Alteration of testicular response to long photoperiod by transient exposure to short photoperiod in collared lemmings (*Dicrostonyx groenlandicus*)

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The reproductive response of collared lemmings (*Dicrostonyx groenlandicus*) to photoperiod is unique for rodents. Whereas most reproductively photoresponsive rodents show maximal gonadal growth when exposed to long photoperiod (long day), collared lemmings show delayed maturation when born and maintained under this condition. However, transfer of lemmings from short photoperiod (short day) to long day results in maximal gonadal growth, indicating that the response to long day depends upon photoperiod history. We hypothesized that the slowing of maturation observed in animals born and maintained on long day reflects an inability to respond fully to long day, resulting from the absence of previous exposure to short day. To determine whether young lemmings born in long day are capable of being stimulated by long day, we exposed them at weaning (19 days of age) to 1, 6 or 10 weeks of short day, and then challenged them with a second exposure to long day. Relative to animals transferred permanently to short day at weaning, lemmings exposed to 6 weeks of short day showed accelerated gonadal growth after both 5 and 10 weeks of subsequent exposure to long day, and those exposed to 10 weeks of short day had larger testes after 6 weeks of long day. Thus, during transient exposure to short day, the animals acquired sensitivity to the stimulatory effects of long day. The responses of body mass, bifid claw width and pelage colour to the photoperiod manipulations did not parallel that of the gonads, indicating independent regulation of somatic and reproductive parameters. The unique way in which the reproductive system of collared lemmings responds to photoperiod may reflect evolution in an environment where the production of offspring during periods of unchanging long day (for example, the Arctic summer) is not selectively advantageous.

Introduction

The Arctic rodent *Dicrostonyx groenlandicus* (collared lemming) shows several physiological and morphological responses to changes in day length. In the laboratory, exposure to photoperiods ranging from 2 h light and 22 h dark per 24 h (2L:22D) to 24L:0D affects body mass, pelage colour, bifid claw width and serum hormone concentrations (Hasler *et al.*, 1976; Reynolds and Lavigne, 1989; Maier and Feist, 1991; Nagy *et al.*, 1993a, b). Exposure to long photoperiod is associated with a small body mass and a grey–brown pelage. Exposure to short photoperiod results in body mass gain, moult to a white winter pelage, and growth of second, bifid claws below the primary claws on the third and fourth digits of the forepaws.

The reproductive response of collared lemmings is likewise sensitive to photoperiod, but in a manner atypical to rodents.

When born in long photoperiod (22L:2D; long day (LD)) in the laboratory, reproductive maturation is impeded by continued maintenance in long day (Nagy *et al.*, 1993a, b). This response is not due to the lack of melatonin production (Gower *et al.*, 1996) and therefore is not analogous to the slow sexual maturation observed in Siberian hamsters maintained in constant light (Stetson *et al.*, 1989). When born in short photoperiod (8L:16D; short day (SD)) and transferred at weaning to LD, lemmings have heavier testes 10 weeks after weaning than the testes of animals exposed to all other photoperiod manipulations tested (Nagy *et al.*, 1993a), indicating that LD can be stimulatory, but only under certain circumstances. Transfer from LD to SD permits gonadal growth but results in testes smaller than those observed in animals transferred from SD to LD (Nagy *et al.*, 1993b). Taken together, laboratory data indicate that collared lemmings mature at three statistically distinct rates, as indicated by testes masses 10 weeks after weaning: slow (animals born and maintained on LD); intermediate (animals born on LD and transferred to SD, or born and maintained on SD); and rapid (animals transferred at weaning from SD to LD).

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Among other rodents in which the reproductive response to photoperiod has been studied, none show a response similar to that of collared lemmings; that is, impedence of maturation when exposed to long photoperiod and enhancement of maturation when transferred from long to short photoperiod. Reproductive maturation in many temperate small mammals is stimulated by long days (regardless of photoperiod history) and inhibited, at least transiently, by short days (Hoffmann, 1978; Bronson, 1989; Horton, 1994), whereas most rodents from south-temperate and tropical latitudes show either an attenuation of the temperate-type response or no response to changes in photoperiod (Carlson *et al.*, 1989; Bronson and Heideman, 1992; Heideman and Bronson, 1992, 1994). Inhibition of maturation by long photoperiod has not been observed in a rodent other than the collared lemming. However, impeded maturation in response to long photoperiod is observed in several avian species. For example, starlings (*Sturnus vulgaris*), which are born in the spring under the influence of long day lengths, do not mature reproductively in the spring or summer of their birth. Data from wild-caught, hand-reared birds have shown that offspring are refractory to the stimulatory effects of long day lengths from the time of hatching (McNaughton *et al.*, 1992). Maturation is dependent upon development of photosensitivity, which occurs during exposure to the short days of autumn and winter (Williams *et al.*, 1989). In wild starlings, as in temperate small mammals (Bronson, 1989; Steinlechner and Niklowitz, 1992), gonadal growth and breeding are induced ultimately by exposure to long photoperiod. This strategy is thought to have evolved in response to the negative selective pressure associated with producing young during unfavourable environmental conditions (for example, low food availability; Dawson and Goldsmith, 1982).

The present experiment was conducted to test the hypothesis that, much like starlings, collared lemmings born in LD are unable to respond maximally to the stimulatory effects of LD on gonadal growth without prior exposure to SD. Under natural conditions, a prolonged period of unchanging LD would occur for 10 weeks in late spring or early summer (mid-May to late July). Although this natural, prolonged, long photoperiod would be 24L:0D, we used 22L:2D in this experiment to be consistent with previous laboratory data indicating that prolonged exposure to 22L:2D is inhibitory. A further aim of this study was to characterize the nature of the somatic responses to the indicated photoperiod manipulations, and to determine whether somatic responses are regulated similarly to reproductive responses.

Materials and Methods

Animals

Collared lemmings were obtained from our colony maintained at the University of Delaware. The progenitors of the colony were captured in 1985 on Igloodik Island, Northwest Territories, Canada (69°23'N, 81°50'W). Experimental animals were produced from pairs bred in 22L:2D. At weaning (19 days of age), animals were entered into an experimental group (at least eight animals per group). All animals were housed

two or three per 38 cm × 20 cm × 15 cm polypropylene cage. Food (Prolab Rabbit Diet, Agway, Syracuse, NY) and water were freely provided and temperature was maintained at approximately 20°C. For all lighting regimens, lights-off occurred at 20:00 h.

Experimental design

At weaning, male lemmings either remained in LD or were transferred to 8L:16D (SD; Fig. 1). One group of animals remained in SD permanently (SD). Others were transferred to SD for 1, 6 or 10 weeks after weaning (SD-1, SD-6 and SD-10, respectively) before being transferred back to LD. Representatives ($n \geq 8$) of groups subjected to the appropriate photoperiod were killed by decapitation 6, 11 and 16 weeks after weaning.

Measurements

Carcasses were weighed to the nearest 0.1 g. Testes were excised, trimmed of fat and weighed to the nearest mg. Seminal vesicles were excised, fluid was expressed and tissue was weighed to the nearest mg. Bifid claw widths were measured with Vernier calipers to the nearest 0.1 mm. Pelage colour was rated on a scale of 1 to 5, with 1 for the grey-brown summer pelage and 5 for the white winter pelage (Maier and Feist, 1991).

Statistical analysis

All data were log-transformed and analysed with a one-way analysis of variance for an effect of treatment, with each postweaning group at each sampling time being a treatment (for a total of 12 treatments). Data (mean $\pm$ SEM) shown in the figures were back-transformed following statistical analyses. Between-group differences of $P < 0.05$ were considered significant.

Results

Testes mass

When examined 6 weeks after weaning, paired testes mass was greater in animals transferred to 8L:16D for any length of time (SD and SD-1) than in those never seeing SD (LD; Fig. 2). When examined 11 weeks after weaning, paired testes mass was greater in the SD-6 group than in the LD and SD groups, which did not differ from each other ($P = 0.87$). At 16 weeks after weaning, paired testes mass was greatest in the SD-6 and SD-10 groups, both of which differed from the LD and SD groups ($P < 0.05$ for SD versus SD-6; $P < 0.01$ for SD versus SD-10; $P < 0.001$ for LD versus SD-6 and SD-10). In addition, the SD-10 group differed from the SD-1 group. SD-6 and SD-10 did not differ from each other ($P = 0.66$).

Seminal vesicle mass

Seminal vesicle mass was unaffected by photoperiod in animals killed 6 weeks after weaning (no differences among

Fig. 1. Experimental design. The gestation, birth and weaning period of collared lemmings (*Dicrostonyx groenlandicus*) took place under long photoperiod conditions of 22 h light and 2 h dark per 24 h (22L:2D); that is, long day (LD). At weaning, lemmings either remained in LD or were transferred to short photoperiod (short day (SD); 8L:16D). A portion of the animals transferred to SD remained there for 1, 6 or 10 weeks before being transferred back to LD. These groups are designated SD-1, SD-6 and SD-10, respectively. One group remained in SD (designated SD). At 6, 11 and 16 weeks after weaning, representatives of appropriate groups were killed, and data on testes mass, seminal vesicle mass, body mass, bifid claw width and pelage colour were collected (for example, representatives of the SD-6 group were killed 11 and 16 weeks after weaning.)

groups; $P = 0.51$; Fig. 3). At 11 weeks after weaning, seminal vesicle mass in the SD-6 group was greater than that in all other groups ($P < 0.05$ versus SD; $P < 0.01$ versus LD and SD-1), which did not differ from each other. At 16 weeks after weaning, seminal vesicle mass was greatest in the animals from the SD-6 and SD-10 groups, both of which were different from the LD and SD-1 groups ($P < 0.01$ for SD-6 versus SD-1; $P < 0.001$ for all other comparisons). In addition, the SD-10 group was different from the SD group.

Somatic parameters

Body mass, bifid claw width, and pelage colour at time of death are given in Figs 4, 5 and 6, respectively. At 6 weeks after weaning, body mass and claw size reflected the length of time animals had been exposed to 8L:16D, whereas pelage colour was different from stage I only in the SD group. At 11 weeks after weaning, body mass was significantly lower in the LD group than in all other groups, which did not differ from each other. In contrast, claw width and pelage colour score were lower in the LD and SD-1 groups than in the SD-6 and SD groups. At 16 weeks after weaning, body mass and claw width were greatest in the SD-10 and SD groups (which did not differ); there was no difference in these parameters between the LD, SD-1 and SD-6 groups. In contrast, pelage colour

reflected the length of time in SD and differences between all groups were significant.

Discussion

The present study further characterizes the reproductive response to photoperiod of an Arctic rodent, the collared lemming, and illustrates another aspect of this response that is unique among small mammals. Collared lemmings were stimulated to mature rapidly when exposed to LD only when shown a period of SD, a requirement not observed in other photoperiodic rodents. Although such a photoperiod manipulation would never occur naturally, the scheme used in the present experiment was useful for clarifying the type of information about day length used in the wild to stimulate or suppress maturation.

Past and present laboratory data suggest that wild collared lemmings born in winter (with a minimum day length of 6 h light) would mature rapidly in response to increasing day length. Conversely, young born in late spring, under conditions of unchanging LD, would not mature until after day lengths begin to shorten in late August, presumably due to the adverse environmental conditions present during early summer (Banfield, 1974; Chapin *et al.*, 1975; Fuller *et al.*, 1975). For those LD-born individuals that over-winter, maximal gonadal

Fig. 2. Paired testes mass ($\pm$ SEM) of the collared lemming *Dicrostonyx groenlandicus* 6, 11 and 16 weeks after weaning. Histograms are for LD (□), SD-1 (▤), SD-6 (▥), SD-10 (▧) and SD (■) animals, where SD is short day, LD is long day and numerals indicate number of weeks in SD (for example, SD-1 animals were in SD for 1 week, and then were transferred back to LD and held there until they were killed at the indicated week after weaning). Histograms with different lower-case letters indicate significant differences between groups ($P < 0.05$) within a given week after weaning.

Fig. 4. Body mass ($\pm$ SEM) of the collared lemming *Dicrostonyx groenlandicus* 6, 11 and 16 weeks after weaning. Histograms are for LD (□), SD-1 (▤), SD-6 (▥), SD-10 (▧) and SD (■) animals, where SD is short day, LD is long day and numerals indicate number of weeks in SD (for example, SD-1 animals were in SD for 1 week, and then were transferred back to LD and held there until they were killed at the indicated week after weaning). Histograms with different lower-case letters indicate significant differences between groups ($P < 0.05$) within a given week after weaning.

Fig. 3. Seminal vesicle mass ($\pm$ SEM) of the collared lemming *Dicrostonyx groenlandicus* 6, 11 and 16 weeks after weaning. Histograms are for LD (□), SD-1 (▤), SD-6 (▥), SD-10 (▧) and SD (■) animals, where SD is short day, LD is long day and numerals indicate number of weeks in SD (for example, SD-1 animals were in SD for 1 week, and then were transferred back to LD and held there until they were killed at the indicated week after weaning). Histograms with different lower-case letters indicate significant differences between groups ($P < 0.05$) within a given week after weaning.

Fig. 5. Bifid claw width ($\pm$ SEM) of the collard lemming *Dicrostonyx groenlandicus* 6, 11 and 16 weeks after weaning. Histograms are for LD (□), SD-1 (▤), SD-6 (▥), SD-10 (▧) and SD (■) animals, where SD is short day, LD is long day and numerals indicate number of weeks in SD (for example, SD-1 animals were in SD for 1 week, and then were transferred back to LD and held there until they were killed at the indicated week after weaning). Histograms with different lower-case letters indicate significant differences between groups ($P < 0.05$) within a given week after weaning.

growth would be expected during the increasing photoperiods that occur after the winter solstice. These hypotheses are supported by existing field data suggesting that the major

reproductive efforts of collared lemmings occur in early spring and late summer (Banfield, 1974; Negus and Berger, 1987), that autumn and winter breeding occur (Krebs, 1964; MacLean *et al.*,

Fig. 6. Pelage colour ($\pm$ SEM) of the collared lemming *Dicrostonyx groenlandicus* 6, 11 and 16 weeks after weaning. A score of 1 represents the grey-brown summer pelage and a score of 5 represents the winter pelage (completely white). Histograms are for LD (□), SD-1 (▤), SD-6 (▨) and SD (■) animals, where SD is short day, LD is long day and numerals indicate number of weeks in SD (for example, SD-1 animals were in SD for 1 week, and then were transferred back to LD and held there until they were killed at the indicated week after weaning). Histograms with different lower-case letters indicate significant differences between groups ($P < 0.05$) within a given week after weaning.

1974), but that very few young are born around the time when the snow melts in June (Banfield, 1974).

In a relatively short-lived species such as the collared lemming (microtine rodents rarely live beyond one season; Leslie and Ranson, 1940; Kalela, 1957), rapid sexual maturation could have a significant impact on fecundity during the lifetime of an individual. Neither field data on the timing of sexual maturation nor laboratory data on the importance of testes size for fecundity in this species are available. Thus, knowledge of the relative fecundity of male lemmings exposed chronically to LD versus those transferred to LD from SD awaits breeding experiments. However, female collared lemmings, 40, 70 or 100 days old, chronically exposed to LD produce fewer young than do females of the same age transferred at weaning from SD to LD, when both are mated to fertile, stud males (B. A. Gower, T. R. Nagy and M. H. Stetson, unpublished). The data from females suggest that photoperiod history has an impact on reproductive function.

The present experiment was conducted to test the hypothesis that collared lemmings gestated, born and reared in LD can be stimulated by LD if shown a transient period of SD. Support for the hypothesis depended upon demonstration that gonadal growth of LD-born animals given a transient exposure to SD would exceed that of animals transferred permanently to SD. The data reported here support the hypothesis. At 11 weeks after weaning, the paired testes mass and seminal vesicle mass of animals given a transient 6 week exposure to SD (SD-6) were greater than those of animals transferred permanently to SD (SD). Likewise, 16 weeks after weaning, the testes mass of animals in both the SD-6 and SD-10 groups was greater than

that of animals in the SD group. One week of SD exposure (SD-1) apparently was insufficient to confer sensitivity to LD. These data are the first to demonstrate that LD-born collared lemmings can show gonadal stimulation in response to LD.

We have demonstrated previously that the inhibitory effect of chronic LD exposure on gonadal growth persists for at least 10 weeks after weaning (Nagy *et al.*, 1993a, b). The present data indicate that after 11 and 16 weeks of chronic exposure to LD after weaning, the gonadal mass of animals born and raised in LD was not different from that of animals transferred at weaning to SD. Thus, chronic LD exposure eventually permits maturation, albeit with lighter testes than those of same-aged animals transferred from SD to LD. Since, in the wild, collared lemmings would not see unchanging LD for more than 10 weeks, the limited effectiveness of maturational impedance by LD seems logical.

Unlike testes and seminal vesicles, somatic parameters responded to day length in a manner that was independent of photoperiod history. Transient exposure to SD stimulated a gain in body mass that occurred even after the animals were transferred back to LD. This response was most apparent 11 weeks after weaning, when the SD-1, SD-6 and SD groups did not differ in body mass (even though the first two groups had been back in LD for 10 and 5 weeks, respectively). Similarly, transfer to SD caused claw growth and a lightening of pelage colour that was eventually, but not immediately, interrupted and reversed by transfer back to LD. However, unlike body mass, pelage colour in the SD-1 group never reached that displayed by SD animals. This difference in response between parameters suggests that induction of the moult to winter pelage requires a longer period of continuous exposure to SD than does induction of the large body mass. Taken together, the somatic data indicate that certain developmental or cyclical programmes are set in motion by changes in photoperiod and are played out regardless of subsequent photoperiod changes. These programmed responses may reflect the adaptive value of a large body mass, white pelage and bifid claws for surviving the Arctic winter. The present observations also suggest that reproductive and somatic parameters are independently regulated in this species, consistent with earlier data from our laboratory (Nagy, 1993; Nagy *et al.*, 1993a, b).

In conclusion, the present data indicate that maturation in male collared lemmings born and maintained on LD proceeds slowly unless interrupted by exposure to SD. Thus, LD-born animals can show accelerated gonadal growth in response to LD but only after SD exposure. This type of response, although not documented among temperate zone rodents, bears some similarity to that of the ferret (*Mustela putorius*) (Sisk, 1990; Sisk *et al.*, 1992) and the starling. Under natural conditions, LD-born male lemmings probably would breed only after exposure to SD (late summer, autumn or winter) or after exposure to increasing day length (late winter or early spring of the year after their birth). The evolution in collared lemmings of this pattern of photoresponsiveness may be related to environmental conditions in the Arctic when photoperiods are long (Nagy *et al.*, 1995). Chronic long photoperiod (constant light) occurs from mid-May to late July at a latitude of 66°N (Nautical Almanac Office, 1991). During this time, the availability of food is low, standing biomass from

the previous year's growth is diminished and the present year's growth has not yet begun (Chapin *et al.*, 1975). Also, the melting of snow during June floods the lemmings' habitat (Fuller *et al.*, 1975) and interrupts breeding (Banfield, 1974). Thus, reproductive quiescence during this stressful period may allow young animals to postpone maturation and reserve resources for times when environmental conditions are more favourable to reproduction.

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