$ at 28°C, decreased $6 \pm 3\%$ at 22°C, and decreased $21 \pm 5\%$ at 5°C ($P < 0.05$ for each comparison). By *week 2*, however, there was no longer a significant relation between changes in body mass and testis size ($P > 0.7$); there were similar body mass changes at all T_a values with most hamsters maintaining or increasing body mass independent of changes in testis size. By *week 3*, hamsters at 5°C had regained their initial body mass, and body mass values at 5°C did not differ significantly from those at 22 or 28°C. Body mass for all SD R animals considered together increased by 4.5 ± 0.8 g from *weeks 3–6*, but the absolute values were 7 g lower

at 5°C than 22 or 28°C (Fig. 3). During *weeks 6–14*, body mass increased in the LD group by 5.5 ± 1.3 g but decreased in the SD group by 2.0 ± 1.5 at 5°C, 7.1 ± 0.7 g at 22°C, and 6.2 ± 2.8 g at 28°C. By *week 12*, the differences among the SD R hamsters held at different T_a values were no longer significant because of the greater body mass loss at 22 and 28°C than at 5°C. Body mass increased spontaneously in all SD animals beginning on *week 16* (Fig. 3). By *week 24*, hamsters at 5°C were heavier ($P < 0.001$) than all other groups except the 28°C NR hamsters.

α -Expansion. The α -value remained short (10.4 ± 0.1 h) for hamsters kept in LDs (Fig. 4) but expanded in all animals transferred to SDs. The α -value was significantly longer during the first 2 wk at 5°C than at 22 or 28°C ($P < 0.005$ and $P < 0.01$, for each comparison on *weeks 1 and 2*, respectively). At a T_a of 22°C, the α -value did not expand in hamsters during the first week in SDs and was equivalent to that of LD animals. At 28°C, the α -value increased but not significantly during the first week in SDs. By the second week, the α -value had lengthened significantly in both 22 and 28°C groups and reached steady-state SD values at all T_a values. By *week 4*, the α -value no longer differed between T_a values and remained long (>12 h) in SDs at all T_a values through the end of the experiment on *week 24*. In the 5°C group, the α -value became highly variable and at times difficult to characterize during the weeks before and during the appearance of torpor. The α -expansion was comparable in R and NR animals at 28°C (Fig. 4). Activity records for individual animals from each of the three SD groups are shown in Fig. 5.

The interval between α -expansion and testicular regression was temperature dependent (Fig. 6, *top*), but the latency to onset of gonadal recrudescence relative to time of α -expansion to >13 h was not affected by T_a (Fig. 6, *bottom*). There was no delay in gonadal regression relative to α -expansion at 5°C. By the end of the first week in 5°C, testis volume had decreased slightly but significantly, and the α -value had expanded to >12 h (see Figs. 1 and 4). By *week 2* at 5°C, testicular

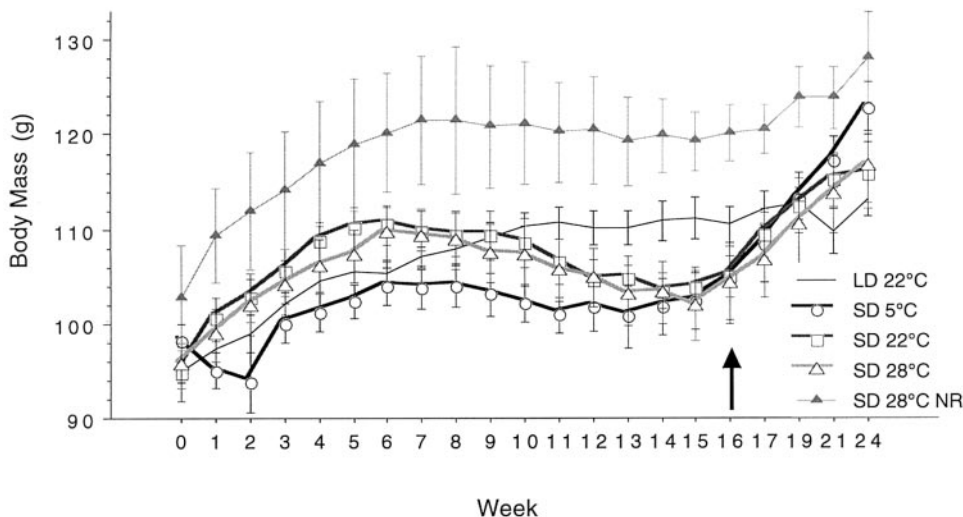
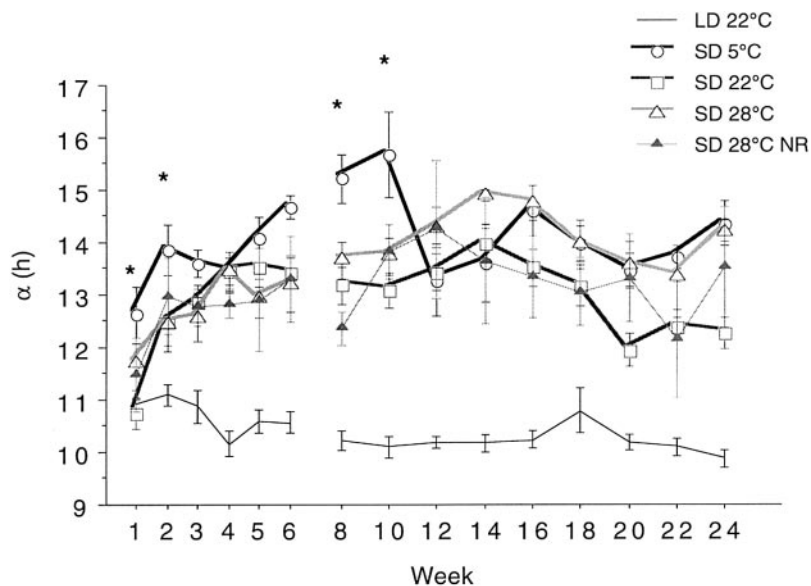


Fig. 3. Body mass of hamsters kept in LD photoperiod at T_a of 22°C or in SD photoperiod at 5, 22, or 28°C for 24 wk. Arrow indicates the week when body mass increased in all groups of SD photoreponsive hamsters.

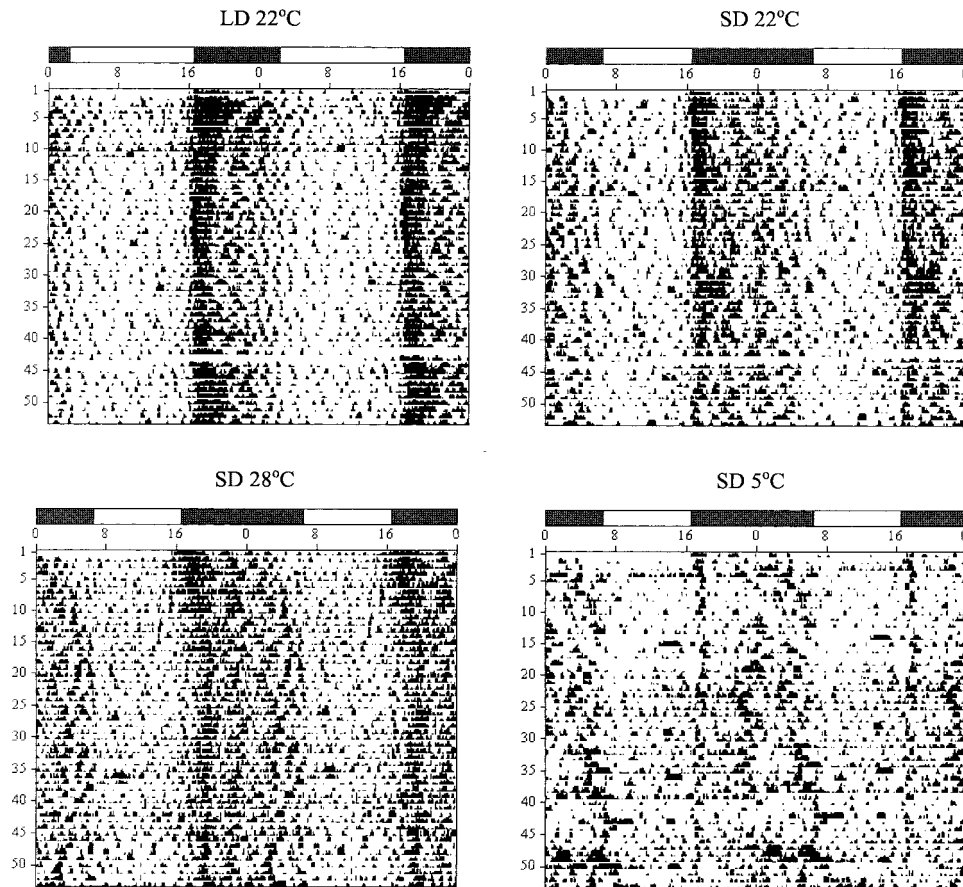
Fig. 4. Duration of nocturnal locomotor activity (α) of hamsters kept in LD photoperiod at T_a of 22°C or in SD photoperiod at 5, 22, or 28°C for 24 wk. *Significantly longer α -value in 5°C hamsters relative to all other groups. Weekly mean α -values are presented for the first 6 wk when the α -value was lengthening in the SD-exposed animals; thereafter the α -value was calculated in 2-wk intervals, $P < 0.05$.



regression was nearly complete and the α -value had expanded to >13 h. Although α -expansion was delayed by only 1 wk at 22 and 28°C compared with 5°C (see Fig. 4), the latency to gonadal regression was substantially longer at the higher T_a values ($P < 0.005$ for each comparison to 5°C). Despite the similarity in the timing of α -expansion at 22 and 28°C, latency to testicular

regression was doubled at the higher T_a , and 25% of hamsters held at 28°C never underwent gonadal involution. In contrast to its marked effect on timing of testicular regression, the latency to testicular recrudescence was not affected by T_a ; recrudescence occurred 11.8 ± 0.4 wk after α -expansion with no differences attributable to T_a (Fig. 6, bottom).

Fig. 5. Double-plotted actograms of spontaneous activity from individual hamsters recorded by passive infrared motion detectors during the first 8 wk in SD photoperiod at 5, 22, and 28°C and in LD photoperiod at 22°C.



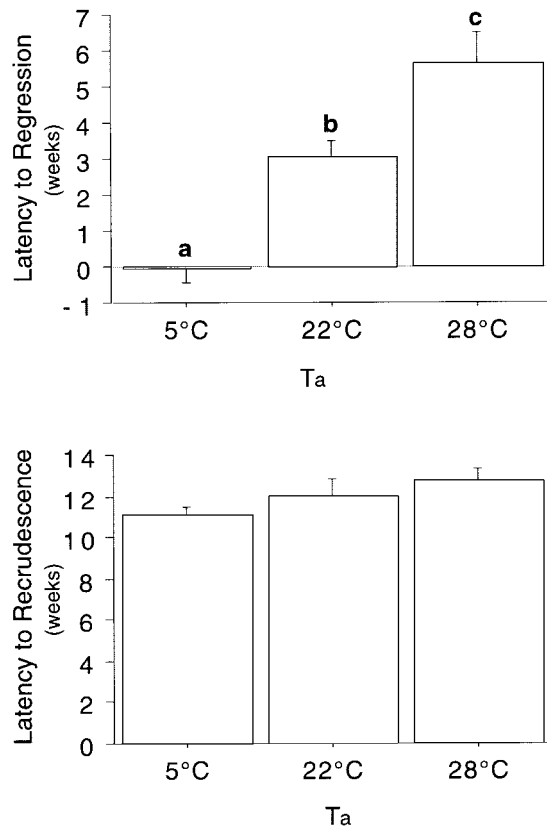


Fig. 6. Latency of testicular regression (*top*) and recrudescence (*bottom*) in photoresponsive hamsters kept in SD photoperiod at 5, 22, and 28°C. Latency was calculated as number of weeks to regression and recrudescence relative to the week in which the α -value first expanded to ≥ 13 h in each animal. Bars with different letters differ significantly, $P < 0.05$.

DISCUSSION

In Syrian hamsters exposed to SD lengths, low and high T_a may accelerate and delay the appearance of winter traits, respectively, by modulating the responsiveness of target tissue to melatonin. The amplitude of the melatonin signal does not consistently increase in Syrian hamsters housed at low temperatures: no differences were detected in plasma melatonin concentrations of males held at 5 and 20°C, respectively (31, 33), but in a third investigation (40), serum melatonin concentrations were higher at 5 than 22°C. It is unknown whether amplitude changes of the magnitude reported in the latter investigation affect rates of gonadal regression.

Cold exposure accelerated α -expansion, which presumably implies an earlier appearance of long-duration melatonin signals. This conclusion must remain tentative pending verification of the high positive correlation of these variables at low as well as higher T_a values. In any case, the more rapid entrainment in cold-exposed hamsters was insufficient to fully account for the marked acceleration of testicular regression in the cold and does not explain the markedly delayed reproductive responses at 28°C. The latency to onset of testicular regression after α -expansion, which may

provide a valid measure of how rapidly neuroendocrine tissues respond to the SD melatonin signal, was strongly temperature dependent with shorter latencies at lower T_a values. At 5°C, hamsters experienced rapid gonadal regression coincident with α -expansion, whereas an increase from 22 to 28°C doubled the latency to gonadal regression from 3 to almost 6 wk. Furthermore, 25% of the hamsters housed at 28°C were NR, as neither testes volume nor body mass changed significantly in response to SDs. Variations in T_a may also affect reproduction independently of the pineal axis, e.g., by modifying secretion of gonadotropins or thyroid hormones (13). It remains uncertain whether the inadvertent decline in T_a from 28 to 22°C for 3 days during *week 7* facilitated gonadal regression.

At 28°C, the α -value expanded similarly in both R and NR Syrian hamsters, which indicates that the circadian system of NR Syrian hamsters responded in the typical manner to the shortened day length. In deer mice (*Peromyscus maniculatus*), T_a also modulates the timing of SD testicular responses (7, 37), and some individuals are NR (3). In common with the Syrian hamster, NR deer mice entrain their circadian rhythms appropriately to SDs with expanded melatonin signals and lengthened α -values but nevertheless fail to undergo gonadal regression; this suggests that loss of target tissue responsiveness to long melatonin signals is the cause of nonphotoresponsiveness in deer mice and possibly in Syrian hamsters. A genetic component has been implicated in the nonphotoresponsiveness of deer mice, which occurs with greater frequency in populations from more southerly latitudes (28, 47). In contrast to deer mice, nonphotoresponsiveness in Siberian hamsters appears to be due to a change in the generation of the melatonin signal rather than to tissue insensitivity to melatonin. Nonresponder Siberian hamsters do not maintain extended α -values when transferred to SDs (18, 32), but they respond appropriately to long melatonin signals produced endogenously in constant darkness or exogenously by daily melatonin infusions (12, 16, 25, 32). Nonphotoresponsiveness in a primarily photoperiodic species allows for more opportunistic reproductive responses to environmental conditions (5). To our knowledge, the present study provides the first documented instance of environmentally induced nonphotoresponsiveness in Syrian hamsters.

Nonphotoresponsiveness in Syrian hamsters at 28°C may reflect either decreased target tissue responsiveness to long melatonin signals or a masking effect of high T_a that is unrelated to circadian control of the pineal gland. In the latter instance, melatonin secretion could be compromised at 28°C, even as the α -value indicates normal entrainment of the locomotor activity rhythm to SDs; decreased amplitude and/or duration of the melatonin signal in SDs at 28°C may explain nonphotoresponsiveness in some individuals. The observation that melatonin secretion in European hamsters is attenuated at a T_a of 30°C supports this conjecture (45). The α -value is a reliable indicator of the duration of the nocturnal melatonin signal in Syrian hamsters

at 22°C (11, 20); whether this relation holds at lower (5°C) or higher (28–32°C) T_a values is not known and therefore requires qualification of these conclusions. In Syrian hamsters held in LDs and treated with supplementary midafternoon melatonin injections, the gonadal response was diminished at T_a values of 30–32°C compared with responses at 22°C (26, 35). It is not possible, however, to definitively conclude on the basis of these studies that neuroendocrine target tissue responsiveness is blunted at the higher T_a ; if melatonin secretion were abbreviated in Syrian hamsters at T_a values of 30–32°C, the afternoon melatonin injections might not be sufficient to produce the long-duration melatonin signal that this treatment induces at 22°C. Whether high T_a values attenuate or eliminate SD responses by decreasing target-tissue responses to long melatonin signals as occurs in Siberian hamsters (25) can be determined in studies in which pinealectomized hamsters held at 22 and 28°C are administered standardized melatonin infusions.

The onset of spontaneous testicular recrudescence occurred 6.3 wk after testes had regressed irrespective of the T_a at which hamsters were housed but at quite different times after animals were placed in SD environments. If neuroendocrine refractoriness is triggered after a fixed number of SD lengths and long melatonin signals, then clearly this mechanism is highly temperature sensitive. Testicular recrudescence was initiated after ~8, 13, and 15 wk of SD exposure, respectively, for hamsters held at 5, 22, and 28°C. This issue is complicated by the potential masking effects of T_a on gonadal function; testicular recrudescence in SDs typically only occurs when gonadal regression has ceased. Hamsters at 5°C initiated recrudescence at *week 8*, at which time animals at 28°C were still weeks away from complete testicular regression.

More than half of the Syrian hamsters kept at 5°C initiated hibernation 9 wk after transfer to SDs, which corresponded to the week on which testicular recrudescence was initiated but before substantial testicular growth was evident. In the closely related Turkish hamster (*Mesocricetus brandtii*) (6, 14), hibernation onset was also coincident with the earliest phases of testicular recrudescence, and hibernation was terminated after substantial testicular growth accompanied by increased androgen secretion had occurred. Hibernation is generally associated with diminished androgen secretion, and high plasma concentrations of testosterone terminate hibernation in several hamster species (15, 23). Some species, such as the golden-mantled ground squirrel, terminate hibernation before initiating testicular development (1); in general, gonadal recrudescence may be prevented or greatly diminished during torpor.

Hibernation and food hoarding were observed only in hamsters kept at 5°C and appeared to be mutually exclusive behaviors. Hamsters either entered torpor or cached food in their nests. These behaviors were first noted after 9 wk in SDs, which suggests that their spontaneous appearance may be controlled by day length. We cannot, however, discount the possibility

that low T_a is the primary proximate controller of hoarding behavior (21). Neither behavior was noted in hamsters kept in SDs at 22 or 28°C.

Syrian hamsters transferred to 5°C sometimes incur severe energy imbalances that may contribute to rapid inhibition of the hypothalamic-gonadal axis (9, 36). Rapid onset of gonadal quiescence associated with cold exposure in female hamsters kept in LDs coincided with profound (20%) losses of body mass; this effect was completely eliminated by providing more palatable ground chow that sustained increased food consumption and normal body mass (9). In the absence of profound losses of body mass, cold exposure of male Syrian hamsters housed in LDs sometimes (22, 27) but not always (8, 30) resulted in moderate testicular regression similar to that measured during the first week of cold exposure in the present study. Thus in the present study, the moderate (21%) decline in testis size measured during the first week at 5°C may result at least partially from the inhibitory effects of cold exposure and the associated minor (<5%) body mass loss. In contrast, the rapid and substantial gonadal involution during the second week at 5°C was independent of changes in body mass, which suggests that it may represent an accelerated, SD-induced gonadal regression. Body mass loss was not the major determinant of testicular regression; hamsters that gained body mass and those that lost <1% of their initial body mass during the first 2 wk of cold exposure ($n = 5$) showed significant testicular regression that was indistinguishable from that seen in animals that lost 1–5% of their body mass ($n = 6$). Reflecting the possible role of limited energy supplies in inhibiting reproduction in the cold, the NR hamsters at 28°C, which retained reproductive function throughout SDs, had the highest body masses. Increased energy reserves may contribute to maintenance of testicular function in SD animals.

Timing of testicular regression and onset of recrudescence but not changes in body mass were affected by T_a values between 5 and 28°C. The sole exception to this generalization was the acute decrease in body mass during the first week of cold exposure. Testicular regression occurred 4 wk earlier at 5°C and 3 wk later at 28°C relative to latency at 22°C. Testicular recrudescence occurred 2 wk earlier at 5°C than at 22 or 28°C, during *week 13* versus *week 15*, respectively. In contrast to the variability in timing of gonadal regression and recrudescence at several T_a values, body mass in R Syrian hamsters reached a nadir on *week 15* and increased starting on *week 16* at all T_a values. There were no differences in body mass between the 22 and 28°C R hamsters despite the striking differences in the timing and extent of their testicular regression. The effector pathways that govern somatic and gonadal responses to day length may be differentially affected by T_a with gonadal status the more labile trait.

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