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

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Running head: Photoperiod, testosterone, and hamster pelage

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ABSTRACT

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 re-shaved 3 weeks later to assess fur regrowth (mg re-grown fur/cm² skin). Fur density was greater in SD than LD Siberian hamsters after 11 weeks of differential phototreatment. The onset of increased fur density in SDs was accompanied by a transient increase in fur regrowth (dorsal surface: weeks 11-14; ventral surface: weeks 7-10 and 11-14), 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 SD treatment (>27 weeks) 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 all greater in SD than LD males. Castration increased and testosterone (T) treatment decreased both dorsal and ventral fur regrowth in LD and SD hamsters, but the effects of T manipulations on fur density were limited to decreased 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.

Keywords: pelage, Siberian hamster, Syrian hamster, photoperiodism, testosterone
INTRODUCTION

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 results 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 both the number of hairs per hair follicle and 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 (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 compared to long day (LD) males (20). Figala et al. (8), however, noted the appearance of increased 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, the number of hair follicles, and the 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 both LD and SD hamsters, suggesting that Siberian hamsters undergo a continuous rather than 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 than 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 (reviewed in 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 for 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 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.

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 treatment 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 proximally influence the seasonal transitions of some pelage characteristics. In this view, SD-induced decreases in circulating T either 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, regardless of 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-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 for 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 the underlying morphological changes.

**MATERIALS AND METHODS**

*Animals and housing conditions*

Siberian hamsters were obtained from our breeding colony that was derived from animals originally provided by Katherine Wynne-Edwards (Queen’s University). The breeding colony was maintained on a light-dark cycle of 14 h of light/day (14L; dark onset at 1800h PST). Syrian hamsters (*HsdHan:AURA*) were purchased from Harlan (Indianapolis, IN) and maintained on a similar 14L photoperiod (dark onset at 1600h PST). Hamsters were housed at 22±2°C in polypropylene cages (Siberian hamsters: 25×14×12cm, 1-3 per cage; Syrian hamsters: 48×25×21cm, 1-2 per cage) furnished with Tek-Fresh Lab Animal Bedding (Harlan Teklad, Madison, WI). Hamsters were fitted with ear tags for individual identification, and those that fought were separated into individual cages. Tap water and Purina rodent chow 5015 and Lab Diet Prolab 5P00 were available *ad libitum* for all Siberian and Syrian hamsters, respectively.
Adult reproductive status was confirmed in all animals by measuring the length and width of the testis externally under light isoflurane anesthesia. The product of testis width squared times the length is highly correlated with testis weight and can be used as a measure of estimated testis volume (ETV in mm$^3$; 11). Only hamsters with an initial ETV greater than 400mm$^3$ for Siberian hamsters or 3000mm$^3$ for Syrian hamsters were considered to have achieved adult LD reproductive status; any hamster with an initial ETV less than their species-specified cut-off was not included in the study. ETV measures of Siberian hamsters were recorded again after SD transfer to confirm photoperiodic responsiveness. Animals that did not exhibit the typical gonadal response to photoperiod (ETV > 200mm$^3$; 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 externalized. The testicular veins were ligated, the testes and epididymis 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 mid-dorsal surface just posterior to the head of the hamster. Two 15mm blank or T-filled Silastic capsules were inserted sc above or below the area to be shaved to minimize local effects of T on fur growth, and the incision closed with wound clips. Capsules were sterilized overnight in Benzal solution and then rinsed with sterile saline prior to implantation. Castrated hamsters were treated with the analgesic Buprenorphine (0.2ml of 0.015mg/ml, sc).
Blood sampling

Hamsters were anesthetized with isoflurane vapors; ~ 0.6ml of blood was withdrawn from the retro-orbital plexus into 1.5ml microfuge tubes kept on ice using non-heparinized micro-hematocrit capillary tubes (VWR, West Chester, PA). After ~1 h, samples were centrifuged at 3500 rpm for 15 minutes. The supernatant was transferred to a clean microfuge tube and stored at –80°C until assayed.

Radioimmunoassay

Serum T concentrations were determined in a single assay using a solid-phase $^{125}$I radioimmunoassay kit (Diagnostic Systems Laboratories, Webster, TX), previously validated in our laboratory (28, 29). Samples were divided into duplicate 50µl 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 0.08ng/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 4 point scale into a 7 point scale by adding 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 (patch size ~ 2×2cm in exps. 1 and 2, 2×3cm in exp. 3, and 3×3cm in exp. 4). The hairs were gathered and weighed on a Sartorius R200D balance (±0.02mg). To correct for inter-individual
variations in patch size, the length and width of the shaved patch were measured to the nearest 0.1mm 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/cm²/3 weeks).

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 weeks later recorded the amount of fur regrowth. To minimize the number of animals needed, most hamsters contributed to 2 initial shave time points by having 2 separate patches shaved on the dorsal and ventral surfaces, one on each side of the midline; the side of initial shaving was randomized. The small body size of Siberian hamsters restricted ventral shaving to only one location along the midline.

Experimental design

Siberian hamsters

Experiment 1: Male hamsters aged 2-6 months were randomly assigned to 5 groups and either transferred to 10L (dark onset at 1800 PST; SD; n=82) or maintained in 14L (n=70). Initial dorsal patches were shaved at weeks 7, 10, 11, 14, 15, 18, 27, 30, and 49 after photoperiod transfer. Many of these patches were re-shaved 3 weeks later, providing re-growth time points at weeks 10, 14, 18, 30, 33, and 52. Initial ventral patches were shaved at weeks 7, 11, 15, 27, and 49 and then re-shaved 3 weeks later at weeks 10, 14, 18, 30, and 52. Body mass and pelage color ratings were recorded at each shave. Because individual hamsters within each group could accommodate only 2 initial shaves, some shave points contain data from the same hamsters while other shave points come from completely separate groups of hamsters. After exclusion of photo-
nonresponsive hamsters, sample sizes for LD and SD groups at each time point ranged from 11 to 16.

Experiment 2: Seven male hamsters aged 3-5 months were transferred to 10L and 8 remained in 14L. Eleven weeks later hamsters were euthanized by CO₂ inhalation and a 4cm² patch of fur was shaved on the lateral dorsal surface. Hamsters were then washed in 95% ethanol to remove sebaceous secretions, dried under a heat gun, and shaved again on the contralateral dorsal surface. Shavings were weighed as described above to compare measures of fur density of LD and SD groups before and after washing.

Syrian hamsters

Experiment 3: Forty male hamsters aged 2-4 months were castrated and 20 were left unoperated. Castrates either received two 15mm T-filled (T1500, Sigma, St. Louis, MO) or two 15mm empty capsules (Silastic tubing, Dow Corning, Midland, MI; i.d. 1.98mm, o.d. 3.18mm). One to three 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: LD intacts (LDi), LD castrates with blank capsules (LDx), LD castrates with T capsules (LDt), and the analogous SD groups (SDi, SDx, and SDt). Hamsters were initially shaved at 2 and 8 weeks after photoperiod transfer, and these patches were re-shaved at weeks 5 and 11, respectively. Each hamster was shaved at all time points. Capsules that were extruded during the study were replaced with fresh ones. Hamsters were inspected at least every 3 days, which limited the duration any hamster lacked a capsule. Nonetheless, only LDt and SDt hamsters with blood T concentrations greater than or equal to 2.14 ng/ml (the lowest value obtained from LD intact hamsters)
were included in the analyses. Four LDt and 5 SDt animals were excluded; final sample sizes for these groups were 6 and 5, respectively.

Experiment 4: Nine male hamsters aged 4-5 months were transferred to 8L and 8 remained in 14L (dark onset at 1600 PST for both photoperiods). Eight weeks after photoperiod transfer, dorsal fur density was recorded from a 9cm² patch of fur. Two weeks later, 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 2-3 guard hairs and 5 underhairs, selected at random, were measured under a dissecting microscope using a metric ruler and averaged to provide mean guard hair and underhair lengths for each hamster. Three dorsal hair samples and 1 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 (73.2mg ketamine, 7.2mg xylazine, and 1.2mg acepromazine per kg body mass) 4 weeks before photoperiod transfer and received sham lesions just dorsal to the dorsomedial hypothalamus in which no current was passed. Buprenorphine (0.2ml of 0.015mg/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; Abacus 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 PLSD. 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 both dorsal (Fig. 1A) and ventral (Fig. 1B) fur densities compared to values for LD hamsters. This effect was first observed at week 11 and persisted through the 27th week of SD treatment, but was not evident at weeks 30 or 49. The significantly increased dorsal fur density of SD hamsters 11 weeks after photoperiod transfer was still present after washing the fur with ethanol (exp. 2, data not shown).

Fur Regrowth

Fur regrowth on the dorsal surface of SD hamsters exceeded that of their LD counterparts at weeks 11-14 (Fig. 2A) and on the ventral surface at weeks 7-10 and 11-14 (Fig. 2B). No photoperiodic differences were observed in the weight of re-grown 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 (week 7); this effect persisted until week 30 (not illustrated). At all later time points (wk 33 – 52), this difference was no longer significant. Pelage color ratings were
significantly higher (indicating a whiter fur coat) in SD versus LD hamsters from weeks 10 through 33 (not illustrated). This difference was no longer significant at weeks 49 and 52.

**Syrian hamsters**

*Testosterone concentrations*

As expected, LDi hamsters had significantly higher circulating T concentrations than did SDi males (mean ± s.e. [T] = 2.6 ± 0.1 and 0.23 ± 0.07 ng/ml for LDi and SDi hamsters, respectively); T concentrations were undetectable for all castrates in both photoperiods. Mean blood T concentrations of LDt and SDt hamsters were significantly higher than those of LDi hamsters (mean ± s.e. [T] = 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 of SDi hamsters was significantly greater than that of LDi hamsters after 8 weeks of SD treatment (Fig. 3B); no differences were detected at week 2 (Fig. 3A). Castration did not affect dorsal fur density in either LD or SD hamsters and did not prevent development of photoperiodic differences in dorsal fur density at week 8. Nevertheless, T treatment decreased dorsal fur density in both photoperiods to values below those of their respective intact control groups at week 8 (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. 3C and D).
**Fur Regrowth**

SDi hamsters re-grew more dorsal fur than did LDi hamsters during weeks 2-5 and weeks 8-11 (Fig. 4A and B); this effect was evident on the ventral surface only during weeks 8-11 (Fig. 4D). Castration increased and T treatment decreased the rate of both dorsal (Fig. 4A) and ventral (Fig. 4C) fur regrowth from weeks 2-5 in both 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 weeks 8-11. In LDs, dorsal (Fig. 4B) and ventral (Fig. 4D) fur regrowth did not differ between LDi, LDx, and LDt groups at this time. In SDs, 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 SDi controls (Fig. 4D). Photoperiodic effects on fur regrowth of T-treated animals emerged at weeks 8-11, but differences between LD and SD castrates fell just short of statistical significance (p = 0.05 and 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 weeks after photoperiod transfer (exp. 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 the dorsal fur density (not illustrated).
DISCUSSION

Siberian hamsters

Short day lengths 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 both dorsal and ventral surfaces beginning at week 11 and persisting through the 27th week of SD treatment (Fig 1). These findings provide quantitative support for the observations of Figala et al. (8) and contrast with results of Kuhlmann et al. (20), who reported no difference in hair density between SD and LD Siberian 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, number of active hair follicles, or decreases in the spacing between follicles each 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 non-fur substances. Increased fur density likely contributes to the more insulative fur coat characteristic of SD Siberian 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 week 33, the magnitude of this difference progressively decreased from weeks 18 to 33; the transition to the LD phenotype was initiated between weeks 18 and 27. The return to the LD fur density after prolonged SD treatment appears
to be triggered by an endogenous mechanism with interval timing properties, and is thus a Type 1 seasonal rhythm (37).

Both 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, occurring immediately before (ventral fur), or concomitant 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 due to lack of inter-individual synchrony in the development of photorefractoriness.
Syrian hamsters

As in Siberian hamsters, photoperiod altered fur density, fur regrowth, and hair lengths. SD dorsal fur density was significantly greater than that of LD hamsters by the 8th week of SD treatment. This was accompanied by increased dorsal fur regrowth rates during weeks 2-5 and 8-11. In contrast, SDs did not affect ventral fur density in this experiment; ventral fur regrowth was not increased until weeks 8-11, 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. Ten weeks after SD transfer, lengths of guard hairs and underhairs from both 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.

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 supraphysiological T concentrations.

Ventral fur density, on the other hand, was not altered by castration or T administration, demonstrating site specificity to these T effects. Insensitivity of ventral fur density to changes in T may account, in part, for the absence of decreased ventral fur density.
Differential responsiveness to T has also been reported for fur regrowth within versus around the flank organ of Syrian hamsters (26) and a stimulatory response has been reported for the vibrissae of albino mice (13). Ventral fur regrowth, however, was altered by both T manipulations and in a similar manner to dorsal fur regrowth. Thus, T can differentially affect fur regrowth rate and fur mass per area. Fur density is undoubtedly a complex pelage characteristic determined by multiple factors (e.g., hair length, hair width, hair density, follicle density, fur growth, and shedding).

T manipulations had the greatest effect on fur regrowth and were reminiscent of findings in the laboratory rat (14). T suppressed and castration triggered fur regrowth in hamsters housed in both photoperiods, suggesting that the typical LD T blood concentrations suppress the rate of fur regrowth. Alternatively, decreased T availability may provide a signal to increase fur regrowth. The transient increase in fur regrowth of castrated Syrian hamsters was similar to that of SD Siberian hamsters undergoing gonadal regression, suggesting that decreased circulating androgens facilitate synchronized fur replenishment (molting waves) and the transition to the winter pelage. Transient suppression of fur regrowth by supraphysiological T was also reported by Mezick et al. (26).

Prolactin has recently been shown to inhibit developmental fur growth waves in laboratory mice (*Mus musculus*) by slowing entry of the hair follicle into anagen (4). Castration decreases and androgen replacement increases pituitary prolactin in the laboratory rat (25), raising the possibility that altered fur density and regrowth after castration/T replacement are the indirect result of altered prolactin secretion. In the Syrian hamster, however, neither castration nor T replacement alters circulating prolactin
suggesting that effects of T on fur are prolactin-independent. Thus, the seasonal molt 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 interactions between prolactin, T, and other hormones in regulating the seasonal molt remain challenges for future investigations.

Whether these effects are exerted on androgen receptors or estrogen receptors after aromatization is unknown. A topical estradiol antagonist stimulates hair growth, whereas topical 17-β-estradiol treatment retards hair growth in several strains of laboratory mice (27, 34). Further, E2 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 has been 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 short days 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. Ovariectomy 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 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 overwinter survival by increasing the insulative capacity of the fur coat at a time when energetic challenges are greatest (12, 16).
ACKNOWLEDGEMENTS

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REFERENCES


FIGURE LEGENDS

Figure 1. Mean ± s.e. dorsal (A) and ventral (B) fur density (mg fur/cm² of skin) of Siberian hamsters maintained in a LD or transferred to a SD at week 0. *Significant difference between LD and SD groups.

Figure 2. Mean ± s.e. dorsal (A) and ventral (B) fur regrowth (mg regrown fur/cm² of skin) of Siberian hamsters maintained in a LD or transferred to a SD at week 0. *Significant difference between LD and SD groups.

Figure 3. Mean ± s.e. dorsal (A and B) and ventral (C and D) fur density of intact, castrated, and castrated plus T treated (T capsule) Syrian hamsters maintained in a LD or transferred to a SD at week 0. *Significant difference between LD and SD hamsters within each hormone condition; †significantly different from respective LD or SD intact control groups.

Figure 4. Mean ± s.e. dorsal (A and B) and ventral (C and D) fur regrowth of intact, castrated, and castrated plus T treated (T capsule) Syrian hamsters maintained in a LD or transferred to a SD at week 0. *Significant difference between LD and SD hamsters within each hormone condition. †Significantly different from respective LD or SD intact control groups.
Table 1. Mean (cm) ± s.e. hair lengths of Syrian hamsters housed in LDs or transferred to SDs 10 weeks earlier.

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<td>0.99 ± 0.02*</td>
<td>0.68 ± 0.02*</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Significant differences from LD hamsters (p<0.05).
Figure 1

A

Dorsal Fur Density (mg/cm²)

Week

0  4  8  12  16  18

B

Ventral Fur Density (mg/cm²)

Week

0  1  2  3  4

Legend:

LD  SD

* Indicates significant difference.
Figure 2

A

Fur Weight (mg/cm²)

Dorsal

Ventral

Weeks

0 1 2 3 4 5 6

7-10 11-14 15-18 27-30 30-33 49-52

* *

B

Fur Weight (mg/cm²)

Weeks

LD SD

0 1 1.5 2 2.5

7-10 11-14 15-18 27-30 49-52

* *

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Figure 3

(A) Week 2

(D) Week 8

Ventral Fur Density (mg/cm²)

Dorsal Fur Density (mg/cm²)

Intact Castrated T capsule

Intact Castrated T capsule

Intact Castrated T capsule

Intact Castrated T capsule

* * † †

SD LD

■ LD □ SD
Figure 4

A  Weeks 2-5
  Dorsal Fur Regrowth (mg/cm²)
  Intact Castrated T capsule

B  Weeks 8-11
  Dorsal Fur Regrowth (mg/cm²)
  Intact Castrated T capsule

C  Weeks 2-5
  Ventral Fur Regrowth (mg/cm²)
  Intact Castrated T capsule

D  Weeks 8-11
  Ventral Fur Regrowth (mg/cm²)
  Intact Castrated T capsule

* Significant difference
†† Significant difference

LD  SD