Photoperiodic and hormonal influences on fur density and regrowth in two hamster species

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Paul MJ, George NT, Zucker I, Butler MP. Photoperiodic and hormonal influences on fur density and regrowth in two hamster species. Am J Physiol Regul Integr Comp Physiol 293: R2363–R2369, 2007. First published September 26, 2007; doi:10.1152/ajpregu.00520.2007.—Temperate and boreal mammals undergo seasonal changes in pelage that facilitate thermoregulation in winter and summer. We investigated photoperiodic influences on pelage characteristics of male Siberian and Syrian hamsters. Fur density (mg fur/cm² skin) was measured by weighing the shavings of fur patches removed from the dorsal and ventral surfaces of hamsters maintained in long days (LDs) or transferred to short days (SDs). Patches were resheared 3 wk later to assess fur regrowth (mg regrown fur/cm² skin). Fur density was greater in SD than in LD Siberian hamsters after 11 wk of differential phototreatment. The onset of increased fur density in SDs was accompanied by a transient increase in fur regrowth (11–14 wk on the dorsal surface and 7–10 and 11–14 wk on the ventral surface), suggestive of a seasonal molting process. Fur density, body mass, and pelage color of Siberian hamsters returned to values characteristic of LD males after a similar duration of prolonged (>27 wk) SD treatment and appear to be regulated by a similar or common interval-timing mechanism. In Syrian hamsters, dorsal fur density, fur regrowth, and hair lengths were greater in SD than in LD males. Castration increased and testosterone (T) treatment decreased dorsal and ventral fur regrowth in LD and SD hamsters, but the effects of T manipulations on fur density were limited to a decrease in dorsal fur density after T treatment. Decreased circulating T in SDs likely contributes to the seasonal molt of male hamsters by increasing the rate of fur growth during the transition to the winter pelage.

Siberian hamster; Syrian hamster; photoperiodism; testosterone

FOR MANY TEMPERATE AND BOREAL species, winter conditions present serious energetic challenges. Several energy-saving behavioral and physiological modifications, including hibernation/torpor, huddling, nest building, reproductive quiescence, and altered body mass, facilitate overwinter survival (24). In many mammals, properties of the fur coat vary seasonally and provide greater insulation in winter and greater ventilation in summer (15). In the field vole (Microtus agrestis), seasonal fur growth and hair replacement result in a sparse summer pelage, composed mostly of coarse guard hairs that aid air circulation, and a dense fine-haired winter pelage, with greater numbers of underhairs that trap air and increase insulation (15, 18). The more dense winter coat is achieved by an increase in the number of hairs per hair follicle and in the number of active follicles, resulting in more hairs per unit area of skin (18).

Siberian hamsters (Phodopus sungorus) housed in short “winter-like” day lengths [short days (SDs)] grow a more insulative fur coat (12, 16), yet the pelage changes that afford these thermoregulatory savings in this species are not known. Investigation of pelage characteristics in Siberian hamsters has been largely restricted to changes in fur color: transfer of Siberian hamsters to SDs induces a molt from the summer agouti pelage to a white winter coat. Some added insulation is likely achieved by a lengthening of hairs on the dorsal surface of SD-housed Siberian hamsters (12, 20); the lengths of abdominal hairs appear to be unchanged (20). No differences were detected in dorsal hair density (number of hairs per hair funnel) and a decrease was noted in ventral hair density of SD-exposed males compared with long-day (LD)-exposed males (20). Figala et al. (8), however, noted an increase in ventral pelage density in SD hamsters but did not provide a quantitative measure. The absence of changes in the number of hairs per hair funnel in SD males (20) does not preclude changes in the length/thickness of the hairs, spacing between hair follicles, number of hair follicles, and proportion of hair types, each of which can alter fur mass per unit area of skin (fur density); the latter likely constitutes a more functional measure of pelage density than the number of hairs per hair funnel (hair density). Molting patches are present on the skin of LD and SD hamsters, suggesting that Siberian hamsters undergo a continuous, rather than a seasonal, molt (20). Thus the process by which Siberian hamsters transition between the summer and winter pelage is not clear and appears to be different from that of most species investigated. To our knowledge, seasonal pelage changes of Syrian hamsters (Mesocricetus auratus) have not been investigated.

Winter adaptations of Siberian and Syrian hamsters are triggered by the decreasing day lengths of late summer and autumn; the return to the spring phenotype is governed by an endogenous process with interval-timing properties (for review see Refs. 9, 30, 31); prolonged exposure to SDs results in a spontaneous reversion to the spring phenotype attributed to the development of neuroendocrine refractoriness to SD melatonin signals (9).

Photoperiodic control of seasonal fur changes is mediated by the same pineal-melatonin mechanism implicated in other seasonal traits (7). Decreasing day lengths of late summer are mirrored by increasing durations of nocturnal melatonin secretion, which trigger the SD phenotype (for review see Ref. 31). Photoperiodic changes in melatonin alter prolactin secretion, which influences coat color in Siberian hamsters (6) as well as seasonal changes in fur depth, fur density, and guard hair length in meadow voles (Microtus pennsylvanicus) (33). The control of the seasonal pelage has not been fully characterized for any mammal and likely involves complex interactions of several hormones.

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Steroid hormones influence the hair growth cycle. Castration increases and testosterone (T) administration decreases the rate at which developmental molting waves spread over the dorsal surface of the male rat (*Rattus norvegicus*) (14). T administration significantly slows the rate of fur regrowth around the flank organ of Syrian hamsters (26). The principal effect of androgens may be interference with initiation of the anagen phase and prolongation of the telogen phase of the hair cycle (22, 36). These data raise the possibility that photoperiod-induced changes in circulating T concentrations proximately influence the seasonal transitions of some pelage characteristics. In this view, SD-induced decreases in circulating T trigger or facilitate the molt to the winter pelage. In support of this conjecture, castration of field voles increases the rate of the spring molt, advances the onset of the autumnal molt, and leads to the development of a winter-like coat, with increased hair density, whether the voles are housed in LDs or SDs (17). The onset of the annual molt in European badgers (*Meles meles*) is also advanced by castration (23). Castration did not induce a molt to the white winter coat in LD-housed Siberian hamsters, but maintenance of LD-like T concentrations in hamsters transferred to SDs delayed and attenuated the SD-induced change in coat color; other pelage characteristics were not measured (5).

The present experiments investigated the effects of photoperiod on pelage characteristics of Siberian and Syrian hamsters and the role of T as a mediator of these changes in Syrian hamsters. We determined whether fur density (fur mass per area) of Siberian hamsters is affected by ambient photoperiod and whether prolonged exposure to SDs would result in a spontaneous reversion to the LD fur density phenotype. We also tested whether molting in Siberian hamsters is a continuous process that proceeds at the same rate in LD and SD hamsters. A second experiment assessed the contribution of changes in sebaceous secretion to the photoperiodic differences in fur mass. Finally, two experiments determined whether SDs alter fur density, fur regrowth, and hair lengths of Syrian hamsters and whether photoperiodic changes in circulating T contribute to these morphological changes.

**MATERIALS AND METHODS**

**Animals and Housing Conditions**

Siberian hamsters were obtained from our breeding colony, which was derived from animals originally provided by Katherine Wynee-Edwards (Queen’s University). The breeding colony was maintained on a 14:10-h light-dark cycle (14L; dark onset at 1800 PST). Syrian hamsters (*HsdHan: AURA*) were purchased from Harlan (Indianapolis, IN) and maintained on a similar 14L photoperiod (dark onset at 1600 PST). Hamsters were housed at 22 ± 2°C in polypropylene cages (1–3 Siberian hamsters per 24 × 14 × 12 cm cage and 1–2 Syrian hamsters per 48 × 25 × 21 cm cage) furnished with Tek-Fresh laboratory animal bedding (Harlan Teklad, Madison, WI). Hamsters were fitted with ear tags for individual identification, and those that were killed were separated into individual cages. Tap water and Purina rodent chow 5015 and Lab Diet Prolab SP00 were available ad libitum for all Siberian and Syrian hamsters, respectively.

For confirmation of adult reproductive status, the length and width of the testis were measured externally under light isoflurane anesthesia. Testis width squared times testis length is highly correlated with testis weight and can be used as a measure of estimated testis volume (ETV, in mm³) (11). Only Siberian hamsters with an initial ETV >400 mm³ and Syrian hamsters with an initial ETV of 3,000 mm³ were considered to have achieved adult LD reproductive status; any hamster with an initial ETV less than their species-specified cutoff was not included in the study. ETV of Siberian hamsters was measured again after SD transfer to confirm photoperiodic responsiveness. Animals that did not exhibit the typical gonadal response to photoperiod (ETV >200 mm³, n = 21 of 152) were excluded from all analyses.

All animal procedures were approved by the Animal Care and Use Committee at the University of California, Berkeley.

**Castrations and Capsule Implantations**

Syrian hamsters were deeply anesthetized with isoflurane vapors. An incision was made lateral to the midline of the abdomen, and the testes were exteriorized. The testicular veins were ligated, the testes and epididymides were removed, and the extraneous tissue was returned to the body cavity. The incision was closed with sterile surgical sutures and wound clips. Next, an incision was made on the middorsal surface just posterior to the head of the hamster. Two 15-mm blank or T-filled Silastic capsules were inserted subcutaneously above or below the area to be shaved to minimize local effects of T on fur growth, and the incision was closed with wound clips. Capsules were sterilized overnight in benzol solution and then rinsed with sterile saline before implantation. Castrated hamsters were treated with 0.2 ml of the analgesic buprenorphine (0.015 mg/ml sc).

**Blood Sampling**

Hamsters were anesthetized with isoflurane vapors; ~0.6 ml of blood was withdrawn from the retroorital plexus into 1.5-ml microfuge tubes kept on ice in nonheparinized microhematocrit capillary tubes (VWR, West Chester, PA). After ~1 h, samples were centrifuged at 3,500 rpm for 15 min. The supernatant was transferred to a clean microfuge tube and stored at −80°C.

**Radioimmunoassay**

Serum T concentrations were determined in a single assay using a solid-phase 125I radioimmunoassay kit (Diagnostic Systems Laboratories, Webster, TX), which was previously validated in our laboratory (28, 29). Samples were divided into duplicate 50-μl aliquots and incubated with tracer for 1 h at 37°C. Cross-reaction of the antibody with 5α-dihydrotestosterone and the lower limit of hormone detection for this kit were 5.8% and 0.08 ng/ml, respectively, as reported by the manufacturer. Eight replicate samples of LD-pooled serum yielded an intra-assay coefficient of variation of 3.9%.

**Pelage Color**

For Siberian hamsters, pelage color was rated using the scale described by Duncan and Goldman (5), with conversion of their four-point scale into a seven-point scale by addition of half units (2).

**Fur-Shaving Procedures**

Hamsters were anesthetized with isoflurane vapors, and patches of the fur were shaved with an electric razor on the dorsal and ventral surfaces (~2 × 2 cm patch in experiments 1 and 2, 2 × 3 cm patch in experiment 3, and 3 × 3 cm patch in experiment 4). The hairs were gathered and weighed on a Sartorius R200D balance (±0.02 mg). To correct for interindividual variations in patch size, the length and width of the shaved patch were measured to the nearest 0.1 mm with calipers, and the area derived from the product of these measures was used to determine fur density (mg fur/cm²) and fur regrowth (mg fur-cm⁻²·3 wk⁻¹).

In most cases, each patch was shaved twice: an initial shave provided a measure of fur density, and a re-shave of the same area 3 wk later yielded the amount of fur regrowth. To reduce the number of animals needed, most hamsters contributed to two initial shave time points; i.e., two separate patches were shaved on the dorsal and ventral
surfaces, one on each side of the midline, with the side of initial shaving randomized. The small body size of Siberian hamsters restricted ventral shaving to only one location along the midline.

**Experimental Design**

**Siberian hamsters.** In experiment 1, 2- to 6-mo-old male hamsters were randomly assigned to five groups and transferred to 10L (dark onset at 1800 PST; SD; n = 82) or maintained in 14L (n = 70). Initial dorsal patches were shaved 7, 10, 11, 14, 15, 18, 27, 30, and 49 wk after photoperiod transfer. Many of these patches were resheared 3 wk later, providing regrowth time points at 10, 14, 18, 30, 33, and 52 wk. Initial ventral patches were shaved at 7, 11, 15, 27, and 49 wk and resheared 3 wk later at 10, 14, 18, 30, and 52 wk. Body mass and pelage color ratings were recorded at each time point. Because individual hamsters within each group could accommodate only two initial shaves, some shave points contain data from the same hamsters, whereas other shave points contain data from completely separate groups of hamsters. After exclusion of nonphotoresponsive hamsters, sample sizes for LD and SD groups at each time point ranged from 11 to 16.

In experiment 2, seven 3- to 5-mo-old male hamsters were transferred to 10L and eight remained in 14L. After 11 wk, hamsters were euthanized by CO₂ inhalation, and a 4-cm² patch of fur was shaved on the lateral dorsal surface. Hamsters were then washed in 95% ethanol for removal of sebaceous secretions, dried under a heat gun, and shaved again on the contralateral dorsal surface. Shavings were weighed as described above for comparison of measures of fur density of LD and SD groups before and after washing.

**Syrian hamsters.** In experiment 3, forty 2- to 4-mo-old male hamsters were castrated and twenty were left intact. Castrated animals received two 15-mm T-filled capsules (T1500, Sigma, St. Louis, MO) or two 15-mm empty capsules (Silastic tubing, Dow Corning, Midland, MI; 1.98 mm ID, 3.18 mm OD). At 1–3 days after surgery, half of the hamsters from each group were transferred to 10L (dark onset at 1600 PST); the remaining animals were maintained in the original 14L photoperiod. The resulting groups, each containing 10 hamsters, were as follows: LD intact animals (LDi), LD castrated animals with blank capsules (LDx), LD castrated animals with T capsules (LDt), and the analogous SD groups (SDi, SDx, and SDt). Hamsters were initially shaved 2 and 8 wk after photoperiod transfer, and these patches were resheared at 5 and 11 wk, respectively. Each hamster was shaved at all time points.

Capsules that were extruded during the study were replaced with fresh capsules. Inspection of the hamsters at least every 3 days limited the duration any hamster lacked a capsule. Nonetheless, only LDi and SDt hamsters with blood T concentrations ≥2.14 ng/ml (the lowest value obtained from LDi hamsters) were included in the analyses. Four LDi and five SDt animals were excluded; final sample sizes for these groups were six and five, respectively.

In experiment 4, nine 4- to 5-mo-old male hamsters were transferred to 8L and eight animals remained in 14L (dark onset at 1600 PST for both photoperiods). At 8 wk after photoperiod transfer, dorsal fur density was recorded from a 9-cm² patch of fur. At 10 wk, small hair samples on the dorsal and ventral surfaces were removed by clipping the base of the hairs, just above the skin, with surgical scissors. Hair clippings were placed in a petri dish containing a thin layer of 100% peanut oil. The lengths of two to three guard hairs and five underhairs, selected at random, were measured under a dissecting microscope with use of a metric ruler and averaged to provide mean guard hair and underhair lengths for each hamster. Three dorsal hair samples and one ventral hair sample contained only a single guard hair and were excluded from analyses. Hamsters in this experiment were controls for an unpublished study. In addition to the procedures outlined above, these hamsters had been deeply anesthetized (73.2 mg of ketamine, 7.2 mg of xylazine, and 1.2 mg of acepromazine per kg body mass) 4 wk before photoperiod transfer and subjected to sham lesions just dorsal to the dorsomedial hypothalamus, in which no current was passed. Buprenorphine (0.2 ml of 0.015 mg/ml) was administered after sham-lesion surgery.

**Statistical Analyses**

All LD and SD comparisons, except pelage color, in experiments 1, 2, and 4 were made using two-tailed Student’s t-tests (Statview 5.0, Abacaus Concepts, Berkeley, CA). Photoperiodic differences in pelage color were analyzed using the Mann-Whitney U test. Effects of photoperiod and T treatment on fur density and fur regrowth in Syrian hamsters in experiment 3 were assessed using ANOVA; when the overall ANOVA was significant, planned comparisons were made using Fisher’s protected least significant difference test. Differences were considered significant if P < 0.05 and are reported as such, regardless of actual P values below this threshold.

**RESULTS**

**Siberian Hamsters**

**Fur density.** SD treatment resulted in significant increases in dorsal (Fig. 1A) and ventral (Fig. 1B) fur densities compared with values for LD hamsters. This effect was first observed at 11 wk and persisted through 27 wk of SD treatment but was not evident at 30 or 49 wk. The significantly increased dorsal fur density of SD hamsters 11 wk after photoperiod transfer remained after the fur was washed with ethanol (experiment 2; data not shown).

**Fur regrowth.** Fur regrowth on the dorsal surface of SD hamsters exceeded that of their LD counterparts at 11–14 wk (Fig. 2A) and on the ventral surface at 7–10 and 11–14 wk (Fig. 2B). No photoperiodic differences were observed in the weight of regrown fur at any other time point.

**Body mass and pelage color.** SD hamsters weighed significantly less than LD hamsters at the first time point measured (7 wk); this effect persisted until 30 wk (not illustrated). At all later time points (33–52 wk), this difference was no longer significant. Pelage color ratings were significantly higher (indicating a whiter fur coat) in SD than in LD hamsters from 10 through 33 wk (not illustrated). This difference was no longer significant at 49 and 52 wk.

**Syrian Hamsters**

**T concentrations.** As expected, circulating T concentrations were significantly higher in LDi than in SDi males (2.6 ± 0.1 ng/ml) in experiment 4 (Fig. 3). The small body size of these hamsters limited the duration any hamster lacked a capsule. Nonetheless, only LDi and SDt hamsters with blood T concentrations ≥2.14 ng/ml were included in the analyses. Four LDi and five SDt animals were excluded; final sample sizes for these groups were six and five, respectively.

![Fig. 1. Dorsal (A) and ventral (B) fur density (mg fur/cm² skin) of Siberian hamsters maintained on a long-day (LD) regimen or transferred to a short-day (SD) regimen at week 0. Values are means ± SE. *Significantly different from LD.](http://ajpregu.physiology.org/)

*Fig. 1.* Dorsal (A) and ventral (B) fur density (mg fur/cm² skin) of Siberian hamsters maintained on a long-day (LD) regimen or transferred to a short-day (SD) regimen at week 0. Values are means ± SE. *Significantly different from LD.
vs. 0.23 ± 0.07 (SE) ng/ml); T concentrations were undetectable for all castrated animals in both photoperiods. Mean blood T concentrations were significantly higher in LDt and SDt than in LDi hamsters (8.6 ± 3.7 and 13.5 ± 4.6 ng/ml for LDt and SDt hamsters, respectively) and did not differ significantly from each other.

**Fur density.** Dorsal fur density was significantly greater in SDi than in LDi hamsters after 8 wk of SD treatment (Fig. 3B); no differences were detected at 2 wk of treatment (Fig. 3A). Castration did not affect dorsal fur density in LD or SD hamsters and did not prevent development of photoperiodic differences in dorsal fur density at 8 wk. Nevertheless, T treatment decreased dorsal fur density in both photoperiods to values below those of their respective intact control groups at 8 wk (Fig. 3B) and prevented the development of photoperiodic differences in this measure. Ventral fur density did not differ between LDi and SDi hamsters at either time point, and there were no effects of castration or T treatment (Fig. 3, C and D).

**Fur regrowth.** SDi hamsters regrew more dorsal fur than did LDi hamsters at 2–5 and 8–11 wk (Fig. 4, A and B); this effect was evident on the ventral surface only at 8–11 wk (Fig. 4D). Castration increased and T treatment decreased the rate of dorsal (Fig. 4A) and ventral (Fig. 4C) fur regrowth from 2 to 5 wk in LD and SD hamsters; both manipulations prevented the development of photoperiodic differences in dorsal fur regrowth at this time point. The effects of castration and T administration on fur regrowth waned by 8–11 wk. Dorsal (Fig. 4B) and ventral (Fig. 4D) fur regrowth did not differ between LDi, LDx, and LDt groups at this time. Dorsal fur regrowth did not differ significantly between SDi, SDx, and SDt groups (Fig. 4B). Ventral fur regrowth of SDx and SDt hamsters was significantly lower than that of SDi animals, which appeared to reflect an elevated rate of fur regrowth in the latter group (Fig. 4D). Photoperiodic effects on fur regrowth of T-treated animals emerged at 8–11 wk, but differences between LDx and SDX animals fell just short of statistical significance (P = 0.05 and P = 0.06 for LDx vs. SDX comparisons of dorsal and ventral fur regrowth, respectively).

**Hair lengths.** Guard hairs and underhairs from the dorsal and ventral fur of SD hamsters were longer than those of LD-housed controls 10 wk after photoperiod transfer (experiment 4; Table 1); for dorsal guard hairs, however, this difference fell short of statistical significance (P = 0.06). These animals also exhibited the SD-induced increase in dorsal fur density (not illustrated).

**DISCUSSION**

**Siberian Hamsters**

SDs trigger a transition to a thicker pelage as measured by the weight of fur shavings per area of skin, referred to here as fur density. Fur density increased on dorsal and ventral sur-

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<td>SD</td>
<td>1.29 ± 0.03</td>
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Values are means ± SE in cm. LD, long day; SD, short day. *Significantly different from LD (P < 0.05).

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Fig. 2. Dorsal (A) and ventral (B) fur regrowth (mg regrown fur/cm² skin) of Siberian hamsters maintained on an LD regimen or transferred to an SD regimen at week 0. Values are means ± SE. *Significantly different from LD within each hormone condition. †Significantly different from respective LD or SD intact control.

Fig. 3. Dorsal (A and B) and ventral (C and D) fur density of intact, castrated, and castrated + T-treated (T capsule) Syrian hamsters maintained on an LD regimen or transferred to an SD regimen at week 0. Values are means ± SE. *Significantly different from LD within each hormone condition. †Significantly different from respective LD or SD intact control.

Fig. 4. Dorsal (A and B) and ventral (C and D) fur regrowth of intact, castrated, and castrated + T-treated (T capsule) Syrian hamsters maintained on an LD regimen or transferred to an SD regimen at week 0. Values are means ± SE. *Significantly different from LD and SD hamsters within each hormone condition. †Significantly different from respective LD or SD intact control.
faces beginning at 11 wk and persisting through 27 wk of SD treatment (Fig. 1). These findings provide quantitative support for the observations of Figala et al. (8) and contrast with the results of Kuhlmann et al. (20), who reported no difference in hair density between SD and LD Syrian hamsters. That the number of hairs per hair follicle does not increase in SDs (20), does not preclude an increase in fur mass per area. Increases in hair lengths, hair widths, or number of active hair follicles or decreases in the spacing between follicles can affect fur density. Photoperiodic differences in fur density persisted after a postmortem ethanol wash designed to remove sebaceous secretions, suggesting that the increased fur weight in SDs is not attributable to greater amounts of nonfur substances. Increased fur density likely contributes to the more insulative fur coat characteristic of SD Syrian hamsters (12, 16).

After prolonged maintenance in SDs, hamster fur density reverted to the lower LD values; the time course of this transition was similar to that of other photoperiodic traits of this species (body mass and pelage color). Although the difference in pelage color ratings persisted through 33 wk, the magnitude of this difference progressively decreased from 18 to 33 wk; the transition to the LD phenotype was initiated between 18 and 27 wk. The return to the LD fur density after prolonged SD treatment appears to be triggered by an endogenous mechanism with interval-timing properties and, thus, is a type 1 seasonal rhythm (37).

LD and SD hamsters exhibit molting patches (20) and regrow fur after shaving (Fig. 2); fur growth in this species is a continuous process. Our data, however, indicate that the rate of fur regrowth is increased in SDs. The timing of increased fur regrowth, immediately before (ventral fur) or concomitantly with (dorsal fur) the appearance of increased fur density, suggests that this process aids in the transition to the winter fur coat. This effect is transient, and resumption of the LD fur regrowth rate occurs many weeks before the recrudescence of other LD traits. Therefore, the reversion to LD fur regrowth is unlikely to be regulated by a loss of responsiveness to SDs or to melatonin. Rather, the SD effect on fur regrowth is reminiscent of the transient increase in fur regrowth of castrated Syrian hamsters, suggesting that it is a consequence of decreased androgen secretion associated with testicular regression (see below).

We did not detect changes in fur regrowth rates as hamsters molted back to the LD pelage. This molt may be achieved by normal hair replenishment coupled with increased hair shedding. The Syrian hamster data suggest that the rate of fur regrowth should increase during the molt to the winter pelage when T concentrations are decreasing, but not during the molt to the summer pelage when circulating T is increasing. Nonetheless, it remains possible that differences in fur regrowth were not detected because of lack of interindividual synchrony in the development of photoperiodic influences on pelage characteristics in Syrian hamsters. The photoperiodic molt in this species has likely gone unnoticed, because it is not accompanied by the prominent changes in fur color seen in other species.

The decrease in circulating T appears to be a permissive factor for increased dorsal fur density in SDs. Although castration did not trigger increases in dorsal fur density or prevent the development of photoperiodic differences, treatment of SD hamsters with T capsules blocked the photoperiod-induced increase in dorsal fur density and even led to a significant decrease in hamsters housed in LDs, possibly due to supra-physiological T concentrations.

Ventral fur density, on the other hand, was not altered by castration or T administration, demonstrating the site specificity of these T effects. Insensitivity of ventral fur density to changes in T may account, in part, for the finding that ventral fur density does not decrease in SDs. Differential responsiveness to T has also been reported for fur regrowth within vs. other LD traits. Therefore, the reversion to LD fur density after prolonged SD treatment did not trigger increases in dorsal fur density or prevent the development of photoperiodic differences. Treatment of SD hamsters with T capsules blocked the photoperiod-induced increase in dorsal fur density and even led to a significant decrease in hamsters housed in LDs, possibly due to supra-physiological T concentrations.

Syrian Hamsters

As in Siberian hamsters, photoperiod altered fur density, fur regrowth, and hair lengths. Dorsal fur density was significantly greater in LD than in LD hamsters by 8 wk of SD treatment. This was accompanied by increased dorsal fur regrowth rates at 2–5 and 8–11 wk. In contrast, SDs did not affect ventral fur density in this experiment; ventral fur regrowth was not increased until 8–11 wk, raising the possibility of increased ventral fur density in SD hamsters at later time points. Alternatively, ventral fur may be unresponsive to the photoperiodic signals that trigger increased fur density in SDs. At 10 wk after SD transfer, lengths of guard hairs and underhairs from the dorsal and ventral surfaces were increased, although the increase in dorsal guard hairs failed to reach statistical significance. To our knowledge, these are the first demonstrations of photoperiodic influences on pelage characteristics in Syrian hamsters. The photoperiodic molt in this species has likely gone unnoticed, because it is not accompanied by the prominent changes in fur color seen in other species.

While the decrease in circulating T appears to be a permissive factor for increased dorsal fur density in SDs, the SD effect on fur regrowth is not a simple response to altered prolactin secretion but, rather, is regulated by at least one, and likely several, other hormone(s). Uncovering the precise individual roles and inter-
actions between prolactin, T, and other hormones in regulating the seasonal molt remains a challenge for future investigations.

Whether these effects are exerted on androgen receptors or estrogen receptors after aromatization is unknown. A topical estradiol antagonist stimulates, whereas topical 17β-estradiol treatment retards, hair growth in several strains of laboratory mice (27, 34). Furthermore, estradiol inhibited hair growth at the site of application on the ventral surface of mice but did not influence untreated areas (dorsal hair growth) (3). These findings are consistent with local actions of steroids (35). Recently, it was proposed that the hair follicle is an important melatonin target tissue and prominent source of extrapineal melatonin in humans and laboratory mice and that melatonin indirectly affects hair growth by desensitizing hair follicles to estrogen receptor ligands (19). If confirmed by others, these results raise the possibility that increased duration of melatonin secretion in SDs may act directly on hair follicles to promote growth in seasonal species.

The present experiment leaves open the questions of whether photoperiod influences pelage characteristics in female hamsters and, if so, which hormones are involved. Given that the pelage of female Siberian hamsters affords greater energy savings under SDs than LDs (16), we predict a seasonal molt to a thicker winter fur coat, as observed in males. Ovariecrase and estradiol antagonists accelerate, and systemic estradiol administration suppresses, hair growth in female laboratory rats and mice (14, 27, 34). The effects of decreased circulating T on seasonal molting in male hamsters may be paralleled by decreased circulating estradiol in SD-exposed female hamsters, facilitating the winter molt.

Perspectives and Significance

Siberian and Syrian hamsters utilize changes in day length to vary several pelage characteristics in a manner that facilitates proper thermoregulation in summer and winter: winter-like day lengths increase fur density, fur regrowth, and hair lengths. The return to the less dense LD fur coat in Siberian hamsters maintained under SDs for many months is determined by an endogenous interval-timing mechanism. Although the role of prolactin in seasonal molting has been emphasized for several species, the complete suite of seasonal pelage changes is undoubtedly controlled by a complex process involving several hormones (e.g., prolactin, adrenal, gonadal, and thyroid hormones) (6, 17, 21, 23, 32, 33); a complete understanding of the neuroendocrine regulation of the seasonal pelage will require the investigation of multiple pelage characteristics in addition to color. The present findings extend the limited literature on the role of T in seasonal molting: in Syrian hamsters, decreased circulating T concentrations that accompany testicular regression in SDs are associated with increased fur regrowth and permit the molt to a more dense fur coat. These photoperiodic changes in the hamster pelage likely aid in overcoming survival by increasing the insulative capacity of the fur coat at a time when energetic challenges are greatest (12, 16).

GRANTS

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