

Short-Day Increases in Aggression Are Inversely Related to Circulating Testosterone Concentrations in Male Siberian Hamsters (*Phodopus sungorus*)

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Many nontropical rodent species display seasonal changes in both physiology and behavior that occur primarily in response to changes in photoperiod. Short-day reductions in reproduction are due, in part, to reductions in gonadal steroid hormones. In addition, gonadal steroids, primarily testosterone (T), have been implicated in aggression in many mammalian species. Some species, however, display *increased* aggression in short days despite basal circulating concentrations of T. The goal of the present studies was to test the effects of photoperiod on aggression in male Siberian hamsters (*Phodopus sungorus*) and to determine the role of T in mediating photoperiodic changes in aggression. In Experiment 1, hamsters were housed in long and short days for either 10 or 20 weeks and aggression was determined using a resident-intruder model. Hamsters housed in short days for 10 weeks underwent gonadal regression and displayed increased aggression compared to long-day-housed animals. Prolonged maintenance in short days (i.e., 20 weeks), however, led to gonadal recrudescence and reduced aggression. In Experiment 2, hamsters were housed in long and short days for 10 weeks. Half of the short-day-housed animals were implanted with capsules containing T whereas the remaining animals received empty capsules. In addition, half of the long-day-housed animals were castrated whereas the remaining animals received sham surgeries. Short-day control hamsters displayed increased aggression compared to either castrated or intact long-day-housed animals. Short-day-housed T treated hamsters, however, did not differ in aggression from long-day-housed animals. Collectively, these results

confirm previous findings of increased aggression in short-day-housed hamsters and suggest that short-day-induced increases in aggression are inversely related to gonadal steroid hormones. © 2000 Academic Press

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Individuals of most nontropical rodent species undergo a suite of physiological and behavioral responses across the seasons of the year (reviewed in Bronson and Heideman, 1994; Nelson, Badura, and Goldman, 1990). Despite seasonal fluctuations in a variety of environmental factors (e.g., ambient temperature, rainfall, humidity), photoperiod (day length) appears to be the primary environmental cue used by most mammalian species to coordinate behavioral and physiological responses (Bronson, 1989). Individuals of most mammalian species undergo marked physiological changes when exposed to changes in day length. For example, animals maintained in short “winter-like” days (i.e., <12 h of light/day) undergo gonadal regression (including reductions in gonadotropin secretion, inhibition of gonadal steroid hormones, and subsequent regression of the gonads), as well as changes in body mass, pelage color and density, thermoregulation, general activity, and behavior (reviewed in Bartness, Bradley, Hastings, Bittman, and Goldman, 1993). Animals maintained in short days for prolonged periods of time (i.e., >16–20 weeks) undergo spontaneous gonadal recrudescence at which time the testes return to their long-day condition and reproductive behavior resumes. These physiological

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changes in response to changes in photoperiod are mediated by a multisynaptic pathway that conveys photic information from the retina to the pineal gland and results in changes in the pattern of secretion of the pineal indolamine, melatonin. Interruption of this pathway at any point or removal of the pineal gland blocks short-day patterns of melatonin secretion and consequently gonadal regression (Elliott and Goldman, 1981; Tamarkin, Baird, and Almeida, 1985).

Short-day reductions in reproductive physiology and behavior are due, in part, to reductions in gonadal steroid hormones that accompany gonadal regression. Plasma testosterone concentrations fall to basal levels in animals housed in short photoperiods following regression of the testes. In addition, changes in photoperiod can alter the behavioral sensitivity to steroid hormones. For example, in male Syrian hamsters, castrated animals housed in short days are less sensitive to the stimulatory effects of testosterone on reproductive behavior compared to long-day-housed animals (Campbell, Finkelstein, and Turek, 1978; Morin and Zucker, 1978). In contrast, the reduced behavioral sensitivity to testosterone occurs at a time when hamsters are most sensitive to testosterone negative feedback on pituitary gonadotropin secretion (Tamarkin, Hutchison, and Goldman, 1976; Ellis, Losee, and Turek, 1979). Castration reduces aggression in males in several vertebrate species (reviewed in Knol and Egberink-Alink, 1989). This widely accepted relationship between the presence of the testes (and normal circulating testosterone concentrations) and aggression, however, is based primarily on studies of male-male aggression in highly domesticated species such as laboratory rats (*Rattus norvegicus*) and house mice (*Mus musculus*). In these species, removal of the gonads results in substantial decreases in circulating testosterone and, subsequently, reduced aggression (Edwards, 1969, 1970). When adult males of several nondomesticated species are examined, however, exceptions to the relationship of low circulating testosterone concentrations and reduced aggression begin to emerge (Demas, Moffatt, Drazen, and Nelson, 1999). For example, several species of animals including Mongolian gerbils (*Meriones unguiculatus*) (Christianson, Wallen, Brown, and Glickman, 1972), prairie voles (*Microtus ochrogaster*) (Dewsbury, 1991; Demas *et al.*, 1999), Syrian hamsters (*Mesocricetus auratus*) (Tiefer, 1970; Garrett and Campbell, 1980), and European starlings (*Sturnus vulgaris*) (Davis, 1957; Mathewson, 1961) do not display decreased aggression after castration. Furthermore, there appears to be no consistent correlation between testosterone levels and ag-

gression in some strains of mice (e.g., Selmanoff, Goldman, and Ginsburg, 1977) and, in some instances, exogenous testosterone treatment *reduces* aggression (Compaan, de Ruiter, Koolhaas, van Oortmerssen, and Bohus, 1992; Logan and Carlin, 1991). Collectively, these results suggest that testosterone may not play an important role in the maintenance of aggression in adult animals.

Several studies have examined the role of testosterone in aggression indirectly by manipulation of photoperiod and, thus, gonadal steroid hormones. Interestingly, "functional castration" of male Syrian hamsters by maintaining animals in short days *increases* aggression compared to long-day-housed hamsters, despite basal concentrations of testosterone. After prolonged maintenance in short days (>15 weeks), hamsters undergo gonadal recrudescence and the short-day increases in aggressive behavior largely disappear, returning to long-day levels of aggression by 21 weeks. In addition, males undergoing especially rapid gonadal recrudescence display similarly rapid decreases in aggression. These results suggest that levels of aggressive behavior are inversely related to serum testosterone concentrations, at least in male Syrian hamsters (Garrett and Campbell, 1980). Surprisingly, no other studies to our knowledge have pursued these intriguing results and, thus, the precise hormonal mechanisms underlying short-day increases in aggression remain largely unknown.

Photoperiodic changes in aggression have been demonstrated in females of at least one species, Syrian hamsters (Badura and Nunez, 1989; Fleming, Phillips, Rydall, and Levesque, 1988). Syrian hamsters display a reversed sexual dimorphism in aggressive behavior compared to other rodent species, with females typically displaying significantly more aggression than do their male counterparts except when estrogen concentrations are elevated (e.g., during estrus) (Ciacco, Lisk, and Reuter, 1979; Marques and Valenstein, 1977). Consistent with this pattern, female Syrian hamsters maintained in short days (which reduces circulating estradiol concentrations) display significantly more aggression compared to long-day-housed animals (Badura and Nunez, 1989; Fleming *et al.*, 1988). Interestingly, removal of the pineal gland (i.e., pinealectomy) eliminates the short-day-induced increase in aggression in these animals, suggesting a role for melatonin in mediating this effect. Surgical removal of the ovaries (i.e., ovariectomy) in long-day-housed animals, however, does not result in short-day levels of aggression, suggesting that photoperiodic effects on aggression are not mediated by gonadal steroid hormones in

female Syrian hamsters (Fleming *et al.*, 1988). To our knowledge, no study has examined the role of photoperiod on aggression in males of a rodent species displaying the more typical male-dominant pattern of aggression. Thus, the goal of the present study was to extend the findings from Syrian hamsters to another hamster species, Siberian hamsters (*P. sungorus*). In addition, the present study examined the role of gonadal steroid hormones in mediating photoperiodic changes in aggression by experimentally manipulating circulating testosterone concentrations. Specifically, long-day-housed animals were castrated to mimic short-day levels of testosterone, whereas short-day-housed animals were given exogenous testosterone to mimic long-day profiles.

MATERIALS AND METHODS

Animals and Housing Conditions

Adult (>60 days of age) Siberian hamsters (*P. sungorus*) were obtained from our laboratory breeding colony. This colony was originally derived from stock animals supplied by Dr. Bruce Goldman (University of Connecticut) in 1988 and interbred with wild-trapped hamsters in 1990 from Dr. Katherine Wynne-Edwards (Queens University). Hamsters were weaned at 21 days of age and housed with same-sex siblings. Two weeks before the initiation of the experiments (before photoperiodic manipulation), animals were housed individually in polypropylene cages (27.8 × 7.5 × 13.0 cm) in colony rooms with a 24-h LD 16:8 cycle (lights on 0300 h EST). Temperature was kept constant at 20°C and relative humidity was maintained at 50 ± 5. Food (Purina Rat Chow) and tap water were available *ad libitum* throughout the experiment. Additional animals were used as nonaggressive intruders during behavioral testing and were housed 8–10 per cage. Group-housed hamsters are typically nonaggressive. These animals were of the same age as experimental animals and were housed in long-day conditions. All animals were treated in accordance to the Georgia State University Institutional Animal Care and Use Committee.

Experiment 1

The goal of Experiment 1 was to determine the effects of short-day housing on aggression in adult, male Siberian hamsters. Hamsters ($n = 36$) were selected randomly and assigned to one of two photoperiodic conditions.

Half of the animals ($n = 18$) were housed in a short-day photoperiod to stimulate gonadal regression (LD 8:16), while the remaining animals ($n = 18$) were housed in long-day photoperiodic conditions (LD 16:8). Half of the animals from each photoperiod remained in their respective photoperiodic conditions for 10 weeks before behavioral testing, and their cages were not changed for 2 weeks before behavioral testing. The remaining short-day animals were maintained in their respective photoperiods for 20 weeks to allow spontaneous gonadal recrudescence to occur in short-day-housed animals; this time has been shown previously to be sufficient for recrudescence to occur in Siberian hamsters (Bartness, Hamilton, Wade, and Goldman, 1989). The remaining long-day-housed animals served as age-matched controls. Photoperiodic responsiveness was determined by inspection of pelage color (Duncan and Goldman, 1984). Animals that did not respond to short days by the typical change in pelage color from summer gray to winter white were excluded from subsequent statistical analyses. Resident/intruder aggression was assessed by introducing a nonaggressive intruder into the home cage of an experimental animal for 5 min. Behavioral testing was conducted during the first 2 h of the dark phase to control for circadian rhythmicity of behavior. Intruder males were dye-marked on the tail for purposes of identification. Attack latency, number of attacks, and total duration of attacks were recorded by two observers blind to experimental conditions. A novel pairing of animals was made for each test and nonaggressive intruders were not used more than once per day.

Experiment 2

The goal of Experiment 2 was to assess the role of testosterone in photoperiod-induced changes in aggression. Hamsters ($n = 32$) were selected randomly and assigned to either long or short days. Half of the long-day-housed animals ($n = 8$) were selected randomly and castrated to remove testosterone (mimicking short-day levels) while the remaining animals ($n = 8$) received sham operations. All short-day-housed animals received sham surgeries. Animals were anesthetized deeply using sodium pentobarbital (50 mg/kg). Castrations were performed through bilateral abdominal incisions; both testes were removed, the abdominal wall was sutured, and the incision in the skin was closed with 9-mm wound clips (Clay Adams, Parsippany, NJ). Nitrofurazone antibacterial powder (Phoenix Pharmaceuticals, St. Josephs, MI)

was applied to the skin surface to prevent infection. Animals that were sham castrated underwent a similar procedure but their testes were irrigated with saline and returned to the abdominal cavity before closing. Half of the short-day-housed animals ($n = 8$) were implanted with 10-mm-long Silastic capsule implants (1.47-mm inner diameter, 1.95-mm outer diameter, silicone medical grade tubing, American Scientific Product, McGraw Park, IL) filled with testosterone (Sigma, St. Louis, MO) to mimic long-day levels of testosterone. The remaining short-day-housed animals and all of the long-day-housed animals were implanted with empty Silastic capsules. For capsule implantation, animals were anesthetized lightly with methoxyflurane vapors (Metophane, Pitman-Moore Inc., Mundelein, IL). A 70% alcohol solution was applied to the intrascapular surface and a 5-mm incision was made perpendicular to the midline. Capsules were implanted subcutaneously and the incision was closed with a 9-mm wound clip. Animals remained in their respective photoperiodic conditions for 10 weeks before behavioral testing, and their cages were not changed for 2 weeks before behavioral testing. Resident/intruder aggression was assessed as in Experiment 1, and photoperiodic responsiveness was determined by weighing the testes at autopsy.

Blood Collection and Testosterone Assay

Following behavioral testing in Experiment 2, animals were lightly anesthetized and blood samples (500 μ l) were drawn into capillary tubes via retro-orbital bleeding. Handling time was kept consistent and to a minimum; the time from initial removal from the cage to the end of bleeding was less than 3 min. The samples were allowed to clot for 1 h, then the clot was removed and the samples were centrifuged at 4°C for 1 h at 3500 rpm. Serum aliquots were extracted and stored at -80°C until assayed. Serum testosterone concentrations were determined in a single radioimmunoassay based on a previously reported method (Granger, Schwartz, Booth, and Arentz, 1999) adapted to assess serum testosterone levels of Siberian hamsters. This assay was validated for use with this species. The antiserum used was highly specific for testosterone. Cross-reactivity with other steroid hormones was $<0.01\%$. Assay sensitivity was 0.18 ng/ml and the intra-assay coefficient of variation was 3.5%.

STATISTICAL ANALYSES

In Experiment 1, differences between treatment means were assessed using a one-way between-groups analysis of variance (ANOVA) (Sigma Stat, Jandel Inc., San Rafael, CA). Because aggression did not differ significantly between hamsters housed in long days for either 10 or 20 weeks, the data for all animals from both time points were collapsed into a single statistical analysis. In Experiment 2, differences between experimental conditions were assessed via a 2 (photoperiod) \times 2 (gonadal status) between-groups ANOVA. Post hoc comparisons between pairwise means were conducted using Tukey-HSD tests. In all cases differences between group means were considered statistically significant at $P < 0.05$.

RESULTS

In Experiment 1, there was a significant effect of photoperiod on body mass ($F_{2,35} = 25.31$, $P < 0.05$). Hamsters maintained in short days for 10 weeks weighed significantly less than long-day-housed hamsters ($P < 0.05$) or hamsters housed in short days for 20 weeks ($P < 0.05$). In addition, there was a significant effect of photoperiod on testes mass ($F_{2,35} = 287.27$, $P < 0.05$). Paired testes mass also was significantly smaller in hamsters housed in short days for 10 weeks compared to animals housed in long days ($P < 0.05$) or in short days for 20 weeks ($P < 0.05$) (Fig. 1).

There was a significant effect of photoperiod on the number of attacks ($F_{2,35} = 6.10$, $P < 0.05$). Hamsters housed in short days for 10 weeks exhibited a significantly greater number of attacks than long-day-housed animals ($P < 0.05$) (Fig. 2). In addition, there was a significant effect of photoperiod on initial latency to attack ($F_{2,35} = 3.91$, $P < 0.05$). Latency to initial attack was significantly shorter in short-day-housed animals compared to long-day-housed animals ($P < 0.05$). There was a main effect of photoperiod on the duration of attacks ($F_{2,35} = 9.43$, $P < 0.05$). Hamsters housed in short days for 10 weeks displayed significantly longer duration of attacks compared to long-day-housed hamsters ($P < 0.05$) (Fig. 2). Animals maintained in short days for 20 weeks (i.e., photorefractory) displayed levels of aggression in between that of long-day-housed and 10-week short-day-housed hamsters although levels of aggression were not statistically different than either long-day or

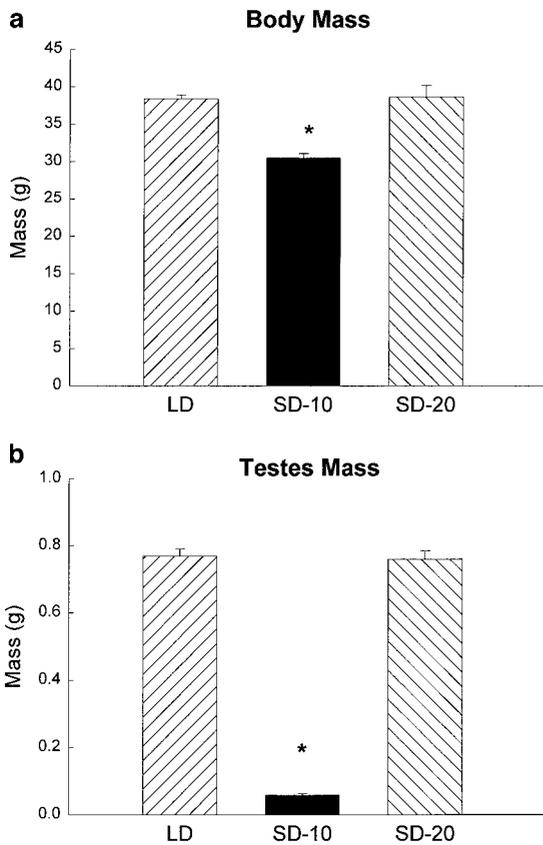


FIG. 1. Mean (\pm SEM) body mass (a) and testes mass (b) of animals housed in long days (LD) ($n = 18$), short days for 10 weeks (SD-10) ($n = 9$), and short days for 20 weeks (SD-20) ($n = 9$). Significant differences between pairwise means are indicated by an asterisk (*) ($P < 0.05$).

10-week short-day-housed animals in all parameters measured (Fig. 2).

In Experiment 2, there was a significant interaction between hormonal treatment and photoperiod on the number of attacks ($F_{1,31} = 3.56$, $P < 0.05$). Short-day-housed sham-operated hamsters displayed a significantly greater number of attacks compared to short-day-housed, testosterone-treated and all long-day-housed animals ($P < 0.05$ in all cases) (Fig. 3). Interestingly, long-day-housed castrated hamsters displayed significantly longer duration of attack compared to long-day testosterone-treated hamsters ($P < 0.05$) and short-day testosterone-treated hamsters ($P < 0.05$). In addition, short-day sham-operated hamsters were not different from long-day castrates in total duration of attack. Finally, the latency to initial attack was significantly shorter in short-day-housed, sham-operated animals compared to short-day-housed, testosterone-treated hamsters ($P < 0.05$) and

long-day-housed sham-castrated animals ($P < 0.05$) (Fig. 3). Serum testosterone concentrations were undetectable both in animals maintained in short days and in castrated animals, regardless of photoperiod, and concentrations did not differ significantly between long-day-housed sham-operated and short-day-housed testosterone-treated animals ($P > 0.05$), (Fig. 4).

DISCUSSION

The present data suggest that short day lengths increase aggression in male Siberian hamsters and that

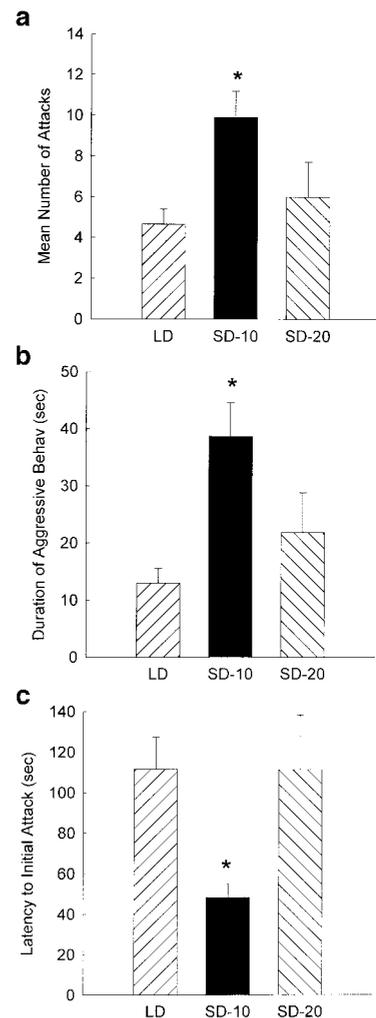


FIG. 2. Mean (\pm SEM) number of attacks (a), total (\pm SEM) duration of attacks (b), and mean (\pm SEM) latency to initial attack(s) (c) of animals housed in long days (LD) ($n = 18$), short days for 10 weeks (SD-10) ($n = 9$), and short days for 20 weeks (SD-20) ($n = 9$). Significant differences between pairwise means are indicated by an asterisk (*) ($P < 0.05$).

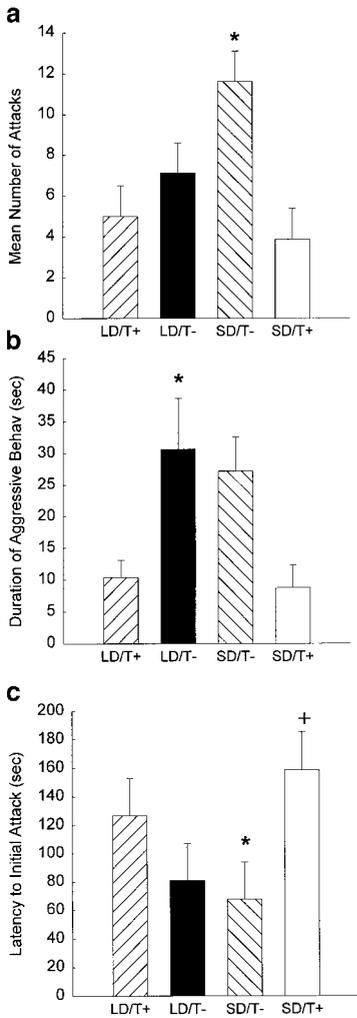


FIG. 3. Mean (\pm SEM) number of attacks (a), total (\pm SEM) duration of attacks (b), and mean (\pm SEM) latency to initial attack (c) of animals housed in long days receiving sham castrations (LD/T+) ($n = 8$), long-day castrated animals (LD/T) ($n = 8$), short-day animals receiving empty capsules (SD/T-) ($n = 8$), and short-day animals receiving testosterone (SD/T+) ($n = 8$). An asterisk (*) indicates a significant difference from both LD/T+ and SD/T+ ($P < 0.05$). A plus (+) indicates a significant difference from both LD/T- and SD/T- ($P < 0.05$).

increased aggression is inversely related to circulating concentrations of testosterone. In Experiment 1, short-day, photoreponsive animals displayed a greater number of attacks, longer duration of attack, and a shorter latency to attack than long-day-housed animals. Short-day photorefractory animals displayed a pattern of aggression in between that of long-day and short-day photoreponsive animals. These data suggest that short photoperiods enhance aggression in male Siberian hamsters. A number of studies have

reported similar increases in aggression in animals housed under short photoperiods in both male (Garrett and Campbell, 1980) and female Syrian hamsters (Fleming *et al.*, 1988; Badura and Nunez, 1989).

In Experiment 2, short-day-housed animals receiving empty capsules displayed more aggressive behavior than short-day-housed, testosterone-treated hamsters and long-day-housed, intact animals. Interestingly, when short-day-housed animals were given testosterone via subcutaneous capsules, levels of aggression were returned to those of long-day-housed intact animals. Taken together, the data from Experiments 1 and 2 suggest that the short-day-induced increases in aggression appear to be inversely related to circulating testosterone concentrations. These data are in contrast with traditional literature suggesting a positive correlation between levels of aggression and levels of circulating testosterone (reviewed in Knol and Egberink-Alink, 1989). The present results, however, are consistent with the sparse literature suggesting that there are photoperiodic-mediated increases in aggression in hamsters (Garrett and Campbell, 1980; Fleming *et al.*, 1988; Badura and Nunez, 1989) and that testosterone may not necessarily contribute to high levels of aggression in adult animals (Demas *et al.*, 1999). It is important to note that the inverse relationship between circulating testosterone levels and aggression does not appear to be a direct one. For exam-

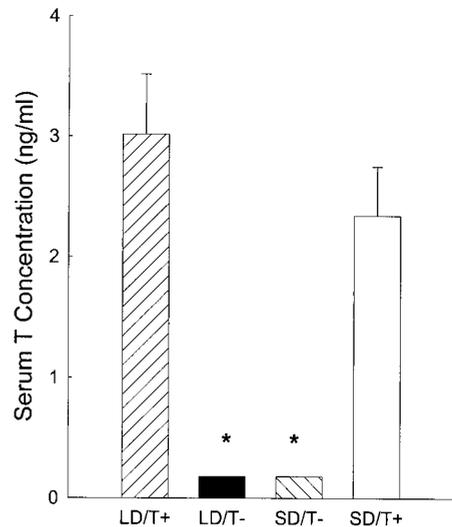


FIG. 4. Mean (\pm SEM) serum testosterone (T) concentration of animals housed in long days receiving sham castrations (LD/T+), long-day castrated animals (LD/T-), short-day animals receiving empty capsules (SD/T-), and short-day animals receiving testosterone (SD/T+). Significant differences between pairwise means are indicated by an asterisk (*) ($P < 0.05$).

ple, if testosterone is the primary factor determining aggression, then long-day castrated animals would display comparable levels of aggression to short-day intact animals. This did not occur in the present study, suggesting that factors in addition to testosterone play a role in mediating short-day increases in aggression.

One possible explanation for the increased aggression observed in hamsters housed in short photoperiods is the size difference between short-day-housed hamsters and nonaggressive intruder animals. For example, previous research has demonstrated that larger animals are typically more dominant and, thus, demonstrate more aggressive behavior than smaller, less dominant animals (Drickamer and Vandenberg, 1973; Payne and Swanson, 1970). This explanation, however, is unlikely in the present studies because hamsters housed in short days had *decreased* body mass and, thus, should display *less* aggression compared to long-day-housed animals.

Another, more interesting explanation for our results is that exposure to short photoperiods increases androgen receptor sensitivity to testosterone. It is important to note that although testosterone in short-day, gonadally regressed hamsters is at basal levels, testosterone is not completely absent. A small amount of testosterone is secreted by the gonads in short-day hamsters; in addition, other sources of androgen secretion (e.g., the adrenal glands) are present. Thus, it is possible that small amounts of testosterone may actually lead to basal or even increased behavioral effects due to increased sensitivity of steroid receptors. It is unlikely that increased steroid receptor sensitivity explains the short-day-induced increased aggression observed in the present study because exogenous testosterone *reduces* aggression in short-day animals.

Vasopressin is another hormone that is involved in mediating aggression in several species (Winslow, Hastings, Carter, Harbaugh, and Insel, 1993; Goodson, 1998; Stribley and Carter, 1999; Bester-Meredeth, Young, and Marler, 1999) and is likely involved in the short-day-induced increased aggression observed in the present study. Injection of vasopressin into the medial preoptic area of Syrian hamsters stimulates aggression, whereas vasopressin antagonists injected into the same nuclei reduce aggression (Ferris and Potegal, 1989; Potegal and Ferris, 1989; Ferris, Melloni, Koppel, Perry, Fuller, and Delville, 1997). It is unclear, however, how photoperiod affects vasopressin levels within the central nervous system. Some studies have shown increased vasopressin immunoreactivity in species exposed to short photoperiods (Juszczak, Luciano, Bozena, Steger, Fadden, and Bartke, 1997; Bitt-

man, Jetton, Villalba, and Devries, 1996; Duncan, Cheng, and Heller, 1995), whereas others have shown no differences or decreases in vasopressin in animals exposed to short photoperiods (Albers, Rowland, and Ferris, 1991; Duncan, 1998). It is possible that photoperiod alters the sensitivity of vasopressin receptors rather than vasopressin itself. Therefore, even if vasopressin levels are not increased during short photoperiods, an increased number of vasopressin receptors or increased receptor sensitivity may explain short-day-induced increases in aggression observed in previous studies and in the present study.

Short-day-induced increases in aggression in Siberian hamsters also may be due to the increased duration of melatonin secretion. Ambient photoperiodic information is transduced by the pineal gland into a melatonin signal with peak concentrations of the hormone occurring during the dark and basal levels occurring during the light portion of the day. Maintenance of animals in short days (i.e., long nights) results in a prolonged duration of melatonin secretion. Although melatonin has traditionally been considered primarily a reproductive hormone, it regulates a wide range of seemingly unrelated physiological, morphological, and behavioral processes (reviewed in Bartness *et al.*, 1993). For example, melatonin appears to mediate the short-day-induced increases in agonistic behavior seen in female Syrian hamsters (Fleming *et al.*, 1988; Badura and Nunez, 1989). Female hamsters housed in short days display increased aggressive behavior compared with long-day-housed hamsters; this short-day-induced increase can be blocked by pinealectomy (Fleming *et al.*, 1988; Badura and Nunez, 1989). Furthermore, long-day-housed hamsters treated with exogenous melatonin to mimic short-day levels also display increased aggression (Fleming *et al.*, 1988). It is not clear, however, whether the relationship is as simple as increased duration of melatonin secretion leading to increased aggression. For example, both previous research (Garrett and Campbell, 1980), and the present data demonstrate that the increases in aggression in short-day-housed hamsters are reversed after prolonged exposure to short days (i.e., when animals become refractory). It is important to note that this "return" to long-day-like levels of aggression occurs despite continued short-day patterns of melatonin secretion. Although the absolute duration of melatonin secretion, and not sensitivity to the hormone, is responsible for the initial gonadal regression, these results suggest that melatonin sensitivity, rather than the absolute duration of melatonin

secretion, mediate photoperiodic changes in aggression in hamsters.

At an ultimate level of analysis, increased aggressive behavior in short days may confer an evolutionary advantage at a time when food availability is presumably low and competition for limited available resources is extremely high. For most nontropical rodents the reduced day length of winter is accompanied by reduced ambient temperature and food availability as well as increased thermogenic demand. Thus, in the field short-day increases in aggression would occur at a time during harsh environmental conditions and limited resources. Specifically, more dominant animals may be more successful in procuring necessary resources to sustain life and, thus, ensure future reproductive success. Regardless of the adaptive significance of short-day-induced aggression, the current data suggest that short-day increases in aggression are inversely related to levels of circulating testosterone.

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