

## Long-term persistence of male copulatory behavior in castrated and photo-inhibited Siberian hamsters

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### Abstract

Gonadal steroids are essential for the long-term maintenance of the full repertoire of sexual behavior in male rodents. Typically, all individuals of several species cease to display the ejaculatory reflex within a few weeks of castration. The present study documents the persistence of the ejaculatory reflex 19 weeks after orchidectomy in 40% of male Siberian hamsters maintained in long or short day lengths; testosterone was undetectable in the circulation of these animals. Intact hamsters transferred from a long to a short photoperiod underwent gonadal regression: 50% of these animals continued to display mating behavior culminating in ejaculation throughout 25 weeks of testing. The remaining animals failed to ejaculate after approximately 11 weeks of short day treatment but resumed mating coincident with spontaneous gonadal recrudescence. Activation of sex behavior in the latter cohort appears to depend on gonadal steroids and is in contrast to the copulatory behavior of the substantial proportion of the study population that sustains the full sexual repertoire in the long-term absence of gonadal steroids. Sex behavior of the latter animals may be dependent on nongonadal steroids or mediation by steroid-independent mechanisms.

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### Introduction

The dependence of male sex behavior on gonadal steroids is well established (Young, 1961). Orchidectomy reduces masculine sexual behaviors in mammals, but the extent of the reduction varies both inter- and intraspecifically (reviewed in Larsson, 1979). Striking interindividual variation in the response to castration has been documented in dogs (Beach, 1970), cats (Rosenblatt and Aronson, 1958), rhesus monkeys (Micheal and Wilson, 1974; Phoenix et al., 1973), and humans (Heim, 1981; Zverina et al., 1990). In rodents and more primitive mammals (musk shrews; Rissman, 1987), the reduction in copulatory behavior after castration is more uniform; in almost all individuals of

several well-studied species, the ejaculatory response disappears within a few weeks of castration (Young, 1961). The single notable exception is the hybrid B6D2F1 mouse (Manning and Thompson, 1976; McGill and Manning, 1976; Thompson et al., 1976) in which 30% of males retain the ejaculatory reflex 25 weeks after castration (Clemens et al., 1988). Plasma testosterone (T) concentrations and hypothalamic nuclear estrogen receptors were reduced to the same extent in males of this strain that ceased or continued to copulate after castration (Clemens et al., 1988). Retention of the ejaculatory reflex after castration apparently is unrelated to differences in circulating concentrations of androgens or to the number of hypothalamic steroid receptors in tissues implicated in the control of male copulation, but may be dependent on nongonadal sources of estrogens (Sinchak and Clemens, 1989; Sinchak et al., 1996).

In seasonally breeding Syrian hamsters, day length profoundly influences copulatory behavior; for example, males cease to display ejaculatory behavior after several weeks of exposure to short day lengths (Campbell et al.,

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1978; Miernicki et al., 1990; Morin and Zucker, 1978; Powers et al., 1989). Furthermore, androgen replacement is less effective in restoring sexual behavior in castrated Syrian hamsters housed in short than long day lengths (Campbell et al., 1978; Morin and Zucker, 1978; Pospichal et al., 1991; Powers et al., 1989). The effects of day length on Syrian hamster sex behavior are exaggerated during hormone withdrawal; long-day castrated males continue copulating longer and more effectively than those in short days several weeks after testosterone treatment is terminated (Pospichal et al., 1991). The threshold for activation of male sex behavior by T may be lower, and residual effects of T may persist longer in long- than short-day animals. Day length may also influence behavior via a steroid-independent mechanism (Howles et al., 1980).

In preliminary work, we unexpectedly observed that adult Siberian hamsters housed in a long-day photoperiod (14L; 14 h of light/day) displayed the ejaculatory reflex in copulo 2 months after castration. This raised the possibility that male sex behavior in this species may be maintained by steroid-independent mechanisms. Alternatively, either low concentrations of androgens present after castration (Park et al., 2003) or long-lasting residual effects of gonadal hormones on neural tissue (Hart, 1974) might account for the persistence of mating behavior in castrated *Phodopus sungorus*.

Suppression of gametogenesis, marked reductions in synthesis and secretion of gonadal steroids, and concomitant elimination of mating behavior are potentially redundant mechanisms that can suppress offspring production during inhospitable autumn and winter months. Decreases in day length and concomitant increases in the duration of nightly melatonin secretion are proximate cues that effect these changes (reviewed in Prendergast et al., 2002). The evidence for photic control of hormone secretion and gametogenesis is extensive; suppression of mating behavior in short day lengths has been inferred often but documented rarely in mammals. The notable exception is the Syrian hamster (*Mesocricetus auratus*) (Campbell et al., 1978; Miernicki et al., 1990; Morin and Zucker, 1978; Powers et al., 1989). Our preliminary observations of castrated Siberian hamsters raised the possibility that exposure to winter day lengths, effective in causing involution of the testes, interruption of spermatogenesis (Bergmann, 1987), and marked reduction in androgen production (Lerchl et al., 1993) might nevertheless be compatible with mating behavior in this species. This proposition was tested by monitoring males as they underwent gonadal regression and eventual recrudescence over the course of 25 weeks of continuous maintenance in short days (SD).

A second goal was to determine whether short day lengths exert gonadal-independent suppression of copulatory behavior. This possibility was assessed by comparing sex behavior of castrated hamsters that remained in the long-day photoperiod with that of males transferred to SD at the time of castration.

## Materials and methods

### Animals

Siberian hamsters (*P. sungorus sungorus*) were from our local breeding colony, descended from stock supplied by Dr. Katherine Wynne-Edwards (Queen's University, Kingston, ONT, Canada; Wynne-Edwards et al., 1999). Hamsters were gestated and maintained in a light–dark cycle that provided 14 h of light/day (14L; light-onset at 0400 h, Pacific Standard Time). Hamsters were weaned at 18 days of age and then housed in polypropylene cages (25 × 14 × 12 cm) in same-sexed groups of two to three animals. Food (Purina rodent chow 5015) and water were provided ad libitum, and the ambient temperature was 22 ± 2°C.

To facilitate behavioral testing during the daytime, 36 male and 36 female hamsters, approximately 60 days of age, were subjected to two 3-h phase advances in the photocycle separated by 10 days. Beginning 10 days after the second phase advance, preoperative tests for male copulatory behavior were conducted 1 h after dark onset during the hamsters' subjective night (1300 h).

Female hamsters used in behavioral testing were ovariectomized and several weeks later were treated with 4-mm Silastic capsules implanted subcutaneously (Dow Corning, Midland, MI, USA; ID 1.98 mm, OD 3.18 mm). Capsules were filled with crystalline estradiol benzoate (EB; Sigma Chemical, St. Louis, MO, USA). To induce behavioral estrus, each female was injected with progesterone (0.6 mg/0.1 ml peanut oil; Sigma) 6 h before testing. Stimulus females were maintained in the 14L photoperiod.

### Somatic and reproductive measures

At predetermined intervals, hamsters were weighed (±0.1 g) and the length and width of the left testis measured externally (±0.1 mm) under light anesthesia induced with isoflurane vapors. The product of testis width squared times testis length provides a measure of estimated testis volume (ETV) that is highly correlated with testis weight in this species (Gorman and Zucker, 1995). Intact hamsters whose testes failed to undergo regression in short days (SD sham-castrates with ETV >250) were judged to be unresponsive to the short day length; their data were excluded from the statistical analyses.

### Behavioral testing

Behavioral testing was conducted under dim red light between 1400 and 1800 h. Males housed in the long-day (LD) photoperiod that successfully ejaculated on 2 consecutive days preoperatively were selected for further study. The occurrence and timing of mounts, intromissions, and ejaculation were recorded. The copulatory pattern in *Phodopus* was as described by Sawrey et al. (1984). Briefly, a series of mounts and intromissions culminates in ejacula-

tion; there is a single brief thrust with each intromission and multiple intromissions precede each ejaculation. Upon ejaculation, the joined pair falls to the side, with the female grasped in the male's forepaws for approximately 10–30 s. There is no vaginal lock.

Behavioral tests conducted in the male's home cage began with the introduction of a hormone-treated stimulus female. If 10 min passed without the male mounting the female, she was replaced with a second stimulus female; if this change failed to elicit copulation, a third female was introduced. Failure to mount the third female resulted in termination of the test. Once the male mounted, the test continued to a criterion of two successful ejaculatory reflexes or for 40 min, whichever occurred first. A stimulus female that became unreceptive during testing was replaced with another stimulus female.

Upon completion of preoperative testing in the LD photoperiod, copulator males were either castrated ( $n = 24$ ) or sham-castrated ( $n = 12$ ) as described in Park et al. (2003); 12 castrates and 12 sham-castrates were transferred to a short-day photoperiod (10L:14D; 10 h of light beginning at 0300 h) and 12 castrates remained in the LD photoperiod. Sex behavior tests were conducted every other week until the majority of the SD sham-castrates achieved testicular recrudescence and resumed copulation (after approximately 25 weeks in SD).

During each postcastration behavioral test, the behavioral components recorded were mount frequency (MF, the number of mounts not accompanied by an intromission that preceded the ejaculation or the termination of the test), intromission frequency (IF, the number of intromissions that preceded the first ejaculation), mount latency (ML; time from the introduction of a receptive female to the first mount), intromission latency (IL; time from the introduction of a receptive female to the first intromission), ejaculation latency (EL; interval between the first intromission and ejaculation), and postejaculatory interval (PEI; interval between the first ejaculation and the next intromission). Animals that did not mount, intromit, and/or ejaculate during a test were assigned a maximum latency of 2400 s.

Males that continued to copulate after castration were considered to be persistent copulators if they demonstrated the ejaculation reflex on at least three occasions between weeks 11 and 17 postcastration.

#### *Blood collection and testosterone radioimmunoassay*

One day after the final behavioral test, blood samples (approximately 500  $\mu$ l) were obtained from the retro-orbital sinus under light isoflurane (Fort Dodge Animal Health, Fort Dodge, IA) vapors between 1900 and 2000 h. Samples were centrifuged at room temperature for 20 min at 2500 rpm, and the serum was collected and frozen at  $-80^{\circ}\text{C}$  until assayed. Testosterone (T) was measured using a double-antibody  $^{125}\text{I}$  radioimmunoassay kit (Prod-

uct number DSL-4100; Diagnostic Systems Laboratories, Webster, TX). Cross-reaction of the T antibody to  $5\alpha$ -dihydrotestosterone for this kit was 6.6% as reported by the manufacturer, and the upper and lower limits of detectability were 25 and 0.1 ng/ml, respectively. This kit has previously been validated for use in Siberian hamsters (Jasnow et al., 2000). Serum samples were aliquoted in 25  $\mu$ l amounts into duplicate assay tubes and incubated with  $^{125}\text{I}$  radiolabelled T tracer and rabbit anti-T antibody for 1 h at  $37^{\circ}\text{C}$ . Pellets were precipitated with goat antirabbit gamma globulin serum and polyethylene glycol, and were centrifuged at room temperature for 20 min at  $1500 \times g$ . The supernatant was then decanted and aspirated, and gamma emissions from each tube were recorded for 1 min using an automated gamma counter (Packard Instrument Company, Meriden, CT, USA). All T values were determined in a single radioimmunoassay for which the intra-assay coefficient of variation was 3.7%.

#### *Statistical analysis*

Cochran  $Q$  tests were used to test for significant changes in copulatory behavior over the course of testing within each group. Post hoc McNemar exact probability tests were conducted where appropriate. Nonparametric Kruskal–Wallis tests were run to determine whether there were differences between groups in copulatory behavior and chi-square tests were used to compare differences in copulatory behavior between groups at certain weeks. Repeated ANOVAs were used to analyze body weight and ETVs of the sham-castrated SD males, and the number of mounts and intromissions, as well as mount, intromission, and ejaculation latencies of all hamsters.

Plasma samples with undetectable T levels were assigned the minimal detectable level of the assay (0.1 ng/ml) and an ANOVA was used to analyze T levels; samples that were reassayed after dilution with the serum blank that still yielded concentrations greater than three standard deviations from the mean were omitted from statistical analyses. Post hoc comparisons were conducted using the Fisher Protected Least Significant Difference test where appropriate. Observed differences were considered significant if  $P < 0.05$ . Statistical tests other than the Cochran  $Q$  test and the post hoc McNemar exact probability tests were run using the Statview program (Statview 5; SAS Institute, Cary, NC, USA).

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

## **Results**

Before surgery, each male successfully ejaculated on two successive mating tests. There was a temporary decline in

some components of mating behavior in all groups 1 week after surgery.

*Ejaculation*

In confirmation of our preliminary study, copulation culminating in the behavioral ejaculatory pattern was documented in a substantial proportion of long-term gonadectomized hamsters. Fifty percent of LD-castrates (6/12) and 36% (4/11) of SD-castrates displayed this behavior 19 weeks after castration (Fig. 1A). Twenty-five weeks after surgery, 30% of castrates (data combined from both photoperiods) were still ejaculating.

The incidence of ejaculation was reduced after surgical castration in males housed in long and short DLs; differences between these groups were not significant at any time point (Fig. 1A). The decline in ejaculatory behavior was more rapid and more pronounced in castrated than in intact males transferred to SD (e.g., SD-castrates vs. SD-sham on week 9;  $P < 0.05$ ).

Transfer of intact males from LD to SD eventually resulted in a decrease in the percentage of hamsters that ejaculated; the nadir was reached after 17 weeks, when 50% of males displayed this behavior (Fig. 1A;  $P = 0.051$  for week 17 vs. each of weeks 3, 5, 7, 9). Between week 17 and 23, the percentage of animals that ejaculated increased from 50% to 100% ( $P < 0.05$  for week 17 vs. week 23). After completion of gonadal recrudescence, the percentage of sham-castrated males that ejaculated exceeded that for either the LD or SD castrates (weeks 23–25;  $P < 0.05$  for each comparison).

The influence of gonadal hormones and DL on mating behavior was assessed separately for animals that continued to copulate throughout 25 weeks of postoperative testing. The EL doubled in the first week of postoperative testing for the SD-castrated and the SD-sham castrated groups, with a return to the preoperative baseline thereafter; there were no differences among the groups (Fig. 2A).

*Intromissions and mounts*

Gonadectomy was associated with a significant decrease in the percentage of males that intromitted and mounted; the decline relative to baseline values was more rapid in SD-castrates than LD-castrates (Figs. 1B,C). Fewer SD- than LD-castrated males intromitted from week 7 to 23 and mounted from week 5 to 19, but the differences were not significant. The incidence of intromissions and mounts of sham-castrated SD males declined to a nadir by week 11 and week 17, respectively, and subsequently increased from 70% to 100% between week 17 and week 23 (Figs. 1B,C), paralleling the pattern of change in ejaculation. By week 9, the percentage of males that intromitted and mounted was significantly lower in SD-castrated vs. SD sham-castrated males (Figs. 1B,C). A greater percentage of the sham-castrated

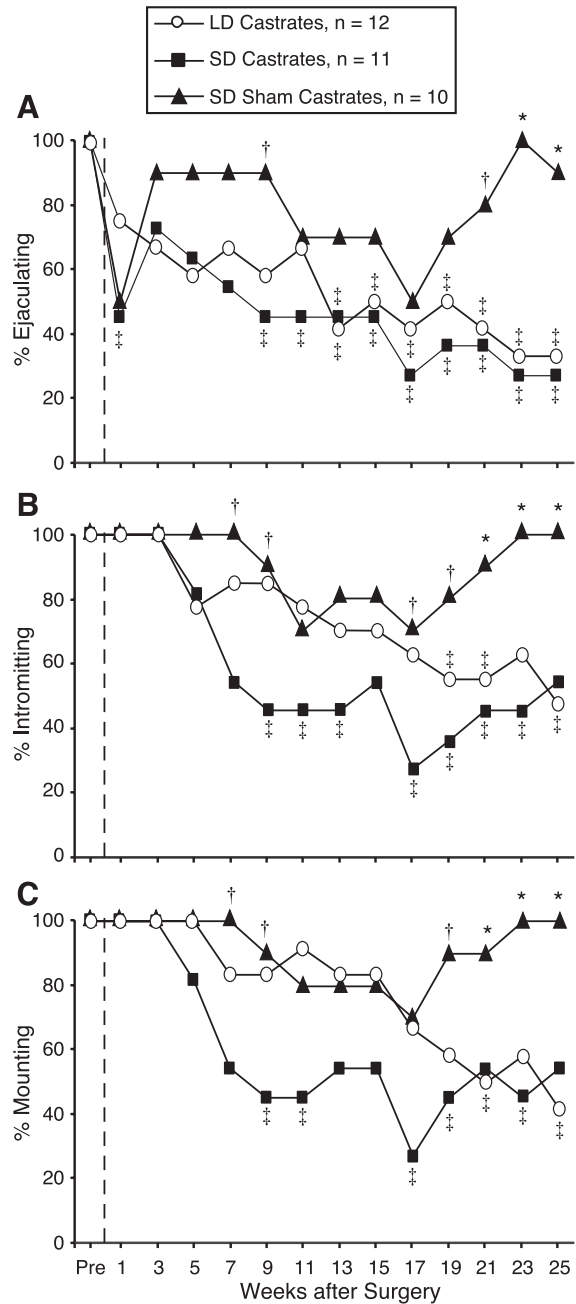


Fig. 1. Percentages of castrated hamsters in long (○) and short (■) day lengths and sham-castrated males in short day lengths (▲) that displayed (A) ejaculatory, (B) intromission, and (C) mounting behaviors during postoperative testing. \*Values of SD sham-castrated males differ from those of both LD and SD castrates ( $P < 0.05$ ). †Differs significantly from values of SD castrates. ‡Significantly different from precastration value for that group ( $P < 0.05$ ).

males intromitted and mounted compared to either the LD- or SD-castrates during weeks 21–25 ( $P < 0.05$ ); this coincided with testicular recrudescence in the sham-castrates (Fig. 3A).

The latency to the first intromission of persistent copulators tended to be longer in the SD castrates than

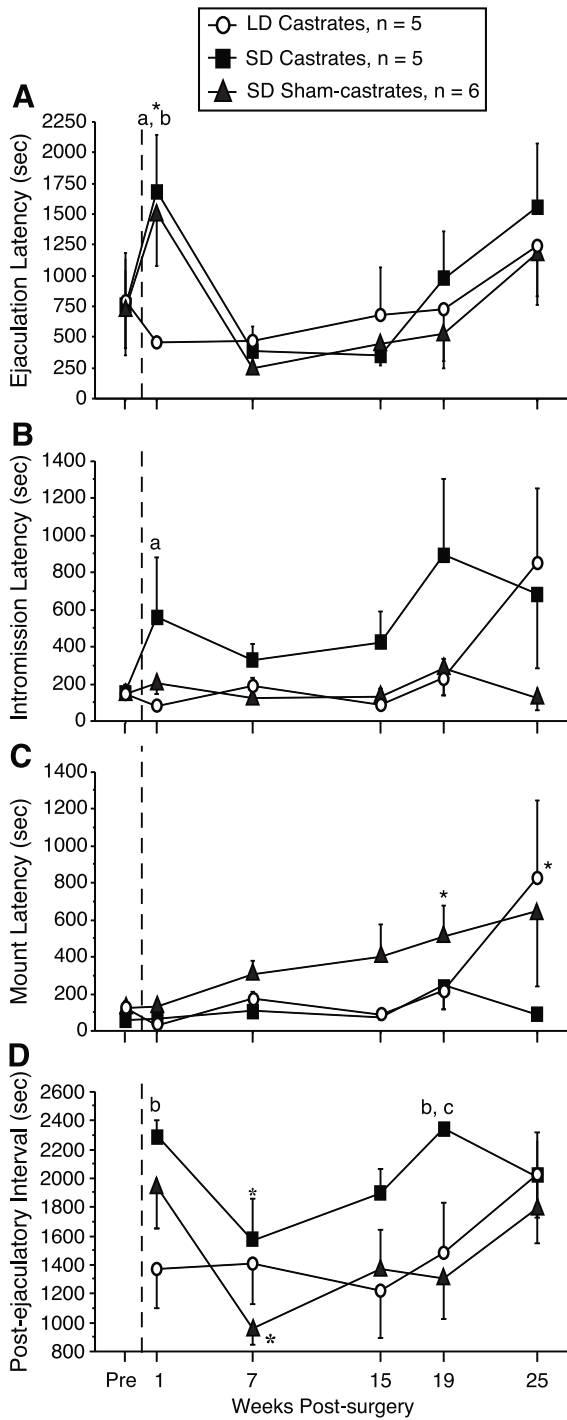


Fig. 2. Mean ± SEM (A) ejaculation latency, (B) intromission latency, (C) mount latency, and (D) postejaculatory interval of castrated hamsters kept in long (○) and short (■) day lengths or sham-castrated males kept in short day lengths (▲) that were persistent copulators. \*Different from preoperative value of this group. <sup>a</sup>Significant difference between LD and SD castrated males. <sup>b</sup>Significant difference between LD-castrated and SD sham-castrated males. <sup>c</sup>Significant difference between SD-castrated and SD sham-castrated males.

for the other groups but the difference was not statistically significant after week 1, perhaps due to small sample size (Fig. 2B).

Mount latency of persistent copulators remained essentially unchanged in LD- and SD-castrates for the first 19 weeks, with a significant increase from week 19 to 25 in the LD group (Fig. 2C).

*Postejaculatory interval of persistent copulators*

The latency to resumption of mating after the first ejaculation was significantly longer in SD-castrates than in the other two groups (Fig. 2D), which did not differ from each other.

*Gonadal size and body mass*

There were no significant differences in estimated testicular volumes (ETVs) between animals that continued or ceased to ejaculate during maintenance in short DLs (Fig. 3A). ETVs decreased during the first 13 weeks hamsters were in SDs; minimum values were recorded between

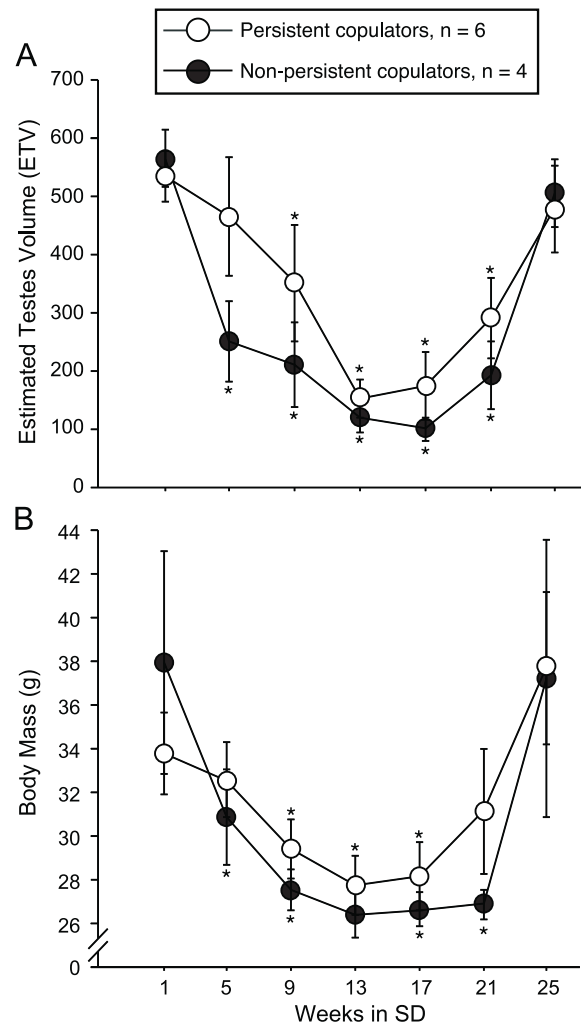


Fig. 3. Mean ± SEM (A) estimated testes volumes and (B) body mass of persistent (○) and nonpersistent (●) copulators kept in short day lengths. \*Differs significantly from corresponding week 1 value ( $P < 0.05$ ).

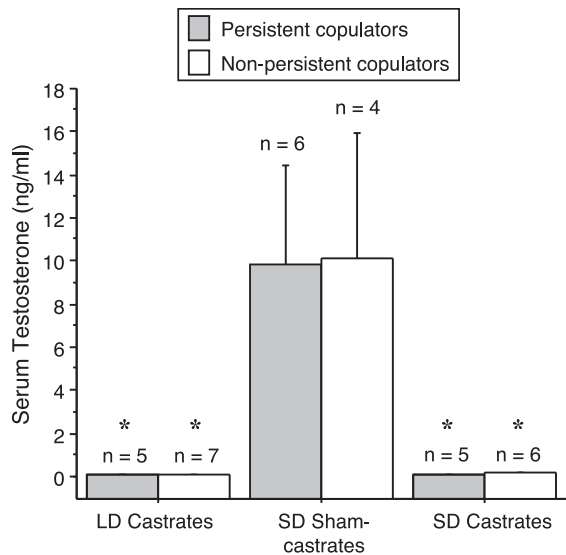


Fig. 4. Mean  $\pm$  SEM serum T concentration 25 weeks after surgery of persistent and nonpersistent castrated copulators in long and short day lengths and sham-castrated persistent and nonpersistent copulators in short day lengths. \*Significantly different from value for the SD sham-castrated males.

weeks 13 and 17 (Fig. 3A). Gonadal recrudescence occurred after week 17, and reached baseline ETV values characteristic of LD males by week 25.

The initial reduction and eventual recovery of body mass in males transferred to SD paralleled the changes in ETV in all essential respects and was similar for persistent copulators and those that no longer displayed the ejaculatory reflex (Fig. 3B).

#### Testosterone

Within each treatment modality (castration or SD treatment), T concentrations did not differ between males categorized as persistent or nonpersistent copulators. The majority of castrates had T concentrations below the lower limits of detectability ( $0.113 \pm 0.008$  and  $0.128 \pm 0.022$  ng/ml for LD and SD-castrates, respectively; Fig. 4). T concentrations of castrated LD or SD males 25 weeks after surgery were significantly lower than those of SD sham-castrated males that underwent gonadal recrudescence (Fig. 4;  $P < 0.05$ ).

#### Discussion

A subset of Siberian hamsters displayed the ejaculatory reflex 25 weeks after surgical castration (33% and 27% of long- and short-day castrates, respectively). Circulating testosterone (T) concentrations were at or below levels of detectability in these animals. The long-term retention of copulation by hamsters is reminiscent of the behavior of orchidectomized male B6D2F1 mice (Manning and

Thompson, 1976; McGill and Manning, 1976), 30% of which copulated to ejaculation 25 weeks after castration (Clemens et al., 1988). This behavior differs markedly from the common pattern of numerous rodents deprived of gonadal hormones (Hull et al., 2002; Larsson, 1979; Young, 1961), but is similar to relations established for bats (Mendonca and Hopkins, 1997) and snakes (Camazine et al., 1980). In rodent species, all males typically fail to ejaculate beginning a few weeks after castration (e.g., Syrian hamsters; Morin and Zucker, 1978). Unlike the hybrid mice in which sex behavior is retained after castration, our colony of Siberian hamsters was derived from animals trapped relatively recently (Wynne-Edwards et al., 1999) and was subjected to random breeding. There was no artificial selection for independence of copulation from hormonal control.

Congruent with these observations, 50% of photo-inhibited hamsters that had undergone testicular regression after 17 weeks of short-day treatment continued to display the full repertoire of male sexual behavior. Persistence of mating behavior in half the Siberian hamsters appears to be unrelated to low plasma androgen concentrations sustained by the photo-inhibited gonads (Park et al., 2003). Our results differ from those of Lerchl et al. (1993) who in preliminary experiments reported no “copulations” in Siberian hamster males maintained in a SD photoperiod. “Copulations” were not defined so it is unclear whether this term encompasses intromissions and ejaculations or only mounting behavior.

Continued copulation in castrated B6D2F1 mice has been attributed to nongonadal sources of estrogens (Sinchak et al., 1996). Whether similar relations obtain in Siberian hamsters is unknown. The possibility of de novo neurosteroids (reviewed in Baulieu, 1998) maintaining male sex behavior after castration also merits investigation. Two behavioral phenotypes emerge after castration in Siberian hamsters: the males that continue copulation for many weeks may differ from those that fail to do so either with respect to availability or responsiveness to estrogens of unknown origin. Mating that survives castration may be mediated via steroid-independent mechanisms or reflects long-term residual effects of gonadal steroids on neural tissue (Hart, 1974).

The subset of hamsters that failed to copulate after undergoing gonadal regression resumed mating activity after they had initiated spontaneous gonadal recrudescence. The recovery of the ejaculatory reflex began after 17 weeks of short day treatment, and was most likely preceded by increased circulating T concentrations. For this subset of hamsters, copulation appears to depend on gonadal hormones, waxing and waning with increases and decreases in testicular steroid hormone production. Exogenous testosterone and/or estradiol treatment likely would restore mating behavior in these hamsters, as was the case for the subset of hormone-treated B6D2F1 mice that ceased copulation after castration (Wee et al., 1988).

The latencies to ejaculation and the postejaculatory interval tended to be longer in castrated persistent copulators housed in short than long day lengths. This suggests either steroid-independent effects of short days on copulation or an enduring impact of day length on steroid sensitive neurons that mediate male sex behavior. The latter conjecture is compatible with findings reported for castrated Syrian hamsters: after testosterone withdrawal copulatory behavior is retained longer in long-day than short-day animals (Pospichal et al., 1991).

It seems unlikely that the retention of ejaculatory behavior in males exposed to short day lengths in nature would result in the production of offspring in mid-winter. This conjecture is based on the arrest of spermatogenesis in males with photoregressed gonads (Bergmann, 1987), and the requirement that males would have to encounter estrous females capable of ovulation in winter. Redundant mechanisms appear to ensure that production of young is restricted to the spring and summer months in this species. The cost, if any, of retaining the ejaculatory reflex and potential for mating behavior in winter remains unknown.

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