Role of photoperiod in reproductive maturation and peripubertal hormone concentrations in male collared lemmings (*Dicrostonyx groenlandicus*)

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Summary. Onset of sexual maturation was determined in weanling male collared lemmings exposed to one of three experimental regimens of different photoperiods before and after weaning. Animals gestated in photoperiods of either 16 h light:8 h dark or 8 h light:16 h dark. Those from 16 h light:8 h dark were transferred at 19 days of age to either 20 h light:4 h dark or 8 h light:16 h dark; those gestated under 8 h light:16 h dark remained in that photoperiod throughout the experiment. After exposure for 15, 20, 25 or 30 days to the postweaning photoperiod, animals were killed and the following parameters assessed: body weight, testes weight, seminal vesicle weight, the presence or absence of epididymal spermatozoa and serum concentrations of prolactin, testosterone and corticosterone. All parameters except serum testosterone were significantly influenced by photoperiod. Animals housed under 8 h light:16 h dark had significantly greater body weights than those housed under 20 h light:4 h dark, a response that differs from that reported for other arvicoline rodents. The group gestated on 16 h light:8 h dark and transferred on day 19 to 8 h light:16 h dark had lower testes and seminal vesicle weights than the other two groups, and mature spermatozoa in the epididymides appeared 5 days later than in the 20 h light:4 h dark group. Serum prolactin was largely undetectable in animals from both 8 h light:16 h dark groups, but all males housed in 20 h light:4 h dark had 2.0–15.0 ng prolactin ml⁻¹. Concentration of serum corticosterone was higher in animals weaned into long photoperiod, and decreased with age. These data indicate that weanling male *D. groenlandicus* are reproductively photoresponsive, but use a decrease in photoperiod, not static short-photoperiod exposure, to alter the rate of development. Prolactin was largely undetectable in animals exposed to short photoperiod, indicating that high concentrations of this hormone are not important for maturation. Low prolactin concentrations in animals in short photoperiods may mediate the annual moult to white pelage. The short-photoperiod-mediated decrease in corticosterone may play a role in seasonal changes in body weight and composition.

Keywords: photoperiod; maturation; prolactin; testosterone; corticosterone; lemming

Introduction

Collared lemmings, *Dicrostonyx groenlandicus*, inhabit the holarctic regions, from Greenland west to Alaska, 60–70° N (Banfield, 1974) and consequently are exposed to dramatic seasonal changes in temperature and photoperiod. The breeding season reflects this temporally harsh and variable environment, generally spanning the months from March to August or September, with a hiatus in June during meltoff (Banfield, 1974; Negus & Berger, 1987). Young born early in the breeding season mature and reproduce during the year of their birth, whereas those born later may

overwinter and reproduce the following year (P. J. Berger and N. C. Negus, pers. commun). Observations of winter breeding in some years (Krebs, 1964; MacLean *et al.*, 1974) suggest that this species is not strictly photoperiodic with respect to reproduction.

Arvicoline rodents (voles and lemmings) use photoperiod to time reproduction and to regulate growth and maturation. Breeding and maturation in the field and laboratory are optimal under conditions of long or increasing photoperiod (Clarke & Forsyth, 1964; Pinter, 1968; Grocock & Clarke, 1974; Hasler & Banks, 1975; Nelson, 1987). Such responses to photoperiod have been observed in many rodent species (for reviews, see Zucker *et al.*, 1980; Bronson, 1989) and are adaptive; production of offspring under long photoperiods results in the weaning of young during the time of year when food is most available and temperatures are most moderate, maximizing the chances of offspring successfully maturing and breeding. Additionally, the energy demands of lactating females are more easily met in seasons of the year when food is readily available. Arvicolines are reproductively opportunistic, however, and also breed when exposed to short or decreasing photoperiod if other environmental cues or conditions are present. Food, water, certain plant chemicals and social factors also affect reproduction in arvicoline species (Pinter & Negus, 1965; Hasler, 1975; Berger *et al.*, 1977, 1981; Nelson *et al.*, 1983; Rissman & Johnston, 1986; Negus & Berger, 1987).

An earlier study (Hasler *et al.*, 1976) examined various reproductive parameters in laboratory-housed adult and weanling male and female *D. groenlandicus* transferred to long (20 h light:4 h dark) or short (6 h light:18 h dark) photoperiods. After 10 weeks of treatment, no differences were found in any of the indices of reproductive function assessed (weights of reproductive tissues, follicle size, epididymal spermatozoa, testosterone concentrations) and the authors concluded that this species was not reproductively photoresponsive; but weanlings were not examined during the period over which sexual maturation would be expected to occur (40–60 days of age, based on findings in other arvicoline species; Grocock, 1979; Kinch *et al.*, 1986; Lee *et al.*, 1987). Consequently, any possible photoperiod-related difference in the onset of maturation may not have been detected. Since the timing of maturation is an important event in the life history of short-lived rodents (Negus *et al.*, 1977; Bronson, 1988), reproductive photoresponsiveness may be selectively manifested before puberty.

We determined the age of reproductive maturation in weanling male *D. groenlandicus* transferred from 16 h light:8 h dark to either short (8 h light:16 h dark) or long (20 h light:4 h dark) photoperiods. These lighting conditions are similar to those used by Hasler *et al.* (1976) and were chosen so that results of the two studies could be compared. The earlier study determined that, when examined as adults, lemmings were reproductively photoinsensitive; the present study examined photoresponsiveness in peripubertal animals. In addition to the above two regimens, we also examined animals gestated and raised in 8 h light:16 h dark. These later conditions would convey short-photoperiod information to animals before and after birth. By using this additional photoperiod treatment and by examining animals at a particularly critical point in their development, we hoped to determine whether *D. groenlandicus* is truly photoinsensitive with respect to reproduction.

Sera from all experimental animals were analysed for prolactin and testosterone, the concentrations of which are known to be influenced by photoperiod in other species (Goldman *et al.*, 1981; Blank & Desjardins, 1986). Prolactin may play a role in sexual maturation in male golden hamsters (Stallings *et al.*, 1985; Stroud *et al.*, 1985) and appears to participate in the annual pelage colour cycle in Siberian hamsters (Duncan & Goldman, 1984a; Duncan *et al.*, 1985). Testosterone is important for reproductive development and function. We also quantified serum corticosterone, since, in arvicoline species, changes in adrenal size and function are associated with changes in environmental conditions, season, maturity and reproductive status (Chitty & Clarke, 1963; Andrews & Ryan, 1971; Andrews & Strohbehn, 1971; Seabloom *et al.*, 1978). The physiological significance of these changes is unknown. Corticosterone is involved in metabolic processes and, when present in high concentrations, can adversely influence reproductive function (Moberg, 1987).

Materials and Methods

Animals and photoperiods

The male *Dicrostonyx groenlandicus* used in this study were obtained from a laboratory colony maintained at the Department of Biology, University of Utah, Salt Lake City, UT, USA. The colony was established from animals trapped at Igloodik Island, Northwest Territories, Canada (69°23' N, 81°50' W). A breeding colony was maintained under a 16 h light:8 h dark photoperiod and an ambient temperature of $18 \pm 1^\circ\text{C}$. For the production of offspring under an 8 h light:16 h dark photoperiod, mated pairs were transferred to that photoperiod 4 days after pairing.

At weaning (19 days old), male lemmings were caged in pairs. Those from the 16 h light:8 h dark colony were transferred at random to either 8 h light:16 h dark (short photoperiod) or 20 h light:4 h dark (long photoperiod), whereas those from 8 h light:16 h dark remained in the natal photoperiod. Animals were housed in $57 \times 17 \times 15\text{ cm}^3$ fibreglass cages, fitted with hardware cloth lids, containing sawdust and cotton batting. Rabbit pellets (Intermountain Farmers Assoc., Salt Lake City, UT, USA) and water were available *ad libitum*.

Hormone measurements

Groups of six animals were killed midway through the photophase every 5 days from 33 to 48 days of age. A pilot experiment showed that sexual maturation, indicated by the presence of spermatozoa in the epididymides, occurred between 33 and 48 days of age. Animals were weighed to the nearest 0.01 g and testes and seminal vesicles were removed, blotted dry and weighed to the nearest 0.1 mg. Epididymides were removed, sectioned histologically and examined microscopically for the presence of spermatozoa. Trunk blood was collected at the time of death and sera were stored at -20°C until analysed for prolactin, testosterone and corticosterone.

Prolactin was measured with a hamster prolactin kit (obtained from A. F. Parlow of the Pituitary Hormones and Antisera Center, Torrance, CA, USA). Reagents included rat antiserum to hamster prolactin (AFP-7472988), highly purified hamster prolactin for iodination (AFP-10302E) and hamster prolactin reference preparation (AFP-10302E). Antigen was iodinated (Iodine-125, ICN) with the chloramine T method, following the guidelines included with the kit, and added to each assay tube at 10 000 c.p.m. Antiserum was used at a final tube dilution of 1:85 000, which bound about 30% of the radioactivity added in an assay volume of 0.425 ml. The standard curve ranged from 0.02 to 5.0 ng. The lower limit of sensitivity, calculated as 90% bound using a regression equation, varied between assays from 0.01 to 0.03 ng. The intra- and interassay coefficients of variation were 3.3 and 7.8%, respectively, based on repeated measures of a serum pool.

The prolactin assay was validated for use with *D. groenlandicus* sera by comparing the slope of serial dilutions of serum pools and pituitary homogenates, obtained from adult males, with the slope of the standard curve. The displacement curves produced by both were parallel to that produced by the hamster prolactin standard (Fig. 1a and b). Serum samples obtained from the juvenile males in the present experiment were assayed in duplicate at either 50 μl (short-photoperiod animals) or 25 μl (long-photoperiod animals); these quantities were chosen from the results of a preliminary assay.

Additivity was determined by assaying 50 μl aliquots of *D. groenlandicus* sera to which known amounts of hamster prolactin had been added. Recovery of hamster prolactin (0.04, 0.08, 0.16, 0.31 and 0.625 ng), when added to *D. groenlandicus* sera, ranged from 100 to 121% (average 108%).

The validations discussed above indicate that the anti-hamster prolactin antiserum crossreacts with prolactin in *D. groenlandicus* sera. Caution should be taken when comparing the prolactin concentrations reported here with those reported elsewhere for other species, since it is not known whether the antiserum binds prolactin with an affinity equal to that for the homologous hormone. Decreased antibody affinity for lemming prolactin, relative to hamster prolactin, would result in an underestimation of hormone content in lemming sera.

Serum testosterone was measured with antiserum S-250 (from G. D. Niswender) used at a dilution of 1:376 000; 100 μl of serum was extracted with 5 ml dichloromethane, reconstituted in assay buffer (0.1 mol phosphate buffer l^{-1} , 1% gelatin, 1% sodium azide) and assayed in duplicate. Extraction recovery was 77% and values were not corrected for extraction losses. Samples were incubated for 24 h at 4°C after which bound and free hormone were separated with dextran-coated charcoal. The standard curve ranged from 3 to 400 pg, 3 pg being the lower limit of assay sensitivity (90% bound). Intra- and interassay coefficients of variation were 3.6 and 6.5%, respectively.

Serum corticosterone was measured with antiserum B3-163 (from Endocrine Sciences, Tarzana, CA, USA) used at 1:120 320; 10 μl of serum was diluted to 1 ml in assay buffer (see above) and heat inactivated (at 65°C for 1 h), after which 100 μl aliquots were assayed in duplicate. Incubation and separation conditions were identical to those given for the testosterone assay. The standard curve ranged from 7.8 to 2000 pg. The lower limit of assay sensitivity was calculated to be 10 pg (90% bound). Intra- and interassay coefficients of variation were 4.8 and 10%, respectively.

Dilutions of a lemming serum pool were heat inactivated, as described for corticosterone and assayed for cortisol (for assay details, see Donham *et al.*, 1988). Cortisol was undetectable in samples, which, when assayed for corticosterone, had concentrations ranging from 7 to 314 pg (92 to 28% bound).

Statistical analysis

Body weights, testes weights, seminal vesicle weights, serum testosterone and serum corticosterone were analysed with a two-way ANOVA and a least-squares means test on log-transformed values (SAS Institute Inc., version 5). The

Fig. 1. Regression plots of displacement curves produced by (a) hamster prolactin reference preparation AFP-10302E (○) and a *Dicrostonyx groenlandicus* serum pool (●) (slopes = -0.81616 and -0.81568 , respectively) and (b) reference preparation and *D. groenlandicus* pituitary homogenates (slopes = -0.78787 , -0.81332 and -0.71077 , for standard (○), pituitaries from 8 h light:16 h dark-housed animals (●) and pituitaries from 20 h light:4 h dark-housed animals (Δ), respectively).

percentages of animals in each group showing epididymal spermatozoa were compared with 2×2 contingency tables. The proportion of detectable versus nondetectable prolactin values were compared between groups with 2×2 contingency tables. Since the samples from the 8 h light:16 h dark to 8 h light:16 h dark group were assayed later than those from the other two groups, absolute prolactin values were not compared.

Results

Body, testes and seminal vesicle weights

Two-way analysis of variance showed that body weights were significantly affected by photoperiod and age (Fig. 2a, $P < 0.0001$). Long-photoperiod animals differed, with respect to body weight, from both of the short-photoperiod groups ($P < 0.0001$). Body weights at 48 days of age were different from those at all other ages ($P < 0.0001$ versus 33 and 38 days; $P < 0.001$ versus 43 days). Testes weights were significantly affected by photoperiod and age (Fig. 2b, $P < 0.0001$). The interaction of photoperiod and age was also significant ($P < 0.005$). Animals transferred to 8 h light:16 h dark had tissue weights that differed from those of the other two groups ($P < 0.0001$). Testes from animals 43 and 48 days old were significantly different from those of animals 33 and 38 days old ($P < 0.01$, 43 versus 33 days; $P < 0.0001$, all other comparisons). Both photoperiod and age influenced seminal vesicle weights (Fig. 2c, $P < 0.0001$). The interaction of photoperiod and

age was significant at $P < 0.05$. Tissue weights from males transferred to 8 h light:16 h dark were different from those of the other two groups ($P < 0.0001$). Seminal vesicles from animals 43 and 48 days of age were significantly different from those of animals 33 and 38 days of age ($P < 0.0005$, 43 versus 38 days; $P < 0.0001$, all other comparisons). Spermatozoa were not found in the epididymides from 33 or 38-day-old males of any photoperiod (Fig. 2b). Males in long photoperiods all had epididymal spermatozoa at 43 days of age, whereas only 33% of those animals transferred to short photoperiod had spermatozoa at this age; this difference was significant ($P < 0.05$). The group raised under 8 h light:16 h dark did not differ from either of the other two groups. At 48 days of age, 83% of males transferred to 8 h light:16 h dark had epididymal spermatozoa; this is not significantly different from the 100% observed in males housed under 20 h light:4 h dark or raised under 8 h light:16 h dark.

Fig. 2. (a) Body weights, (b) testes weights and percentage of animals in each group with epididymal spermatozoa and (c) seminal vesicle weights at the time of death in *Dicrostonyx groenlandicus*. (□) 16 h light:8 h dark-20 h light:4 h dark, (▨) 16 h light:8 h dark-8 h light:16 h dark, (■) 8 h light:16 h dark-8 h light:16 h dark. See Results for significant differences between groups. Data are means $\pm$ SEM.

Table 1. Effects of photoperiod treatment on serum prolactin (ng ml⁻¹) in male collared lemmings

Age (days)	Photoperiod		
	16 h light:8 h dark– 20 h light:4 h dark	16 h light:8 h dark– 8 h light:16 h dark	8 h light:16 h dark– 8 h light:16 h dark
	Number detectable/n Mean ± SEM ^a	Number detectable/n Mean ± SEM ^a	Number detectable/n Mean ± SEM ^a
33	6/6† 5.1 ± 0.4	1/6 0.6	1/6 6.8
38	6/6† 4.1 ± 0.2	0/6 ^b	2/6 4.0 ± 1.0
43	6/6† 4.4 ± 0.8	2/6 2.6 ± 2.1	1/6 2.2
48	6/6† 5.6 ± 1.9	0/6 ^b	0/6 ^c

†Significantly different from both 8 h light:16 h dark groups.

^aMean ± SEM of detectable values only.

^bUndetectable samples <0.4 ng ml⁻¹.

^cUndetectable samples <0.6 ng ml⁻¹.

Fig. 3. Concentration of (a) testosterone and (b) corticosterone in serum of *Dicrostonyx groenlandicus*. (□) 16 h light:8 h dark–20 h light:4 h dark; (▨) 16 h light:8 h dark–8 h light:16 h dark; (■) 8 h light:16 h dark–8 h light:16 h dark. Data are means ± SEM. *n* = 6 for all groups except 16 h light:8 h dark–8 h light:16 h dark at age 43 days where *n* = 4.

Hormone concentrations

Prolactin concentrations were significantly influenced by photoperiod (Table 1, $P < 0.05$, 20 h light:4 h dark versus both 8 h light:16 h dark groups). All males in long photoperiods had detectable concentrations of prolactin, but only seven of the 48 lemmings housed under short photoperiod had a measurable hormone content.

Serum testosterone was not influenced by photoperiod or age alone (Fig. 3a, $P > 0.05$), but the interaction of the two parameters was significant ($P < 0.05$).

Both photoperiod and age influenced serum corticosterone concentration (Fig. 3b, $P < 0.05$). Males in long photoperiods differed from males raised in 8 h light:16 h dark ($P < 0.01$) and those transferred to 8 h light:16 h dark ($P < 0.05$). Serum corticosterone concentration of 48-day-old males differed from that of 33 and 38-day-old animals ($P < 0.05$).

Discussion

The present study was designed to determine whether photoperiod influences the timing of reproductive maturation in male collared lemmings. An effect of photoperiod on maturation has been documented in males of several species of arvicoline rodents (*Microtus pennsylvanicus*: Lee *et al.*, 1987; *M. agrestis*: Grocock, 1979; Kinch *et al.*, 1986; *M. ochrogaster*: Nelson, 1985). In these studies, the appearance of mature spermatozoa was delayed by up to 200 days by exposure to short photoperiod.

The findings presented here clearly demonstrate that weanling male *D. groenlandicus* are also photoresponsive with respect to reproduction. Testes and seminal vesicle weights and the proportion of animals showing epididymal spermatozoa were significantly influenced by photoperiod. This conclusion contrasts with that of Hasler *et al.* (1976), who found no effect on reproductive parameters of exposure to similar photoperiod manipulations at weaning or during adulthood. In this earlier study, however, animals were examined only after 70 days of exposure to the experimental photoperiods. It is possible that, after 70 days, any photoperiodically induced differences in reproductive parameters present early in the treatment period may have disappeared. Our data support this possibility in that the onset of fertility, as indicated by the appearance of spermatozoa in the epididymides, was delayed by only 5 days in animals transferred to 8 h light:16 h dark (present study), while animals switched to 8 h light:16 h dark at weaning and examined after 70 days all had mature epididymal spermatozoa (B. A. Gower & T. R. Nagy, unpublished).

Although, in the present experiment, the effect of photoperiod on the timing of fertility onset was significant, the ecological, or functional, importance of this 5 day delay is not obvious. The possibility exists that, under natural conditions, the reproductive response to a reduction in photoperiod may be more dramatic. When reduced photoperiod occurs simultaneously with reductions in temperature and food quality at the onset of the arctic autumn, maturation in juveniles and reproductive activity in adults may slow or cease. In support of this hypothesis, reproductive activity and gonadal function were compromised when adult lemmings were cold-stressed (Quay, 1960). Mated *D. groenlandicus* pairs failed to produce young when housed at -9 to -5°C , and follicular maturation in females was depressed.

Alternatively, maturation in males may not be strongly affected by environmental factors. Natural selection often has allowed evolution of systems in which, because of the energy constraints associated with reproduction, the timing of puberty in the female is regulated more stringently by environmental conditions than is that of the male (Bronson, 1988). Consequently, further experimentation may find that peripubertal female *D. groenlandicus* show a more pronounced reproductive response to environmental factors than do males.

Only animals that experienced a decrease in photoperiod, not those raised under short photoperiod, responded to 8 h light:16 h dark with a depressed rate of maturation. *Dicrostonyx groenlandicus* have been shown to respond to a decrease in photoperiod with depressed reproductive function. When mated pairs acclimatized to 24 h light were transferred to 14 h light:10 h

dark, the mean number of litters produced and the mean litter size were reduced when compared with pairs remaining in 24 h light (Negus & Berger, 1987). A preferential response to a change in photoperiod, rather than the absolute number of hours of light per day, might be adaptive for a species inhabiting latitudes at which it experiences rapid seasonal changes in photoperiod.

In the present study, lemmings maintained under constant short photoperiod matured more rapidly than those transferred from 16 h light:8 h dark to 8 h light:16 h dark. Since the critical daylengths for triggering short-photoperiod responses have not been determined in this species, we can only speculate as to the ecological relevance of the above-mentioned photoperiod manipulations. Static short-photoperiod treatment in the laboratory may simulate the natural arctic autumn/winter photoperiod (6–8 h light day⁻¹, including civil twilight, from 17 November to 25 January at 66° N; Nautical Almanac Office, 1991). Selection may favour rapid maturation in animals born under these conditions in preparation for spring breeding. The animals switched from long to short photoperiod experienced a decrease in daylength similar to that which occurs in the arctic from 6 September to 17 November (16 h light:8 h dark to 8 h light:16 h dark). Since collared lemmings cease reproducing in August or September, young born in late summer might be expected to mature at a slower rate, possibly under the influence of decreasing photoperiod.

The increase in photoperiod, from 16 h light:8 h dark to 20 h light:4 h dark, experienced by lemmings in this study, simulates photoperiod changes that would be observed in the natural situation by animals born on 1 April (16 h light:8 h dark). These animals would observe a 20 h light:4 h dark photoperiod on 28 April and would reach sexual maturity during the next few weeks. Lemmings with this life history mature rapidly, possibly under the influence of increasing photoperiod, and can breed in the year of their birth. Work underway to determine critical photoperiods in collared lemmings may help in understanding the roles of relative and absolute daylength in seasonal physiological changes in this species.

In the present experiment and in that of Hasler *et al.* (1976), young lemmings exposed to a short photoperiod showed a significant increase in body weight. The decrease in surface to volume ratio resulting from this increase in weight may be of benefit to a small mammal exposed to low temperatures for a long period of the year. This strategy for coping with low winter temperatures differs from that of other arvicoline rodents, which show either a decrease in body weight or growth rate when exposed to decreased or short photoperiod (Horton, 1984; Rhodes, 1989), or no body weight response to changes in photoperiod (Grocock, 1979).

Lemmings also show photoperiod-dependent differences in body composition. Although body weight is increased by short-photoperiod exposure, the relative amount of body fat decreases (Hasler *et al.*, 1976; Nagy, 1992); the mechanism for this change is unknown. In the present study, we observed significant differences in serum corticosterone concentration between animals housed in long and short photoperiods. This hormone influences various metabolic processes, including lipid mobilization and glucose utilization (Granner, 1988) and may play a role in the seasonal changes in body weight and composition observed in *D. groenlandicus*. High glucocorticoid concentrations depress growth in rats (Wehrenberg *et al.*, 1990), suggesting that the decrease in corticosterone associated with short-photoperiod exposure in lemmings may allow the observed increase in growth rate. The reduced corticosterone observed in animals housed in 8 h light:16 h dark may also be involved with thermogenic adjustments. In rats and mice, depression of circulating glucocorticoids, via pharmacological means or adrenalectomy, stimulated brown adipose tissue activity (Hardwick *et al.*, 1989; Kim & Romsos, 1990), a response which prevented obesity in genetically obese mice. Consequently, the short-photoperiod-induced decline in serum corticosterone observed in *D. groenlandicus* may facilitate thermogenesis, a response which would have adaptive value in the autumn and winter, when ambient temperature is low, and may explain the change in body composition observed in animals housed in short photoperiods.

In the present study, serum corticosterone also tended to decrease with maturation. Similar age-related changes in adrenal corticosteroid production were observed in golden hamsters (Donham *et al.*, 1988), brown lemmings, *Lemmus trimucronatus* (Andrews *et al.*, 1975) and

marmots (Armitage, 1991). The physiological significance of these changes is unknown, although the negative effects of glucocorticoids on reproductive function may suggest that a peripubertal decrease in these hormones is permissive to sexual maturation.

Serum prolactin concentration was significantly depressed in lemmings exposed to short photoperiod, when compared with animals housed under long photoperiod. An effect of photoperiod on prolactin has been well documented in hamsters (Bex *et al.*, 1978; Goldman *et al.*, 1981; Duncan *et al.*, 1985) and in deer mice (Blank & Desjardins, 1986). Photoperiodically induced seasonal changes in prolactin are thought to influence gonadal maturation and regression. Treatment of photoregressed adult male hamsters with exogenous prolactin stimulated testicular growth (Bex *et al.*, 1978), as did treatment of juveniles with ectopic pituitary transplants (Stallings *et al.*, 1985). Treatment of juvenile males with bromocryptine, a dopamine agonist which depresses endogenous prolactin, retarded maturation (Stallings *et al.*, 1985; Stroud *et al.*, 1985). The results of the present study, however, suggest that, in *D. groenlandicus*, high concentrations of prolactin are not necessary for the maturation process. This observation may indicate a different role for prolactin in this reproductively opportunistic arvicoline rodent when compared with the highly photoperiodic hamster.

Photoperiod-related changes in prolactin also appear to contribute to the seasonal moults observed in Siberian hamsters (*Phodopus sungorus*). In the laboratory, adult male Siberian hamsters begin to develop a white pelage about 8 weeks after transfer to short photoperiod (Duncan & Goldman, 1984b), whereas animals transferred to 8 h light:16 h dark at birth begin to moult between 30 and 40 days of age (Hoffmann, 1978). When treated with bromocryptine, long-photoperiod-housed, castrated, Siberian hamsters developed a white winter pelage, and hamsters refractory to short photoperiod failed to develop the summer pelage (Duncan & Goldman, 1984a). *Dicrostonyx groenlandicus* also moults to a white winter pelage when exposed to short photoperiod. In the present experiment, the animals raised in 8 h light:16 h dark developed a white pelage immediately after birth, and those transferred to 8 h light:16 h dark at 19 days of age were in the process of moulting to the winter pelage at the time of death (33–48 days of age). Serum prolactin was largely undetectable in all age groups of lemmings housed under 8 h light:16 h dark, indicating that, at most, 15 days of short photoperiod exposure is required to cause a decline in the hormone. This time course is similar to that observed in male *P. sungorus* (Matt *et al.*, 1990). The alteration of serum prolactin by photoperiod may mediate seasonal pelage colour changes in lemmings and Siberian hamsters.

In neither the present study nor in that of Hasler *et al.* (1976) was an effect of photoperiod on testosterone observed; concentrations were similar in the two studies. One would expect testosterone concentration to reflect the weights of testes and seminal vesicles, and therefore to be lower in animals transferred to 8 h light:16 h dark. The lack of such a correlation in this study may reflect the large amount of variability present in the serum testosterone concentrations.

The results indicate that growth of reproductive and somatic tissues and the timing of maturation in male *D. groenlandicus* are influenced by changes in photoperiod after weaning. The effect of photoperiod alone on the timing of maturation is slight, however, and may not be functionally significant. This observation suggests that *D. groenlandicus* is reproductively opportunistic, or facultative, rather than obligately photoperiodic (Negus & Berger, 1972) and may use a combination of environmental cues for timing maturation and breeding. Since other physiological parameters (body weight and composition) respond dramatically to photoperiod, *D. groenlandicus* appears to have uncoupled the regulation of the metabolic and reproductive systems. Serum prolactin was reduced to undetectable concentrations in male *D. groenlandicus* by exposure to 8 h light:16 h dark, suggesting that prolactin is not important for maturation in this species. However, seasonal changes in the concentration of this hormone may play a role in the annual pelage cycle. The observed decrease in serum corticosterone in animals housed in short photoperiods may be important for seasonal changes in body composition or thermogenesis.

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