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Circadian Photosensitive Phase and Photoperiodic Control of Testis Activity in the Mink (Mustela vison Peale and Beauvois), a Short-Day Mammal[1]

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ABSTRACT

Evidence of a circadian photosensitive phase in male mink, whose annual reproductive cycle is characterized by the recrudescence of testicular development in autumn, was based on the study of testicular response after interrupting the dark period by light breaks (0.5 h) offered at various times. In this mammal, the experimental short days 4L:20D and 8L:16D stimulated testicular growth. Short photoperiods, including a main light period of 3.5 h and an additional 0.5 h light break 7.5 h after the beginning of the main photoperiod, were as effective as 8L:16D in stimulating testicular development. On the other hand, when a 0.5 h light break occurred 11.5 or 15.5 h after the beginning of the main photoperiod, the same inhibiting effect on testicular activity was obtained as for long photoperiods. However, when 0.5 h light breaks were given 19.5 h after the beginning of the main light period, some minks recognized, as "dawn," the onset of the shorter of the two light periods offered.

Thus our results proved the existence of a special phase in the day cycle in which light inhibited testicular development in the mink which appears to be a short-day animal. One explanation of the difference between long-day and short-day animals would be the following: if for long-day animals exposure to light during the photosensitive phase led to gonadostimulation, in short-day mammals, like mink, it exerted an inhibiting influence on testicular growth.

INTRODUCTION

Since the first observations by Rowan (1925), Bissonnette (1932), and Benoit (1934), many research studies have shown the importance of photoperiod (i.e., the length of the daily light period and its seasonal changes) in the control of annual breeding cycles in birds and mammals. In temperate and arctic regions, progressive and regressive changes in daylight length form the main environmental variable responsible for the stimulation of the neuroendocrine system which induces recrudescence of gonads and onset of sexual activity in animals with an annual reproductive cycle. The mechanism whereby the organism can follow the annual photoperiod cycle is as yet unknown. Bunning (1936) was first to suggest that endogenous rhythms were involved in the photoperiodic reaction. He developed his hypothesis as a result of his experiments on plants. It envisaged a circadian rhythm of cellular function consisting of two half-cycles, one of which was "light-requiring" (photophil phase) whereas the other was "dark-requiring" (scotophil phase). Thus photoperiodic induction of a process requiring long days occurred only when the duration of the natural or experimental photoperiod extended into the photophil part of the cycle. Bünning's initial hypothesis has been further developed by Pittendrigh (1966). According to the latter, the whole light cycle has a dual action: not only does it induce a photosensitive physiological mechanism but it is also an entraining agent for the circadian oscillation. Bünning's "scotophil phase" is replaced by the concept of a "photoinducible phase," a time sequence of variable but limited length during which the photoinduced physiological mechanism is reactivated.

In vertebrates, the existence of a circadian rhythm of photosensitivity was first demonstrated by Hamner (1963, 1964, 1965) in the house finch. Since then, several authors have

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obtained similar results with other avian models [Farner, 1965; Follett et al., 1974 (white-crowned sparrow); Wolfson, 1966 (slate colored junco and bobolink); Follett and Sharp, 1969; Wada, 1979, 1981 (Japanese quail); Farner et al., 1977 (house sparrow)] or mammalian models [Elliott et al., 1972; Elliott, 1976; Stetson et al., 1975 (golden hamsters); Grocock and Clarke, 1974 (field vole); Boissin-Agasse and Ortavant, 1978 (ferret)].

The different experiments, which have been carried out to show that photoperiodic time measurement is based on a circadian rhythm of photosensitivity, involved birds and mammals whose gonadal response is the "long-day" type, i.e., species in which the onset of testicular activity is concomitant with the increase in length of the daily light. Thus we thought it would be interesting to characterize the circadian cycle of photosensitivty in the mink, as the recrudescence of testicular activity in this mammal occurs at the end of autumn when the daily light duration decreases. Evidence of a circadian photosensitive phase in this mammal, which utilizes short days to signal the onset and maintenance of testicular development, is based on the study of testicular response after interruption of the dark phase by light breaks offered at various intervals during a long dark period. (Experiment I). The testicular response obtained was compared with the one induced by different daily light durations (photoperiodic regimens of 4L:20D; 8L:16D; 16L:8D; 20L:4D) (Experiment II).

MATERIALS AND METHODS

The two experiments were carried out in the Chizé Forest (midwest France; latitude 46° 19′ N; longitude 0° 24′ W). They were begun in October (Experiment I) and November (Experiment II) when the animals born in spring of the same year, were still sexually inactive. The male minks came from the breeding unit at the National Institute for Agricultural Research (Jouy-en-Josas, France).

Experiment I

The minks were divided into six groups of six. Each animal was in an individual wire cage. In the control group (group 1), the animals were maintained outdoors in natural conditions of photoperiod and temperature. The five other groups were housed in photoperiod-controlled rooms. The interiors of the boxes were painted white, and each was illuminated by two 100 W bulbs. The light intensity in the cage was about 200–250 lx. Food and water were provided ad libitum and always during the light period. Temperatures in the boxes were ∿10 ± 1°C. Group 2 animals were exposed to 4L:20D. Groups 3, 4, 5, and 6 were also given light for 4 h, but the light

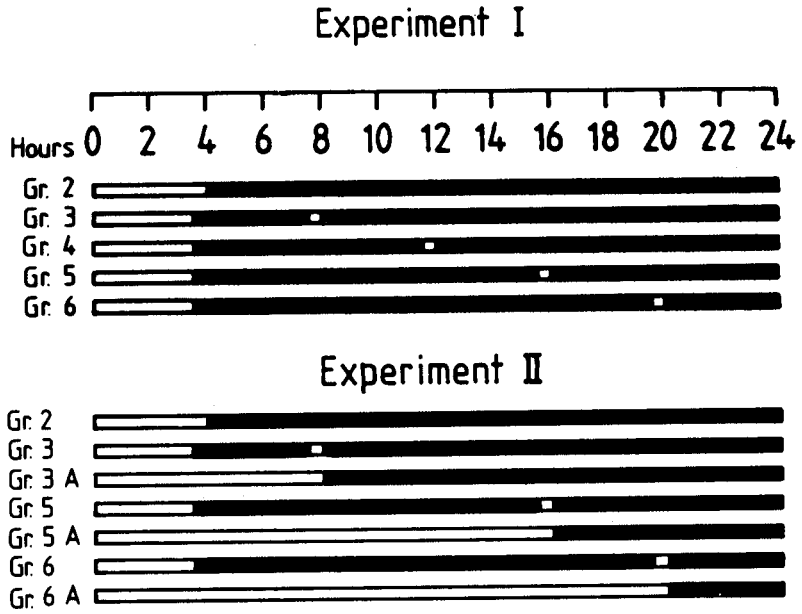

FIG. 1. Design of the two experiments. The white and black bars represent light and dark periods, respectively. Short white bars indicate light breaks of 0.5 h given at selected times after the beginning of the main photoperiod.

phase was divided into two photofractions of 3.5 h and 0.5 h. The shorter light period (0.5 h) broke into the dark phase at various intervals: 7.5, 11.5, 15.5, and 19.5 h after the beginning of the main light period. The onset of the 3.5 h light period was always 0800 h (Fig. 1).

Experiment II

This experiment required eight groups of six male minks. The animals in group 1 were kept under natural environmental conditions. The animals in groups 2, 3, 5, and 6 were kept in the same conditions as the corresponding groups in experiment I. The results obtained for groups 3, 5, and 6 where the animals received a light complement 7.5, 15.5, or 19.5 h, respectively, after the beginning of the main photofraction, were compared with those obtained for the animals in groups 3A, 5A, and 6A, with the following photoperiods: 8L:16D (group 3A), 16L:8D (group 5A), and 20L:4D (group 6A) (Fig. 1).

Measure of Testicular Activity

Two parameters were considered: testis volume (cm^3) and plasma testosterone levels (ng/ml). Testicular measurement and collection of blood samples were carried out under light anesthesia (halothane, I.C.I.) at the beginning of the experiments, and then 15 (mid-October), 30 (beginning November), 45 (mid-November), and 75 (mid-December) days later (Experiment I) or 30 (December), 60 (January), 90 (February), 120 (March), and 150 (April) days later (Experiment II).

The testes were measured through the scrotum without surgery with a caliper to the nearest 0.1 mm. After measurement of the three dimensions (L x W x T, length X width X thickness), we were able to calculate testicular volume from the formula of Setchell and Waites (1964):

$$TV = \frac{4}{3} \pi \frac{L}{2} \cdot \frac{W}{2} \cdot \frac{T}{2}$$

Blood samples (5 ml) were taken from the jugular vein. Heparinized blood was immediately centrifuged, and the plasma was stored frozen at −25°C until the testosterone levels were determined.

Testosterone levels were measured using radioimmunoassay already described and validated (Boisin-Agasse and Boissin, 1979). The sensitivity of the assay

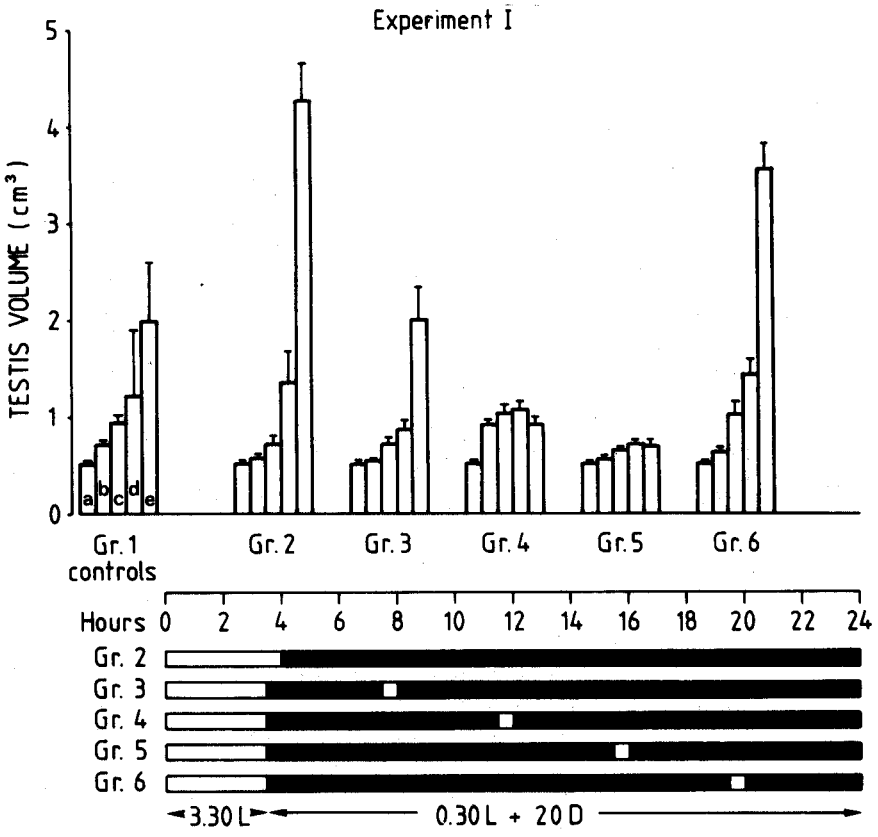

FIG. 2. Photoperiodic induction of testicular growth in the mink subjected to 4L:20D with main photoperiod of 3.5 h and additional short photoperiod of 0.5 h offered at the times indicated in the long dark period. Animals in group 1 were exposed to natural environmental conditions. Six minks per group were used. Vertical bars represent SEM. a, Beginning of the experiment; b, 15; c, 30; d, 45; and e, 75 days later.

was 8 pg/tube. The intraassay and interassay coefficients of variation were 2–5% and 10%, respectively.

Results and Statistic Analysis

The mean values for testis volume and plasma testosterone concentration have been shown with their standard error.

Variance analysis (test F) was used for the statistical exploitation of the results (comparison of the mean values).

RESULTS

Experiment I. Study of Testicular Response in Relation to the Time of the Light Break

As shown in Fig. 2, in minks kept in natural conditions of light and temperature, testis volume (TV) increased significantly from October to December ($P<0.01$). At the beginning of December, before winter solstice, the value for this parameter was 4 times greater than the initial calculation in October. On the other hand, if we consider the variations in plasma testosterone levels (PT) (Fig. 3), we can observe that the endocrine testicular activation came later and was evident only after a decrease in plasma testosterone concentration during the first half of November ($P<0.05$). The increase was significant only between the November and December results (PT November vs December: $P<0.05$).

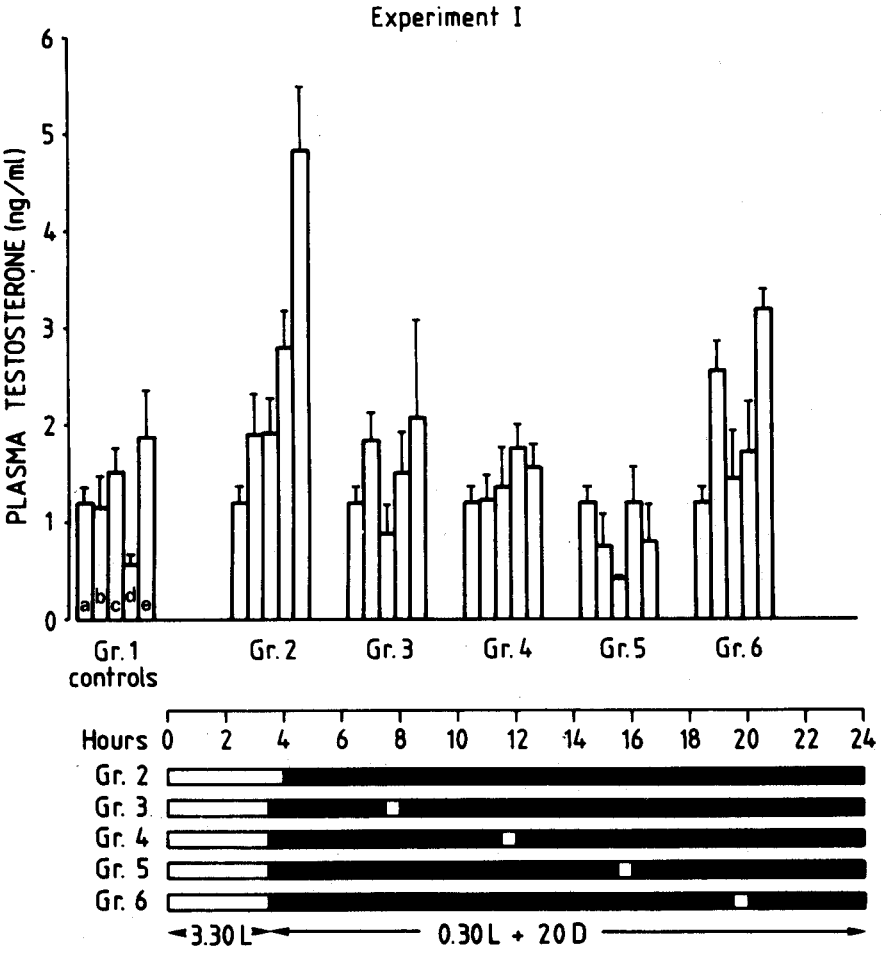

FIG. 3. Photoperiodic induction of testosterone secretion in the mink subjected to 4L:20D with main photoperiod of 3.5 h and additional short photoperiod of 0.5 h offered at the times indicated in the long dark period. Animals in group 1 were exposed to natural environmental conditions. Six minks per groups were used. Vertical bars represent SEM. a, Beginning of the experiment; b, 15; c, 30; d, 45; and e, 75 days later.

For the group 2 animals (4L:20D), a marked increase in testis volume could be observed (Fig. 2), and gonadostimulation was greater than for the animals in the control group (December: TV control group vs TV group 2; $P<0.001$). At the end of the experiment, testis volume calculated for the minks in group 2 was twice that measured in the control group. The plasma testosterone concentration followed a similar pattern (Fig. 3). Forty-five days after the beginning of the photoperiodic treatment, the increase in testosterone level was statistically significant (PT beginning of October vs PT end of November: $P<0.01$), and 30 days later (mid-December) the hormonal level was twice the level measured at the same stage of the experiment for the control group.

The variations in the two parameters observed for the animals in group 3 showed that if the light break interrupts the dark period 7.5 h after dawn (beginning of the main light period), the gonadostimulation is less than if the animals have 4 h uninterrupted light. The evolution of testicular growth is statistically comparable to that observed in the animals in group 1, and the testosterone level is the same for animals in groups 1 and 3 in mid-December, after 75 days of experiment (Figs. 2, 3). It seemed interesting to compare the results obtained for group 1 and group 3 animals since the photoperiodic conditions for both groups were similar. In the natural environmental conditions of light (group 1) during the month of December, daylength is about 8 h (mean duration of daylight in December: 8.15 h); for group 3 animals the shorter light period came to an end 8 h after the beginning of the main light period.

When the light break interrupted the dark period 11.5 h after dawn (group 4), a statistically significant increase ($P<0.05$) in testicular growth was observed during the first 15 days (Fig. 2). The value for this parameter then stopped increasing and remained constant at a relatively low level until the end of the experiment. On the other hand, the plasma testosterone concentrations remained unchanged throughout the experiment. The variations exhibited no statistical significance (Fig. 3).

The testicular activity of the animals in group 5 was characterized by the total absence of testicular growth (Fig. 2). The minks in this group were offered a light break 15.5 h after the beginning of the main light period. After a month, the plasma testosterone levels decreased significantly ($P<0.05$). The endocrine testicular activity then increased slightly but remained at a very low level until the end of the experiment (Fig. 3).

When the light break came 19.5 h after the beginning of the main light period, the increase in testis volume was statistically comparable to that observed for group 2 animals (Fig. 2) where marked testicular growth was observed. There was a similar large increase in plasma testosterone concentration; an extremely significant increase in the hormonal level was evident after only 15 days of photoperiodic treatment (PT beginning of October vs PT mid-October: $P<0.01$, Fig. 3).

Experiment II. Influence of Daylight Length on Testis Activity in the Mink

Experiment II lasted 6 months, from November 2, 1979, to April 2, 1980. The results obtained for the animals under 4L:20D (group 2), 8L:16D (group 3A), 16L:8D (group 5A), and 20L:4D (group 6A) were compared with those obtained when the light break interrupted the dark period (groups 3, 5, and 6: experimental design was the same as in experiment I).

As Experiment II was sufficiently long, we were able to study the seasonal onset and decrease of testis activity in group 1 animals kept in natural conditions of photoperiod and temperature. The testis volume, as noted, increased in autumn (daylength <12 h). The most rapid growth was observed between December and January when natural daylength was shortest (mean duration of daylight in December: 8.15 h). The highest values were calculated for February. Testis volume then decreased (TV February vs TV March: $P<0.05$) (Fig. 4). The variations in plasma testosterone level followed a similar pattern (PT November vs PT December: $P<0.05$; maximum: February; PT February vs PT March: $P<0.01$; PT March vs PT December: NS) (Fig. 5).

It is important to note that the results obtained throughout experiment II for the animals in groups 2, 3, 5, and 6 confirmed the results obtained in experiment I; however, if we take into account the prolonged photoperiodic treatment, the gonadostimulation observed in the animals in groups 2, 3, and 6 was greater at the end of experiment II.

A 4L:20D photoperiod led to an increase in testis volume and in plasma testosterone concentration equivalent to the increase due to autumn and winter changes in daylength (TV

January group 1 vs TV January group 2: NS; TV February group 1 vs TV February group 2: NS), but whereas testis activity decreased from February to March in minks kept in natural environmental conditions, it remained at a high level after February in group 2 animals (Figs. 4, 5).

If we consider the results obtained for groups 3 and 3A animals, we see that the gonadostimulating effects brought on by 8L:16D (group 3A) were the same as those produced by the light break interrupting the dark period 7.5 h after the onset of the main light period (group 3) (Figs. 4, 5). The increase in testis volume was statistically the same for groups 2, 3, and 3A animals (Fig. 4). On the other hand, the plasma testosterone levels were higher for group 2 minks than for groups 3 and 3A (Fig. 5).

The photoperiodic regimens given to groups 5 and 5A did not bring about any increase in testis volume nor in plasma testosterone concentrations which remained at their lowest levels throughout the experiment.

Testicular response was similar for groups 3 and 3A (gonadostimulation) and for groups 5 and 5A (absence of gonadostimulation) whether the light was continuous (group 3: 8L; group 5: 16L) or given in two periods of different duration (3.5 h and 0.5 h), whereas in groups 6

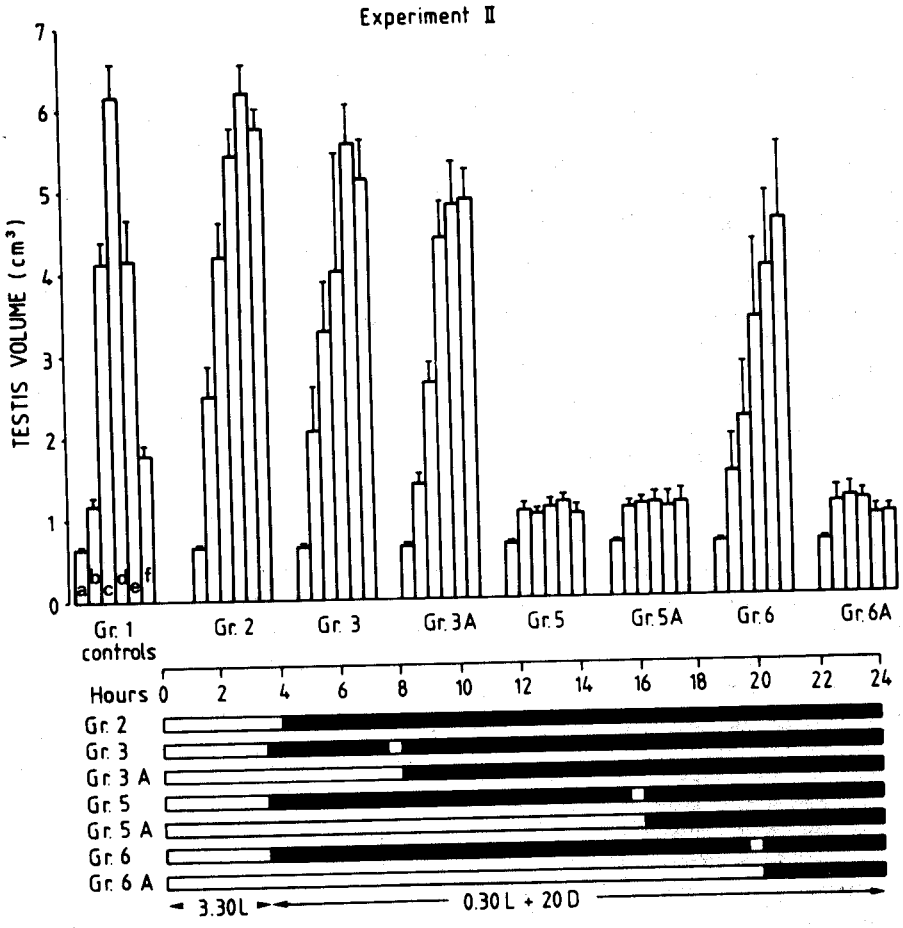

FIG. 4. Influence of daylength on testicular development in the mink. The results obtained for the animals under 8L:16D, 16L:8D, and 20L:4D were compared with those obtained when an additional short photoperiod (0.5 h) interrupted the dark period. Animals in group 1 were maintained under natural environmental conditions. Six minks per group were used. Vertical bars represent SEM. a, Beginning of the experiment; b, 30; c, 60; d, 90; e, 120, and f, 150 days later.

and 6A gonadostimulation was different for each group. For group 6, testis volume and plasma testosterone levels were similar to those obtained for groups 2, 3, and 3A, but for group 6A no testicular activity could be observed and the plasma concentration in testosterone remained at a level similar to the one measured for groups 5 and 5A (Figs. 4, 5).

The mean values of testis volume and plasma testosterone concentrations calculated for group 6 animals showed an exceptionally high standard error. The variability in testicular response can be explained by the fact that the first series of measures, 30 days after the beginning of the experiment, showed no increase in testis volume and testosterone level for two of the minks whereas there was a high level of gonadostimulation for the four remaining animals. For these two minks following the same photoperiodic regimen as the others, no sexual

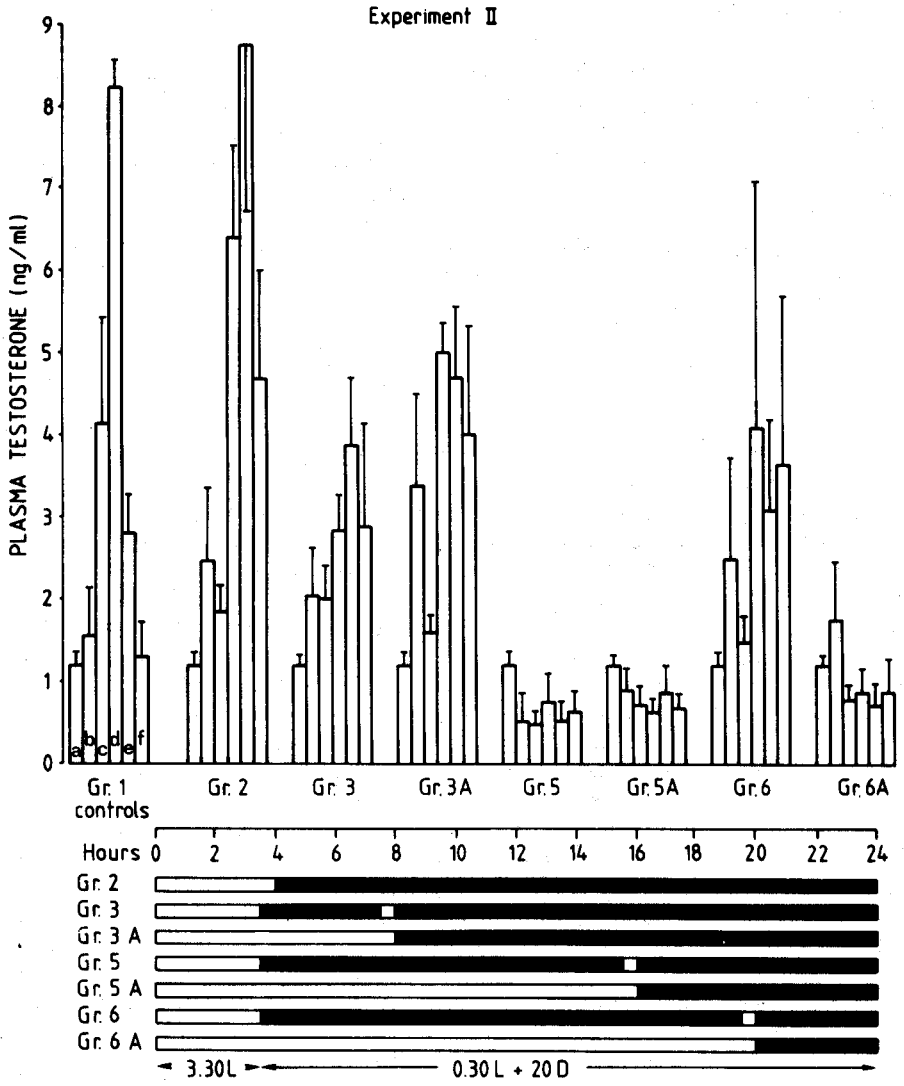

FIG. 5. Influence of daylength on testosterone secretion in the mink. The plasma testosterone levels obtained for the animals under 8L:16D, 16L:8D, and 20L:4D were compared with those measured when an additional short photoperiod (0.5 h) interrupted the dark period. Animals in group 1 were maintained under natural environmental conditions. Six minks per group were used. Vertical bars represent SEM. a, Beginning of the experiment; b, 30; c, 60; d, 90; e, 120; and f, 150 days later.

activity could be observed up until the end of experiment II.

DISCUSSION

The results obtained for the minks maintained under natural conditions of photoperiod or submitted to different photoperiods have led us to make the following observations:

Seasonal testis activity begins in autumn, when daylight length is less than 12 h and decreasing, and is at its maximum after winter solstice when daylight length is on the increase; it decreases at the beginning of spring when daylight exceeds darkness.

The 4L:20D photoperiod is gonadostimulating. This also occurs when the time interval from the beginning of the main light period to the end of the light break does not exceed 8 h in our experimental conditions. When time interval is equal to or greater than 12 h, the gonads remain inactive.

The results obtained for the animals in groups 4 and 5 would seem to prove the existence of a special phase in the day cycle during which a light break of 0.5 h inhibits testicular activity.

Exposure to 3.5L with an additional 0.5 h light break 7.5 h after the beginning of the main photoperiod (group 3) was as effective as short photoperiods (8L:16D) (group 3A) in stimulating testicular development. Long photoperiods (16L:8D) (group 5A) have an inhibiting effect on testicular activity, and the same result is obtained when a 0.5 h light break occurs 15.5 h after dawn (group 5). However, different results were observed for groups 6 (photostimulation) and 6A (photoinhibition). The results obtained for group 6 animals, where a high rate of testicular activity was found even though the light break came 19.5 h after dawn, can be explained if we consider that in this case the beginning of the shorter photoperiod was taken to be dawn because of the short interval separating the secondary photoperiod from the following main photoperiod. The same hypothesis has already been suggested by Menaker (1965) to explain a similar result for the sparrow. This also explains why the testicular response observed in group 6 minks (0.5L + 4D + 3.5L + 16D) is the equivalent of the response observed for group 3 (3.5L + 4D + 0.5L + 16D). However, 2 of the 6 minks in group 6 did not react to the secondary photoperiod; they behaved as if exposed to long days (3.5L + 16D + 0.5L + 4D) and no testicular development was observed for them. The result in their case can be compared to the group 6A result.

The two parameters considered, testis volume and plasma testosterone concentrations, gave concordant indications on the state of the testes. However, the increase in testis volume was always greater then the increase in plasma testosterone concentration. Furthermore, testosterone is released in pulsatile fashion in minks during sexual activity, but short-term variations of plasma testosterone levels disappear when testicular activity is strongly reduced (Boissin-Agasse and Boissin, 1979). The existence of circhoral changes explains the wider dispersion found in the values of this parameter in group exhibiting gonadostimulation.

In minks kept in natural conditions of photoperiod and temperature, the whole reproductive period, from the onset of sexual activity to the regression of the gonads, takes place between the autumn and spring equinoxes when daylight duration is less than 12 h. A similar observation has already been made concerning another European carnivorous animal, the fox (Maurel and Boissin, 1981). Thus it would seem that, in the mink, long nights are necessary if gonadostimulation is to occur and our experiments show that only short days (4L:20D and 8L:16D) stimulate recrudescence of the testes.

These results are, however, very different from those obtained for another mustelid, the ferret. For the latter, testicular recrudescence takes place after the winter solstice, when daylength is on the increase, and the reproductive period is in March-April after the spring equinox (Boissin-Agasse and Boissin, 1979). In the ferret, the experimental design, identical to the one used for the mink (Experiment I), showed that the circadian photosensitive phase occurs 12 h after dawn (Boissin-Agasse and Ortavant, 1978). This result is similar to those found in certain avian species (Hamner, 1963, 1964, 1965; Farner, 1965; Wolfson, 1966; Follett and Sharp, 1969; Turek, 1972, 1974; Follett et al., 1974; Farner et al., 1977; Wada, 1979, 1981) or for other mammals (Elliott et al., 1972; Elliott, 1976; Hoffmann, 1972, 1973, 1974; Grocock and Clarke, 1974; Stetson et al., 1976) where the sensitivity of the hypothalamo-hypophyseal system controlling the annual gonadal cycle is clearly evident. The mechanisms involved in photoperiodic time measurement do not function only in testicular growth. Turek

(1972) in both the white-crowned and golden-crowned sparrow and Stetson et al. (1976) in the golden hamster have shown that in spite of specific differences, an endogenous circadian oscillation of photosensitivity is used in measuring daylength to terminate the refractory condition. However, no published study gives any information about the timing of the circadian photosensitive phase in mammals, like the mink, whose annual reproductive cycle is characterized by recrudescence of testicular development in autumn. According to the results obtained from our experiments, it would appear that a period of darkness equal to at least 16 h is necessary if gonadostimulation is to occur and that exposure to light during this period leads to testicular inhibition. Exactly the same situation occurs in short-day plants in which flowering was inhibited by exposure to light during the second part of the circadian oscillation (Bünning, 1936; Hamner, 1960).

The model of photoperiodic time measurement defined by Bünning's hypothesis (1936, 1960) to explain photogonadal responses of the long-day type also helps us to interpret the results obtained for the mink. All the species studied, whether of the long-day type (golden hamster: Elliott et al., 1972; Elliot, 1976; Stetson et al., 1975, 1976; field vole: Grocock and Clarke, 1974; ferret: Boissin-Agasse and Ortavant, 1978) or short-day type (mink), would seem to be photosensitive only during the second part of the circadian oscillation. However, a fundamental difference would seem to exist between the two types concerning the effects of light present during the photosensitive phase. Whereas for long-day type animals, exposure to light during this phase would seem to stimulate testicular growth, for short-day type animals, it would seem to have an inhibiting effect. Another possibility is that the first part of the circadian cycle is sensitive to light, and if light is given during the scotophil phase, an inhibiting mechanism stops photogonadostimulation even though light has already been given during the photophil phase.

The way to validate one or the other hypothesis would be to study the effects of keeping short-day animals in constant darkness to find out if light has only a negative effect on testicular development. Of course light would still be necessary for the entrainment of the photosensitive or the photoinhibitory rhythm.

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