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Long Day Photoperiods and Temperature of 20°C Induce Spermatogenesis in Blinded and Non-blinded Marbled Newts during the Period of Testicular Quiescence[1]

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ABSTRACT

Adult male marbled newts (Triturus marmoratus) were collected at the end of the spermatogenesis period and exposed to different photoperiods (natural-daylength-simulated photoperiod, total darkness, 8L:16D, 12L:12D, 16L:8D, and continuous light) for 3 mo. Temperature was maintained at 20°C. Two additional groups of newts were blinded and exposed to either the natural-simulated photoperiod and to 16 h of light per day respectively. Quantitative histologic studies on testicular development and germ cell volume per testis were performed. The newts captured in the field at the beginning (initial controls) or at the end of the experiments (final controls) were in the period of testicular quiescence. Newts kept in total darkness or exposed to a short photoperiod (8L:16D) showed germ cell development up to primary spermatocytes, whereas germ cell development in the newts exposed to long photoperiods (12L:12D or 16L:8D) progressed to elongated spermatids. The newts exposed either to intermediate photoperiods (natural-simulated photoperiod) or to constant light showed an intermediate degree of germ cell development (up to round spermatids). No significant differences between non-blinded and blinded animals were found. These results suggest that (1) mild temperature inititiates testicular development in the period of testicular quiescence, (2) long photoperiods associated with mild temperatures produce spermatogenesis in this period, (3) complete darkness or constant light are less effective than some intermediate photoperiod, and (4) the effect of photoperiod on testicular function in newts is not related to ocular photoreception.

INTRODUCTION

The influence of the photoperiod on the regulation of testicular function mediated by the pineal gland has been studied widely in mammals, principally in hamsters (Elliot, 1976; Carter et al., 1982; Goldman et al., 1982, 1984; Hong et al., 1986). These studies have shown that a long photoperiod (14–16 h of light per day) improves spermatogenesis and endocrine testicular function, whereas a reduced exposure to light causes testicular regression. Optic enucleation causes testicular atrophy in hamsters (Gravis and Weaker, 1977; Heindel et al., 1981). Pinealectomy in hamsters (Hagen and Asher, 1983) and pineal tumours that destroy the gland in humans (Ariens-Kappers, 1981) stimulate testicular development.

The effects of the photoperiod on the testis in other vertebrates have been studied in fish (Scott and Sumpter, 1983; Bye, 1984; Skarphedinsson et al., 1985; Borg et al., 1987), amphibians (Werner, 1969; Steinborn, 1984), reptiles (Mayhew, 1964; Licht, 1969; Underwood and Hall, 1982), and birds (Follet, 1976; Balthazart et al., 1981; Ebling et al., 1982; Bachman et al., 1987). The results of these studies suggest that exposure to long photoperiods associated with mild temperature induces testicular growth and increases concentrations of gonadotropins and testosterone, whereas short photoperiods result in testicular regression and decreased concentrations of these hormones.

The study of photoperiod effects in fish, amphibians, and reptiles is of particular interest since in these animals the pineal gland exhibits a photoreceptor structure. The gland may be stimulated directly by light and its function may therefore be independent

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of ocular photoreception. Several experiments suggest that eyes are unnecessary for the photoperiod response in fish (Borg, 1982a; Day and Taylor, 1983) and birds (Farner, 1980; Oliver and Baylé, 1982) due to the occurrence of extraretinal photoreceptors located in the pineal gland or in other sites.

It has been reported that long photoperiods (16L:8D) enhance testicular development in newts during the spermatogenesis period (Werner, 1969; Steinborn, 1984). The objective of the present report was to compare the histological changes induced by different photoperiods (varying from total darkness to continuous light) and mild temperatures during the period of testicular quiescence in the testes of blinded and non-blinded marbled newts.

MATERIALS AND METHODS

Eighty adult male marbled newts (*Triturus marmoratus marmoratus* Latreille) were collected from forested areas of the Province of Leon, Spain (42° 30′ N latitude; 5° 30′–45′ W longitude), on 30 October, at the end of the spermatogenesis period when testicular quiescence initiates. To eliminate the influence of body weight in the experimental results, only newts weighing between 9 and 9.5 g were selected.

Eight newts were killed on 2 November and used as initial controls. Forty-eight newts were alloted to 6 groups (8 newts per group) and maintained in the laboratory up to the end of the experiment on 2 February. Each group of newts was kept in an isolated glass aquarium (1 × 1 × 0.4 m) containing fresh water up to a height of 20 cm. A solid surface (a flat-based, roughly pyramidal-shaped rock) was provided so that the newts could swim or rest on this surface. In no case were the newts protected from light by the surface of the rock. The water was kept clean using a filter with a pump performance of 180 1/h. Lighting was supplied by cool, white, fluorescent lamps with a 14 w output and a wave-length distribution from 350 to 710 nm, with peaks in the blue at 490 nm and in the green at 580 nm. Lighting conditions were controlled by intermatic time switches. Water and air temperatures were maintained at 20 ± 1°C. The animals received food (earth worms and insect larvae) every 2 days. Each group of newts was exposed to a different photoperiod. One group received variable light times according to the natural daylength (from 10.40 to 9 h of light per day in October–December and from 9 to 10 h of light per day in December–January); the intermatic time switches of this group were reprogrammed every 3 days. Another group was maintained in complete darkness. Each of the remaining 4 groups were exposed to a photoperiod of 8L:16D, 12L:12D, 16L:8D, or constant light.

To obtain information about the effects of the photoperiod via pineal gland photoreceptors, 16 newts were blinded by a nonaggressive method: an elastic rubber cap was adjusted to the newt's head covering the eyes but not the pineal photoreceptors. Although the masked animals did not see the food when it was administered, they ate it if it was placed near their mouths. The total amount of food consumed by these animals was similar to that consumed by the newts whose sight was intact. Half of the masked newts were exposed to the natural photoperiod in the laboratory and the other half were exposed to 16 h of light per day. These two photoperiods were considered the most representative. The remaining 8 newts were enucleated and subjected to the natural-simulated photoperiod to determine if both methods of blinding produced similar effects. Other photoperiods were not studied in blinded newts since it seemed unnecessary to blind more animals and subject them to photoperiods that presumably do not have a very different effect on blinded animals than that observed in the normal newts.

To compare the effects of the natural-simulated photoperiod at 20°C with the natural photoperiod at ambient temperature (field temperature during November–January varied from −5°C to 10°C), 8 newts (final controls) were captured in the field at the end of the experiments (1 February). These newts, together with those exposed to photoperiods, were weighed, anaesthetized with methanesulphonate (MS-222; Sandoz, Barcelona, Spain), and perfused through the aortic cone with 3% phosphate-buffered glutaraldehyde-paraformaldehyde (30 min). After this, both testes were removed and weighed, and testicular volumes were calculated by water displacement. The right testes were sliced into small fragments, which were processed for electron microscopy. The left testes were fixed for an additional 6 h in the same fixative, dehydrated, and embedded in paraffin.

Since germ cells in the newt testis progress from the anterior to the posterior pole, only sagittal sections of the whole testis were suitable for quantitative studies. For this purpose, five 6-μm-thick

sagittal sections of each left testis at points 1/6, 1/3, 1/2, 2/3, and 5/6 of the transverse testicular diameter were selected (Figs. 1–9). In each testis, the areas occupied in the 5 sections by each germ cell type (including their accompanying Sertoli cells and connective tissue cells) and the glandular tissue (developed Leydig cells) were measured with a semiautomatic image analyzer (Kontron, Zeiss, Oberkochen, FRG). The resulting values were divided by the total surface of the 5 sections, thus obtaining the volume densities of each cell type. The absolute volumes per testis for each cell type were obtained by multiplying volume densities by testicular volumes and by a correction factor (0.76), which results from transformation of testicular volume after perfusion in testicular volume after embedding. This factor was previously calculated from 50 newt testes.

The means and standard deviations for each group of newts were calculated from the values for each animal. Comparison of the means between the different photoperiods (or controls) was carried out by the one-way ANOVA test and Sheffe's pairwise comparison. For the two photoperiods that included blinded newts, the means of blinded and non-blinded animals were compared by the two sample *t*-test.

RESULTS

Body weights did not vary during the experiment in either non-blinded or blinded animals (Table 1).

Testicular weights and volumes did not change during the experiment in the newts kept in total darkness. However, they did increase slightly (nonsignificantly) in the newts exposed to 8 h of light per day or to the natural-simulated photoperiod and increased significantly in the newts exposed to constant light or to long photoperiods (12 or 16 h of light per day) (Table 1). For the photoperiods that included blinded newts, no significant differences between non-blinded, enucleated, and masked newts were found.

The volume occupied by each germ cell type and the glandular tissue in each group of animals is shown in Table 2. No differences between non-blinded and blinded newts were found in the two photoperiods that included blinded animals. Comparison between both methods of blinding revealed no significant differences.

Initial controls showed abundant spermatozoon bundles formed in the preceding spermatogenetic cycle, a developed glandular tissue, and primary and secondary spermatogonia that had not proliferated to spermatocytes. The final controls presented the same testicular pattern. The newts kept in total darkness and those exposed to 8 h of light per day had initiated the new cycle with germ cell development up to primary spermatocytes. Spermatozoon bundles of the preceding cycle and abundant glandular tissue were also present. The animals exposed to natural photoperiod showed a greater germ cell development up to primary spermatocytes.

The newts exposed to long photoperiods (12 or 16 h of light per day) developed round and elongated spermatids, which were more abundant in the 16L:

TABLE 1. Average body weights and testicular weights and volumes in newts exposed to different photoperiods.*

Treatment	Body weight (mg)		Left testis weight (mg)	Left testis volume (mm^3)
	Initial	Final		
Initial controls	9289 ± 170^{a}	--	116 ± 13^{a}	108 ± 12^{a}
Final controls+	--	9256 ± 162^{a}	113 ± 12^{a}	106 ± 11^{a}
Natural-simulated photoperiod				
non-blinded	9413 ± 165^{a}	9264 ± 163^{a}	135 ± 15^{ab}	126 ± 14^{ab}
blinded (masked)	9179 ± 176^{a}	9324 ± 185^{a}	139 ± 16^{ab}	130 ± 15^{ab}
blinded (enucleated)	9425 ± 172^{a}	9372 ± 173^{a}	136 ± 16^{ab}	127 ± 15^{ab}
Total darkness	9286 ± 158^{a}	9352 ± 189^{a}	121 ± 13^{a}	113 ± 12^{a}
8L:16D	9427 ± 164^{a}	9283 ± 165^{a}	132 ± 15^{ab}	123 ± 14^{ab}
12L:12D	9089 ± 165^{a}	9308 ± 186^{a}	159 ± 19^{bc}	149 ± 18^{bc}
16L:8D				
non-blinded	9452 ± 106^{a}	9377 ± 216^{a}	176 ± 21^{c}	165 ± 20^{c}
blinded (masked)	9325 ± 173^{a}	9256 ± 164^{a}	169 ± 20^{c}	158 ± 19^{c}
Constant light	9112 ± 149^{a}	9245 ± 165^{a}	151 ± 16^{bc}	141 ± 15^{bc}

*Values are expressed as means ± standard deviation; for each parameter, values with different superscript letters (^{abc}) differ significantly ($p<0.05$).

+Natural photoperiod and ambient (cold) temperature.

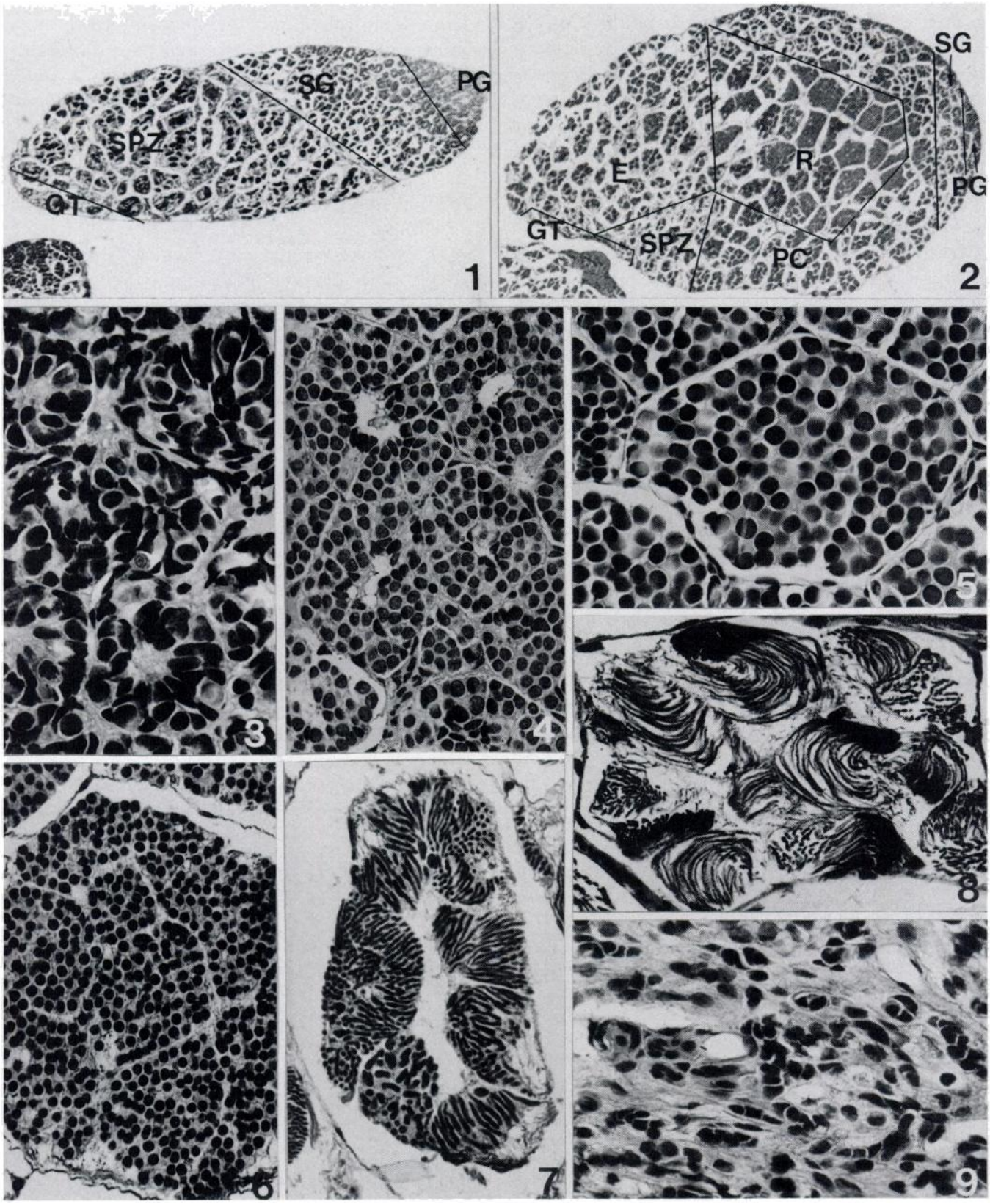

PLATE 1.

FIG. 1. Low-power view of a testicular lobule of marbled newt collected from the field on 30 October and killed 3 days later. A few primary *(PG)* and secondary *(SG)* spermatogonia, numerous spermatozoon bundles *(SPZ)*, and glandular tissue *(GT)* can be seen. Stained with hematoxylin and eosin. X18.

FIG. 2. Low-power view of a testicular lobule of a marbled newt exposed to 16 h of light per day. In addition to spermatozoon bundles *(SPZ)*, glandular tissue *(GT)* and primary *(PG)* and secondary *(SG)* spermatogonia, primary spermatocytes *(PC)*, and round *(R)* and elongated spermatids *(E)* are observed. Stained with hematoxylin and eosin. X18.

FIGS. 3–9. Higher magnification of the different cell types found in marbled newts exposed to a photoperiod of 16L:8D. *(3)* Primary spermatogonia. *(4)* Secondary spermatogonia. *(5)* Primary spermatocytes. *(6)* Round spermatids. *(7)* Elongated spermatids. *(8)* Spermatozoon bundles. *(9)* Glandular tissue. Stained with hematoxylin and eosin. X240.

8D photoperiod. The newts exposed to constant light showed a less pronounced germ cell development, similar to that observed in the final controls exposed to the natural photoperiod.

DISCUSSION

The regulation of testicular activity by the photoperiod in urodele amphibians has been shown to depend on temperature. If long photoperiods are associated with mild temperatures, spermatogenesis is enhanced (Werner, 1969; Steinborn, 1984), whereas cold temperatures present spermatogenesis even with exposure to long photoperiods (Steinborn, 1984).

In the present study, the newts exposed to the natural-simulated photoperiod in the laboratory (average daylength 10 h and temperature 20°C) initiated the spermatogenetic cycle up to primary spermatocytes and a few round spermatids during testicular quiescence, whereas the newts captured from the field (final controls) at the end of the experiment (identical photoperiod and average temperature 5°C) maintained testicular quiescence. The cycle also was initiated in the newts kept in total darkness at 20°C. These findings suggest that it is temperature and not photoperiod that regulates the beginning of the spermatogenetic cycle. Similar results have been reported in teleost fish (Borg, 1982b), anuran amphibians (Crespo, 1974), and reptiles (Licht, 1969). However, the photoperiod is also important since comparison of the results obtained with the different photoperiods revealed that when these ranged from total darkness to 16 h of light per day, the longer the daylength, the greater germ cell development. A long photoperiod combined with mild temperature led to complete spermatogenesis, even in the period of testicular quiescence.

Nevertheless, the effect of constant light on testicular development is more similar to that of a short photoperiod than to that of a long one. This suggests that complete darkness or constant light are less effective than some intermediate photoperiod. Such a result contrasts with that observed in many

TABLE 2. Average volumes (mm^3) per testis of the different cell types* in marbled newts exposed to different photoperiods.+

Treatment	Primary spermatogonia	Secondary spermatogonia	Primary spermatocytes	Secondary spermatocytes + round spermatids	Elongated spermatids	Spermatozoon bundles	Glandular tissue
Initial controls	5.94 ± 0.7^{a}	19.11 ± 2.1^{ab}	--	--	--	78.08 ± 8.6^{a}	4.86 ± 0.6^{a}
Final controls§	5.63 ± 0.6^{a}	18.23 ± 2.1^{ab}	--	--	--	77.16 ± 8.1^{a}	5.01 ± 0.5^{a}
Natural-simulated photoperiod							
non-blinded	5.79 ± 0.8^{a}	11.09 ± 1.4^{c}	22.68 ± 3.0^{ab}	11.34 ± 1.5^{ab}	--	72.89 ± 9.4^{ab}	3.78 ± 0.5^{a}
blinded (masked)	6.24 ± 0.8^{a}	9.49 ± 1.5^{c}	17.81 ± 2.4^{a}	8.84 ± 1.2^{ac}	--	82.94 ± 10.8^{a}	3.02 ± 0.4^{b}
blinded (enucleated)	5.83 ± 0.9^{a}	10.53 ± 1.6^{c}	21.41 ± 2.7^{ab}	9.38 ± 1.4^{ac}	--	77.36 ± 9.8^{ab}	2.98 ± 0.4^{b}
Total darkness	5.65 ± 1.0^{ab}	23.73 ± 4.0^{b}	4.97 ± 0.8^{c}	--	--	73.79 ± 12.5^{ab}	4.86 ± 0.8^{a}
8L:16D	5.16 ± 0.8^{a}	16.97 ± 2.6^{ad}	25.83 ± 3.9^{b}	--	--	71.22 ± 10.7^{ab}	3.81 ± 0.6^{ab}
12L:12D	2.09 ± 0.3^{b}	17.28 ± 2.7^{abd}	57.36 ± 8.9^{d}	12.81 ± 1.0^{b}	2.98 ± 0.5^{a}	55.28 ± 8.6^{bc}	1.19 ± 0.2^{c}
16L:8D							
non-blinded	2.14 ± 0.3^{b}	16.50 ± 2.6^{ad}	37.62 ± 6.0^{ef}	58.91 ± 9.4^{d}	4.95 ± 0.8^{b}	44.22 ± 7.1^{cd}	0.66 ± 0.1^{d}
blinded (masked)	2.84 ± 0.4^{b}	13.59 ± 2.2^{cd}	27.65 ± 4.4^{bf}	62.96 ± 10.1^{d}	6.48 ± 1.1^{b}	43.92 ± 7.0^{d}	0.52 ± 0.1^{f}
Constant light	5.50 ± 1.0^{a}	20.16 ± 3.6^{a}	51.89 ± 9.3^{de}	7.61 ± 1.4^{c}	--	54.28 ± 9.8^{bcd}	1.55 ± 0.3^{c}

*The volume occupied by each type of germ cell includes that occupied by their accompanying Sertoli and interstitial cells.

+Values are expressed as means ± standard deviations; for each cell type, values with different superscript letters ($^{a-f}$) are significantly different ($p<0.05$).

§Natural photoperiod and ambient (cold) temperature.

mammals (Elliot, 1976; Goldman et al., 1982; Kholkute et al., 1987), birds (Bachman et al., 1987), and fish (Ueda and Takahashi, 1981) in which constant light appears to have no effect on testicular function different from that of any other long photoperiod. A optimum photoperiod (from 15 to 17 h of light per day) has been reported in the Turkish hamster (Carter et al., 1982). Both shorter and longer photoperiods induce testicular regression in these mammals. This is the only reference to the negative effects of constant light on testicular function in vertebrate species.

The similar response to lighting in both non-blinded and blinded newts suggests that the maintenance and development of testicular function in these animals are not mediated by ocular photoreceptors. This contrasts with what occurs in mammals (Gravis and Weaker, 1977; Heindel et al., 1981) and even in some of the vertebrates that have pineal photoreceptors (fish, amphibians, and reptiles) or other extraretinal photoreceptors (birds). In some telost fish, optic enucleation has no effects on testicular function (Borg, 1982a), whereas in others such as the channel catfish, optic enucleation delays testicular maturation and pinealectomy has no gonadal effects (Davis et al., 1986). This behaviour has been attributed to the occurrence of abundant amounts of melatonin in the retina of these fish (Gern et al., 1978). In another teleost fish *(Fundulus heteroclitus)*, neither the pineal gland nor the eyes are essential in photoperiod sensitivity, which is attributed to other unknown photoreceptors (Day and Taylor, 1983). Although some reports have emphasized that neither the eyes nor the pineal gland are necessary to perceive changes in the photoperiod in birds (Farner, 1980; Oliver and Baylé, 1982), the importance of the eyes in the testicular function of the quail has been demonstrated by Baylé et al. (1983). These authors implanted radioluminous material in the eyes of quails and found an enhancement in testicular function during exposure to short photoperiods; such an enhancement was not observed when the optic nerves were severed. Although the present experiments indicate that in the marbled newt eyes are unnecessary for photoperiod response, the notion that photoreceptor other than the pineal may be involved in photoperiod sensitivity cannot be ruled out.

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