Timing of puberty and synchronization of seasonal rhythms by simulated natural photoperiods in female Siberian hamsters

Matthew P. Butler,1 Justin J. Trumbull,2 Kevin W. Turner,2 and Irving Zucker1,2

Departments of 1Integrative Biology and 2Psychology, University of California, Berkeley, California

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The proximate cues that determine the breeding season vary between species, populations, and habitats; for many mammals, photoperiod is the principal predictive cue (4, 26). Young born at different times of the breeding season manifest different life history strategies (27). In short-lived rodents, cohorts born early in the season typically breed in their year of birth, whereas later-born offspring delay puberty until the following spring (4, 26). Differences in the age of puberty between cohorts have been documented in the field (voles, Refs. 3, 6, 19; white-footed and deer mice, Refs. 1, 9, 29; and field mice, Ref. 1). Laboratory studies have confirmed the effectiveness of long or short static photoperiods in determining the age of puberty (voles, Ref. 20; white-footed mice, Ref. 18; Siberian hamsters, Ref. 17; and ferrets, Ref. 2). Remarkably little is known, however, about the specific photoperiodic cues that signal the transition from early to delayed puberty.

Male Siberian hamsters (Phodopus sungorus) born in long days grow rapidly and reach puberty at ~5 wk of age, whereas those born in short days gain body weight more slowly, molt to the winter pelage, and delay puberty until ~5 mo of age (17). The reliance on static photoperiods in the great majority of photoperiodism studies with Siberian hamsters limits what we can conclude about the relative salience of different aspects of the natural photic environment (5, 15).

In laboratory studies of Siberian hamsters, postnatal development and puberty timing depend on both ambient photoperiod and a prenatally defined photoperiod history that serves as a reference point (30, 31). The dam imparts photoperiodic information on her fetuses via melatonin secretion in a sensitive period between 5 and 3 days before parturition (34). Pups become sensitive to day length around postnatal day 15 when their endogenous rhythmic melatonin secretion is first evident (32). In males housed in simulated natural photoperiods (SNP), however, prenatal photoperiod history had only small effects on postnatal development (5). Whether females respond similarly is unknown, but the few studies of females point toward sex differences in several aspects of photoperiodism (11, 22, 28, 33). The relevance of prenatal photoperiod to female development is specifically questioned by work that showed that, unlike in males, gestational photoperiod had no effect on early postnatal melatonin rhythms and follicle-stimulating hormone concentrations in females (28).

At the onset of the next breeding season, over-wintering postpubertal but reproducitively quiescent hamsters return to breeding condition, whereas prepubertal animals born late in the previous year first achieve reproductive competence. Spring gonadal growth is driven by the development of refractoriness to short day lengths, the onset of which is controlled by a plastic interval timer (11, 12, 16, 24). Interval timing also differs between sexes: testicular development time was predicted by calendar date, but vaginal patency time was better predicted by age in hamsters raised in SNP and then housed in constant short days from the winter solstice (11). The author speculated that synchronization of female reproductive development might be achieved by increasing day lengths and that the more rapid activation of the ovary compared with the testis obviated the need for an interval timer-dependent trigger (11). Data on the spring transition in females are limited to females born in SNP and then clamped to short days from the time of the winter solstice (11, 12); the synchronizing effects of increasing day lengths are unknown.

To investigate the photoperiod conditions at which rapid maturation gives way to delayed puberty, we monitored devel-

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opment and puberty strategy in female Siberian hamsters born over a 16-wk period (June-September) in SNP. We tested the hypothesis that SNP exposure would, as in males, synchronize fall and spring seasonal transitions across the full range of asynchronously born hamsters, and we assessed whether prenatal photoperiod history influences females’ pubertal strategies.

**METHODS**

Nine cohorts of female Siberian hamsters were born at 2-wk intervals beginning 4 wk before and ending 12 wk after the summer solstice in an SNP corresponding to 53°N (annual range of 7.6–16.9 h of daylight; see Fig. 1 of Ref. 5 for additional details). There was no illumination during the dark phase. The last births correspond to the end of the breeding season in the field in mid-September (35). Other procedural details regarding housing conditions were identical to those described for males (5). Dams were transferred to the SNP 2 wk before pairing with males, and were each used only once. Locomotor activity of the dams was verified to be entrained to the SNP prior to pairing by recording movements in the cage with passive infrared motion detectors (5). Births were distributed over 2–4 days (3.0 ± 0.3, mean ± SE), with the first births 1–3 days before the target birth date (Table 1).

Eighteen pups per cohort were weaned at 23–24 days of age, segregated by sex, and housed three per cage with both littermates and nonlittermates of the same age in clear polypropylene cages furnished with food, water, and bedding. All procedures were approved by the Animal Care and Use Committee of the University of California, Berkeley.

Beginning on the day of weaning and at weekly intervals thereafter, body weight, vaginal patency, and pelage color were assessed for all animals until 41 wk after the summer solstice (April). Body weight and pelage score were assessed for 4 additional weeks. The vagina was rated either patent, closed, or indeterminate; for analysis, each indeterminate score was changed to the nearest preceding certain score of patent or closed. Pelage scores were assigned by using a modified version of the scale of Duncan and Goldman (8) (summer pelage = 1; Ref. 5).

**Responsiveness to short days.** Hamsters were designated potential nonresponders if they met any of the following three criteria: 1) maximum pelage score <2 throughout the experiment; 2) maximum body weight decrease <12%, measured from peak body weight during the first 16 wk of life to the subsequent trough (16); and 3) no period of 4 consecutive weeks between the fall and spring equinoxes during which the vagina is closed.

Hamsters that satisfied all three criteria were deemed unequivocal nonresponders (n = 13). Others that fulfilled one or two of the criteria were evaluated individually by considering the full body weight, pelage, and patency data. Fourteen hamsters satisfied two of the criteria: one was a responder that died before the fall molt and three were deemed indeterminate because different traits showed responder- and nonresponder-typical patterns; 10 were classified as nonresponders. Hamsters that satisfied only one nonresponder criterion were either responders or indeterminate. Indeterminate and nonresponsive hamsters have been removed from all analyses. The maximum body weight decrease criterion was met by most late-born responders and nonresponders alike that typically lack the early peak. Therefore, body weight data for all hamsters that met this criterion were inspected visually for a responder- or nonresponder-typical body weight pattern. Responders in late cohorts typically exhibit a “step” in body weight. After several weeks of rapid weight gain, body weight stabilizes at a constant or slowly increasing plateau, before increasing further in the spring. Body weight gain (g/wk) therefore peaks twice, once in the fall and once in the spring. Nonresponders, on the other hand, grow rapidly and achieve final peak body weight in a smooth manner. Body weight gain peaks once early and then decreases monotonically throughout life.

**Body weight analysis.** Body weight loss and gain were analyzed by fitting moving 11-wk cubic regressions to the raw body weight data (±5-wk window), described in detail in the companion paper published in this issue of *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* (5). Briefly, the second derivative of each successive regression provides a point-wise estimate of body weight acceleration (g/wk²). Each hamster’s time of fall body weight loss was defined as the point of inflection in body weight decline (acceleration = 0), and the time of spring body weight increase was defined as the point of maximum acceleration. For animals in which this occurred on week 40 post-summer solstice (last possible measurement using a ±5-wk window), we reanalyzed the data with a ±3-wk window. This generally corroborated the ±5-wk window, but sometimes revealed a later date of body weight acceleration.

**Vaginal patency and puberty.** Patency onset was defined as the first of 2 consecutive weeks in which the vagina was patent. The first such onset for each animal was defined to be the date of puberty. The transition from a closed to a patent vagina is not abrupt, so this approach ensured that a single isolated occurrence of an open vagina, that may have been borderline, did not define puberty. As a methods check, data were analyzed with a less conservative measure, in which puberty was defined by the first time the vagina was patent. Puberty date differed in 28 out of 122 responders when comparing the more- and less-restrictive definitions; differences were evenly distributed among all cohorts. In only 11 hamsters did it cause reassignment from the delayed- to the early-puberty groups as defined in the results (1 hamster each in cohorts −4, −2, and +6; 2 hamsters in cohorts +4 and +6; and 4 hamsters in cohort +12). Our conclusions were unaffected by this reanalysis. In the results, we note a single, specific test whose significance was affected by our choice of puberty definition.

**Reproductive quiescence was defined as ≥5 consecutive weeks of continuous vaginal closure.** The beginning of the winter interval of vaginal closure was defined as the first of these five closed observations.

In one hamster’s reproductive quiescence, there were two isolated patent vagina observations preceded by 7 wk and followed by 15 wk of vaginal closure. These two observations were discounted in favor of a later second vaginal opening that accompanied a spring body weight increase. In eight hamsters that had previously experienced puberty, spring patency onset was defined by a single patent obser-

### Table 1. Photoperiod, litter, and puberty information for all cohorts

<table>
<thead>
<tr>
<th>Cohort</th>
<th>DOB</th>
<th>Number of Litters</th>
<th>Photoperiod</th>
<th>Puberty Timing</th>
</tr>
</thead>
<tbody>
<tr>
<td>−4</td>
<td>May 24</td>
<td>6</td>
<td>16:31:16:54</td>
<td>22</td>
</tr>
<tr>
<td>−2</td>
<td>June 7</td>
<td>7</td>
<td>16:52:17:00</td>
<td>33</td>
</tr>
<tr>
<td>0</td>
<td>June 21</td>
<td>7</td>
<td>16:59:16:25</td>
<td>35</td>
</tr>
<tr>
<td>+2</td>
<td>July 5</td>
<td>9</td>
<td>16:43:15:50</td>
<td>12</td>
</tr>
<tr>
<td>+4</td>
<td>July 19</td>
<td>7</td>
<td>16:09:15:01</td>
<td>20</td>
</tr>
<tr>
<td>+6</td>
<td>August 2</td>
<td>6</td>
<td>15:36:14:08</td>
<td>0</td>
</tr>
<tr>
<td>+8</td>
<td>August 16</td>
<td>6</td>
<td>14:44:13:11</td>
<td>0</td>
</tr>
<tr>
<td>+10</td>
<td>August 30</td>
<td>5</td>
<td>13:53:12:12</td>
<td>0</td>
</tr>
<tr>
<td>+12</td>
<td>September 13</td>
<td>7</td>
<td>12:53:11:16</td>
<td>13</td>
</tr>
</tbody>
</table>

Cohort number designates birth week relative to the summer solstice. In addition, the target birth date (DOB), the number of litters, and the photoperiods at birth and weaning are shown. %NR, %nonresponders, not including indeterminate hamsters. The puberty timing columns show the number of hamsters assigned to the early and delayed puberty groups. Data from hamsters for whom puberty timing could not be accurately ascertained (occulted water bottle, intermediate puberty, or urethra position; see text) are included in the %NR but not in the puberty timing numbers.
vation on the last week of data collection (week 41). One more hamster had only a single questionable patent score in the last week of observation. These last nine hamsters all had striking body weight increases that confirmed the onset of the spring phenotype, so all nine were included for analysis with vaginal opening set at week 41.

In three hamsters, the urethra was farther posterior than normal, preventing accurate determination of the time of vaginal patency. They were responders based on body weight and pelage, but have otherwise been removed from all patency analyses.

Statistics. One-way ANOVA or Kruskal-Wallis tests were used where appropriate to test for cohort effects on the timing of developmental and seasonal events. Differences between hamsters with different puberty strategies were tested by Student’s t-test or Mann-Whitney U-test. Repeated-measures ANOVA was used to analyze effects of time and time × factor interactions. All main effects of time in these growth curves (age or date) were significant and are not reported. Trends in body weight across cohorts at equal ages were tested with linear regressions. All of the above were calculated by using SPSS 13.0 (SPSS, Chicago, IL). Proportions were tested for significance with the χ²-test for independence (StatView 5.0, SAS Institute, Cary, NC). When multiple χ²-tests were performed in a single analysis, the level for significance was adjusted using the Bonferroni correction to minimize type 1 errors. Means ± SE are reported throughout. The significance level was set at P = 0.05.

To test the competing hypotheses of age vs. date synchronization of life history events, linear regressions were calculated for event date as a function of birth date (cohort) using StatView as described previously (5). A slope of 1 indicates a fixed interval between birth and the event date and thus establishes age synchrony. A slope of 0 indicates a fixed interval between the summer solstice and the event date, thereby indicating synchronization by day length or calendar date. We defined synchronization to be significant if the 95% confidence interval (CI) contained 1 or 0 (5). The competing hypotheses of age vs. date synchronization are not exhaustive, and we use proximity of the regression slopes to 1 or 0 as an index of the primacy of the respective mechanisms.

RESULTS

Nonresponsiveness. Of 162 hamsters, 23 were classified as nonresponders, and 10 more were considered indeterminate. The ratio of nonresponders to responders differed significantly among cohorts; 16/23 nonresponders belonged to the first three cohorts born by the summer solstice (omnibus χ²-test, P < 0.01, Table 1).

Body weight and patency over time. Calendar date of birth (Fig. 1B) was a far better overall predictor of body weight than was age (Fig. 1A). Repeated-measures ANOVA on the intervals for which the full complement of data exist revealed significant effects of cohort and cohort × age interactions for body weight against age (P < 0.01 for both). In contrast, when

![Graph](image-url)
the data were analyzed as a function of calendar date, there was no significant effect of cohort (\( P > 0.1 \)), but different cohorts still differed in the pattern of body weight gain (cohort \( \times \) date, \( P < 0.001 \)). In cohorts \(-4\) to \(+6\), mean body weight increased initially, subsequently declined to a winter trough, and then increased again in the spring. In contrast, cohorts \(+8\) to \(+12\) did not achieve an early peak but instead continued to gain weight gradually through the winter, followed by a further increase in the spring. Despite these differences, winter solstice body weight did not differ between cohorts (ANOVA, \( P > 0.05 \), not shown).

Changes in vaginal patency were also better predicted by calendar date than by age (Fig. 2). As a measure of synchronization, \( \chi^2 \)-tests between cohorts were performed at each time point. There were fewer time points with significant cohort effects when the data were analyzed by date (12 wk, Fig. 2B) than by age (27 wk, Fig. 2A).

**Puberty.** For early-born animals (e.g., cohorts \(-4\) to \(0\) and some hamsters in cohorts \(+2\) and \(+4\), the vagina became patent and then closed in decreasing day lengths. For later-born animals, some showed initial vaginal patency at a young age, but most delayed puberty until the following spring. Overall, both age and date of puberty differed significantly between cohorts (Kruskal-Wallis, \( P < 0.001 \), not illustrated). Hamsters were then categorized into those that experienced early puberty (by 13 wk of age, \( n = 50 \)), intermediate puberty (14 or 16 wk of age, \( n = 2 \)), or delayed puberty (\( \geq 19 \) wk of age, \( n = 67 \), Table 1). Early puberty was synchronized by age (7.4 \( \pm \) 0.3 wk of age), but delayed puberty was synchronized by calendar date at 35.9 \( \pm \) 0.4 wk post-summer solstice (Fig. 3, CIs reported in legend). Inclusion of the two intermediate hamsters into either the early or delayed puberty group did not affect the conclusions. Three cage mates in cohort \(-2\) appeared to experience early puberty based on body weight and vaginal observations but had an occluded water bottle, which prevented them from drinking in the week of expected vaginal patency onset and were not twice observed as patent. These five hamsters were eliminated from all comparisons that relied on classification into early and delayed puberty groups, and consequently, also from later analyses of adults and juveniles.

Hamsters began to delay puberty in substantial numbers beginning with cohort \(+2\) (Table 1). Cohorts \(+2\) and \(+4\) had distinct bimodal distributions: 14 hamsters experienced puberty by 11 wk of age, and 12 delayed puberty until at least 31 wk of age.

**Photoperiod effects on early body weight and puberty.** Hamsters in cohorts \(+2\) and \(+4\) displayed both puberty strategies, despite identical pre- and postnatal photoperiod exposure. Prenatal photoperiods have been posited to play an important role in determining whether postnatal day lengths stimulate or inhibit growth and maturation (30, 31), so we tested for prenatal photoperiod effects by examining body weight in the two puberty strategy groups from weaning to 11 wk of age (the last point of early puberty among these hamsters). We predicted that if prenatal photoperiod history plays a role in delaying puberty, then it should be evident in reduced body weight and slower body weight gain prepubertally. This prediction is based on the significantly lower body weights by 4 wk of age of Siberian hamster females maintained from birth in static short day compared with long day lengths (25). In that study, body weight differences preceded vaginal patency; first detection of puberty and mean puberty age were at 6 and 10.9 wk of age, respectively (25). Because short day reductions in body weight are abolished by ovariectomy (33), differences in body weight may be a sensitive measure of circulating ovarian hormones before vaginal patency is achieved. We reasoned that equal prepubertal patterns of body weight in both strategies would indicate similar development of the ovary in both groups and thus no photoinhibition by prenatal photoperiod history effects.

Although the pattern of body weight over time (3–11 wk of age) differed between puberty strategies, this interaction effect appeared to be caused by late divergence between the groups rather than by early postnatal differences (repeated-measures ANOVA: strategy \( \times \) age effect, \( P < 0.01 \), Fig. 4A). Indeed, body weight only differed significantly at 11 wk of age (Student’s \( t \)-test, \( P < 0.05 \)). There were no significant differences in body weight at weaning (Fig. 4B), body weight gain from age 3 to 5 wk (not illustrated) or maximum body weight attained during this period (but note a trend toward significance in the last comparison, \( P = 0.075 \), Fig. 4B). These data suggest that prenatal photoperiod does not contribute to determining puberty strategy. The achievement of puberty, however, had long-lasting effects on body weight: hamsters that delayed puberty weighed significantly less at their winter trough body weight (\( P < 0.01 \), Fig. 4B). All results were reanalyzed to
ensure that a less conservative definition of puberty (the first observation of vaginal patency) did not change our conclusions. With this definition, two hamsters were reassigned from the delayed group to the early puberty group. Only the comparison of maximum body weight attained by 11 wk was affected (significant under the single patent puberty definition; Student’s t-test, \( P < 0.047 \), not illustrated).

Even across all cohorts, there was no evidence of photoperiod effects on weaning body weight. Among all hamsters, there was a significant cohort effect on body weight at age 3 wk (ANOVA, \( P < 0.05 \)), but body weight did not vary in any consistent manner from early to late cohorts, suggesting that cohort differences were not associated with changes in photoperiod (\( R = -0.02, n = 129, P = 0.8 \), not illustrated). Independence of weaning body weight from photoperiod is restricted to females. Weaning body weight data from a parallel study of males were reanalyzed (5). Like females, body weight of males at 3 wk of age differed significantly between cohorts (ANOVA, \( P < 0.01 \)). Unlike females, there was a small but clear systematic decrease in weaning body weight from the earliest to the latest cohorts as the season progressed (\( R = -0.21, n = 222, P < 0.01 \), not illustrated).

**Fall and spring seasonal transitions.** The onset of the winter phenotype was marked by loss of vaginal patency and a decrease in body weight. Vaginal closure was significantly synchronized across cohorts by calendar date (16.6 \( \pm 0.4 \) wk postsolstice, Fig. 5A). In contrast, body weight loss was not synchronized by either date or age and instead was intermediate (Fig. 5B, regression line for all 9 cohorts not shown). Two distinct patterns were observed, with a transition between the two at 6 wk after the summer solstice. Timing of body weight loss in cohorts \(-4\) to \(+6\) suggested synchronization by date, but this was not significant. Body weight loss in cohorts \(+6\) to \(+12\) was synchronized to constant age (10.9 \( \pm 0.3 \) wk of age, Fig. 5B). The majority of these late-born animals gained and subsequently lost body weight but did not attain puberty in the fall.

The emergence of the spring phenotype was characterized by vaginal patency and body weight gain, both of which were synchronized by calendar date (35.3 \( \pm 0.4 \) and 35.5 \( \pm 0.4 \) wk after the summer solstice, respectively, Fig. 5). There were no significant differences in the date of either measure between adults returning to breeding condition and prepubertal juvenile hamsters.

**Fig. 3.** Regression analysis on the date of puberty (means \( \pm \) SE) plotted against birth date. Regression lines extend only through the data that are included in the regression calculation. Confidence intervals (CI) are denoted by the faint curved lines above and below each regression line [early puberty: CI = (0.64, 1.04), \( n = 50 \); delayed puberty: CI = (−0.35, 0.15), \( n = 67 \)]. Two hamsters with intermediate timing of puberty timing are not included in the regression analyses and are shown separately. Numbers per cohort are the same as in Table 1. The dotted line illustrates perfect age synchronization (slope = 1).

**Fig. 4.** A: body weight of hamsters in cohorts \(+2\) and \(+4\) between 3 and 11 wk of age that underwent early or delayed puberty. \*Student’s t-test, \( P < 0.05 \). Numbers along the early puberty line indicate the number of hamsters that achieved puberty in each week-to-week interval. As a comparison, mean body weight of females housed in 10-h light/day, but in otherwise similar conditions to those here, never exceeded 21 g in this age range (25). B: body weight of females that adopted each puberty strategy in cohorts \(+2\) and \(+4\). Number of hamsters is indicated in A. bw, body weight. All data are plotted as means \( \pm \) SE.
nibles reaching breeding condition for the first time (patency date: Mann-Whitney U-test, \( P > 0.1 \); body weight acceleration date: Student’s \( t \)-test, \( P > 0.1 \); data not shown). Analysis restricted to \( \text{cohorts} +2 \) and \( +4 \), each with substantial representation of both puberty strategies, indicated that adults achieved patency significantly earlier than did juveniles (33.9 ± 1.4 and 37.6 ± 0.6 wk post-summer solstice, respectively; ANOVA: strategy effect, \( P < 0.05 \), cohort and cohort × strategy effects, not significant, Fig. 5A). There were no significant differences, however, in the date of body weight gain between adults and juveniles of \( \text{cohorts} +2 \) and \( +4 \) (ANOVA: all effects not significant, Fig. 5B).

**DISCUSSION**

Age at puberty varied markedly, ranging from 4 to 44 wk of age. All but one female born by the summer solstice developed rapidly and achieved puberty at an early age. Hamsters born 2–4 wk after the summer solstice displayed either early or delayed puberty, and those born 6 or more weeks after the solstice generally delayed puberty until the next spring. Despite the wide ranges in birth date and age at puberty, fall and subsequent spring seasonal events generally occurred at approximately the same calendar dates.

Some July hamsters delayed puberty despite being born only 2 wk after the summer solstice. This onset of delayed puberty was 2 wk earlier than observed in males (5). The long day lengths and moderate decline from gestational to weaning photoperiod for these hamsters prompted us to evaluate the contribution of prenatal photoperiod history to photoinhibition of females. Although prenatal photoperiod history effects have been posited to be important ecologically for accurate assessment of calendar date, the effects in SNP-housed males were small (5), and there is evidence that there may be no effect in females. Circulating concentrations of follicle stimulating hormone, integral to hypothalamo-pituitary-ovarian function, were unaffected by long or short gestational day lengths in females housed from birth in an intermediate day length (28).

In the present experiment, we found no evidence that prenatal photoperiod played a role in delaying puberty. In \( \text{cohorts} +2 \) and \( +4 \), there were no significant differences in prepubertal body weight or body weight gain between hamsters that matured rapidly or delayed puberty. Notably, mean body weight in both groups was much higher than that attained by static short day housed females from our colony and in similar housing conditions as employed here (mean body wt <21 g from 3–11 wk of age, Ref. 25). Body weight can be used in females as an indicator of ovarian state and/or circulating concentrations of ovarian hormones, because body weights of long and short day ovariectomized hamsters do not differ, and both are similar to the mean body weight of short day intact females with atrophic ovaries (33). The similar prepubertal body weights of hamsters displaying both puberty strategies therefore indicate similar development of the ovary, and thus no apparent inhibition by prenatal photoperiod history. Instead, it appears that somatic development proceeds as it would in photostimulated hamsters, and is only arrested later before puberty. Although ovarian development can only be inferred in the present work, direct measurements of testicular development in males support this inference. Testis size increased transiently in the early postnatal period and then decreased again as day lengths shortened in the first males to delay puberty in SNP \( \text{cohorts} +4 \) and \( +6 \) (5).

In a second test of prenatal photoperiod history effects we found no systematic relationship between body weight at
weaning and photoperiod (cohort) in females. This differed from the small progressive decline in weaning body weights of males as the season progressed. Somatic growth of females may be less sensitive or may respond more slowly to postnatal photoperiods compared with males. We suggest that photoinhibition of females in naturally varying day lengths is mediated exclusively by postnatal decreases in ambient day length without reference to prenatal day lengths.

The transition to delayed puberty in females occurred in cohorts +2 and +4, 2 wk earlier than in males housed under identical conditions (5). This may reflect a sex difference in normal rates of pubertal development. Early puberty in males occurred at \(-5\) wk of age, whereas in females, early puberty was not achieved until \(7.4 \pm 0.3\) wk weeks of age. The onset of inhibitory day lengths for both sexes would then be specified as \(\sim 10\) wk after the summer solstice. Day length at this point (\(\sim 14\) h, Table 1) would stimulate rapid development if presented as a static photoperiod (17).

Both age and pubertal status may affect when the spring phenotype emerges, and may do so differently in females and males. In females, puberty strategy had a significant effect on the date of spring vaginal opening, but age was of no consequence despite differing by up to \(16\) wk. The opposite held true for males; puberty strategy had no effect, but older age delayed reproductive and somatic growth in spring (5). Earlier vaginal opening in adult females was not accompanied by earlier weight gain, suggesting that within a sex, different traits may respond differently to the combination of photoperiod, age, and puberty strategy. Sex-specific and trait-specific differences in seasonal regulation have been noted before: in photoinhibited Siberian hamsters born in SNP but then held in short days from the winter solstice, increases in body weight in both sexes and testicular development in males were all synchronized by calendar date, but vaginal opening was not (11). The author concluded that an interval timer controls the first three traits but puberty strategy had no effect, but older age delayed puberty in males. In females, puberty strategy had a significant effect on puberty attainment significantly lower trough body weights during the winter (Fig. 4B). Reduction of body weight in winter (Dehnel’s Phenomenon) allows small animals to reduce their total caloric requirement and thus the total time spent out of the burrow in foraging (21). Female hamsters that delay puberty also do not risk breeding attempts at the end of the breeding season when resources may be degraded and the cost of a litter insupportable. Delaying puberty may ameliorate the decline in female fertility due to reproductive aging. In 40-wk-old age-matched Siberian hamsters, female fertility was significantly higher in short day hamsters that had delayed puberty than in long day hamsters that had undergone early puberty (25). The effects of brief periods of reproductive competence on later fertility are uncharted.

Maturation rate is relevant to understanding dynamics and age structure of populations. Different cohorts contribute differentially to the breeding population in sequential years. Conversely, population structure can also affect maturation rates, especially in species prone to large fluctuations in population size and high densities. For example, the proportion of young voles in a natural population that matured in their year of birth was inversely related to population density (19). This is probably less important for Siberian hamsters that typically exist at very low densities (36) but underscores the importance of determining the cues controlling puberty for our understanding of natural populations.

Nonresponders were mostly limited to the three earliest cohorts, probably because of the environmental induction of nonresponsiveness by long day lengths experienced by these cohorts (14). Very long photoperiods induce nonresponsiveness by altering the circadian system such that the onset of nocturnal activity and melatonin secretion is delayed and is soon truncated by dawn. Consequently, the melatonin duration experienced by these hamsters is short and typical of long days. Even with this effect, we observed only 23 nonresponders in 152 females (indeterminates not included), and 17 in 243 males (5). Among 254 males and females born after the summer solstice, only 11 were nonresponsive (4.3%). Together with recent work showing that dim nocturnal illumination also reduces nonresponsiveness (13), the incidence of nonresponsiveness in natural populations may be quite low.

Vaginal patency and body weight measures complement each other in this experiment. Vaginal patency is a puberty marker and possible indicator of fertility, while body weight may serve as a more sensitive measure of circulating gonadal hormones as discussed above. Body weight more accurately reflects gonadal condition in females compared with males. In males, gonadal steroid-independent processes contribute substantially to the photoperiodic regulation of body weight (10, 23, 33). As a continuous measure, body weight can also reflect gradations in physiological state. There were indications in our data of a nonsystematic dissociation of effects of day length on the timing of vaginal opening vs. changes in body weight. A few hamsters showed transient body weight increases without vaginal opening, while some others showed vaginal opening with little or no concomitant increases in body weight.

The present experiment demonstrates that SNPs can synchronize seasonal events in female hamsters over a wide range of birth dates. Hamsters born as early as July 5 (cohort +2) at a day length of \(16\) h \(43\) min began to delay puberty, and by August (cohort +6) virtually all hamsters delayed puberty until the following spring. Importantly, incrementally decreasing day lengths exert inhibitory effects even at day lengths that stimulate development when presented statically. The response to changing day lengths in females differs in several important ways from that of males. Most notably, photoperiod appears to have no effects on development of females until they are older than \(3\) wk. These data underscore the importance of small daily changes in day length in shaping the seasonal responses of female Siberian hamsters and the importance of including both sexes in the analysis of photoperiodism.

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