LIGHT-INDUCED PROLONGATION OF SPERMATOGENESIS IN THE EUROPEAN STARLING, *STURNUS VULGARIS*

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The annual testicular cycle of the European Starling, *Sturnus vulgaris*, follows the general pattern of many photoperiodic avian species of the north temperate zone. That is, the onset of testicular growth is associated with increasing daily photoperiods following the winter solstice. Captive starlings maintained under natural daylengths at 38° N achieve testicular maturation by mid-April, with the condition persisting until about mid-June. Thereafter, the testes undergo involution and remain quiescent until near the winter solstice (Schwab, unpubl. data).

Bissonnette (1931) believed that seasonally increasing daylengths were responsible for the onset of testicular maturation in the European Starling. Later, an extensive series of experiments on the photoperiodic control of starling testis cycles by Bissonnette and co-investigators showed that the intensity and wave-length of visible light also affected the rate or degree of stimulation of testis activity (for review, see Bissonnette 1937). Essentially, the amount of testis stimulation increases with increased intensity of illumination and exposure to wave-lengths near the red range of the visible light spectrum. Bissonnette and Wadlund (1932) state that "the duration of any phase of the sexual cycle bore an inverse relation to the effectiveness of the stimulating exposure to light, which, in turn, depended on the daily period, intensity, wave-length and rate of change of illumination." These findings suggested the possibility that manipulation of some characteristic of the daily photophase could alter the duration or occurrence of certain phases of the testicular cycle. Thus, it was decided to examine the function of daily light durations with respect to induction of testicular involution in the European Starling.

The specific factor(s) responsible for gonadal involution are not presently known. A number of hypotheses have been proposed, however, including: heat exhaustion (Cowles and Nordstrom 1946; Vaugien 1951); antagonism between the gonadotrophic and thyrotrophic functions of the pituitary (Davis and Davis 1954); an inherent need for a period of gonadal quiescence (Miller 1954); and a variety of other possibilities. Regardless, testicular involution can be induced by manipulation of the daily photoperiod. For example, testicular involution can be induced precociously by exposing the birds to very short daylengths (Burger 1947; Wolfson 1959; Hamner 1968). It seems, however, that this involution is not necessarily followed by insensitivity of the gonads to long daylengths (photorefractoriness), although such insensitivity follows spontaneous involution in most photoperiodic avian species. It appears likely that natural testicular involution is a function of long daily photoperiods, as suggested by a number of authorities (Farner 1964; Wolfson 1964; Farner and Follett 1966; Hamner 1966).

The duration of time that testes remain in a spermatogenic condition can also be influenced by photoperiodic manipulation. Threadgold (1960) documented spermatogenesis for 200 days in English Sparrows, *Passer domesticus*, exposed to a chronic 1L-23D photoperiod. More realistic as to the photoperiods which animals might experience under natural conditions (e.g., equatorial species) is the 12L-12D regimen employed by Wolfson (1959) to prolong spermatogenesis for "almost one year" in Slate-colored Juncos, *Junco hyemalis*. This important finding seems never to have been extended to other avian species.

Extensive prolongation of testicular activity has not been achieved in starlings under 12L-12D (Burger 1953; Schwab and Lott 1969). The results reported here, however, document that certain other chronic daily photoperiods do indeed prolong spermatogenesis in starlings for at least 15 months.

MATERIAL AND METHODS

CAPTURE AND MAINTENANCE OF STARLINGS

The starlings used were juveniles captured in the San Joaquin Valley of central California in June–August 1966. They were maintained on turkey pellets and fresh water ad libitum under natural daylengths in a large outdoor aviary at Davis, California.

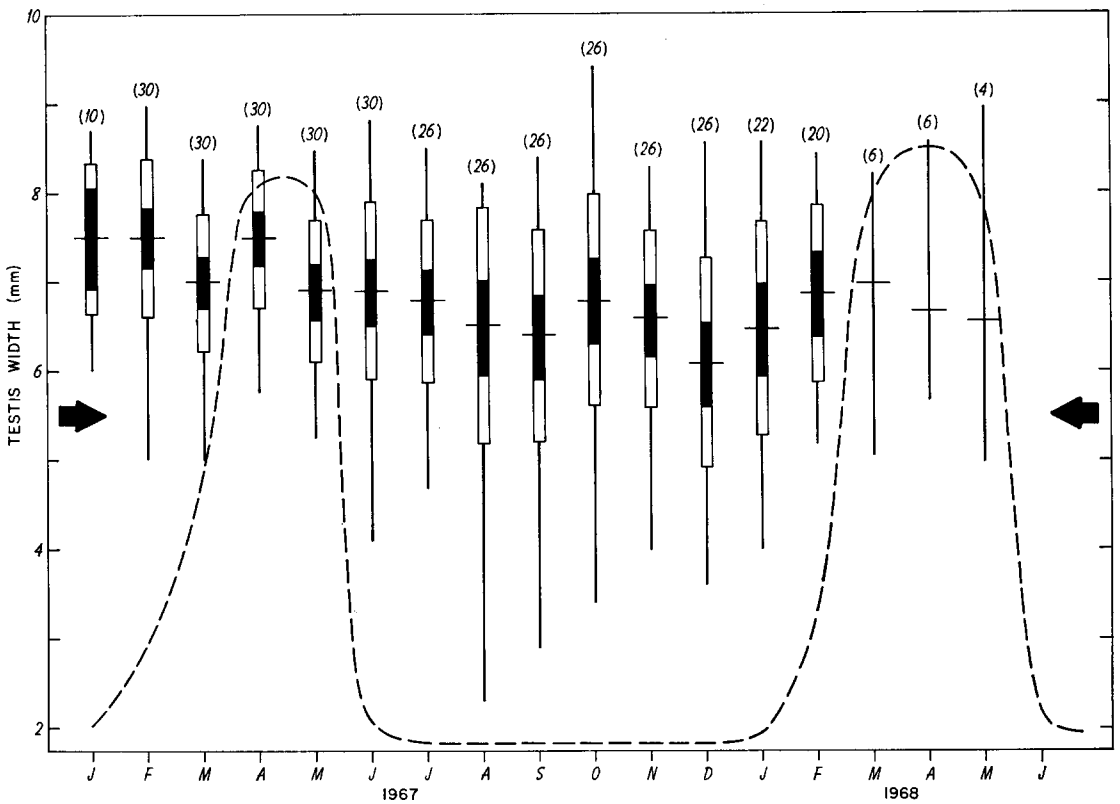

FIGURE 1. Prolongation of spermatogenesis in European Starlings as a function of chronic 10.5L-13.5D and 11L-13D daily photoperiods. Range of testicular measurements is given as a vertical line, mean as a horizontal line, two standard errors above and below the mean as a solid rectangle, one standard deviation above and below the mean as an open rectangle, and number of observations in parentheses. The foregoing combines the testicular measurements taken after spermatogenesis was attained in each of the programmed daily photoperiods (see table 1 for measurement dates and for statistical description of the March, April and May 1968 samples). The broken line approximates average testis size during an initial and a subsequent gonadal cycle in captive starlings under natural daylengths. The testis width at, or above, which spermatogenesis can be expected in all individuals is indicated by arrows.

LIGHT REGIMENS AND TEMPERATURE CONDITIONS

Three groups of male starlings were removed from the outdoor aviaries and exposed to programmed daily photoperiods. They were held in 2 × 2 × 4-ft wire cages enclosed in light-tight plywood "photo-chambers." The light intensity, from incandescent bulbs, was about 60 ft-c at the midpoint of the cage. Daily temperatures within the photo-chambers fluctuated between 22 and 28°C.

The first group of starlings was exposed to 11L-13D on 23 November 1966, the second to 10.5L-13.5D on 22 December 1966, and the third to 11L-13D on 19 January 1967. The control group consisted of starlings in the outdoor aviaries.

ASSAY OF TESTICULAR CONDITION

All gonadal measurements here reported represent the width of the left testis measured *in situ* following unilateral laparotomy. Testicular widths of less than 2 mm could not be measured accurately *in situ*. Hence, width reported as 2 mm may actually have been as much as 1 mm less. Starlings were occasionally selected at random from the programmed-light regimens and sacrificed, and the functional condition of the gonad evaluated by standard histological techniques. Histological assay indicates that testis width is a reliable index of development and that widths of 5.5 mm or greater characterize the spermiogenic phase of testicular metamorphosis in the European Starling.

RESULTS

TESTICULAR CYCLES UNDER NATURAL DAYLENGTH

Determinations of the growth-involution phase of the first and second annual testicular cycles in captive starlings under natural daylength were based on gonadal measurements of 282 and 723 birds, respectively. These cycles will be analyzed in a future report, but the curve in figure 1 presents the general configuration, based on a line fit, by eye, of sample means, for chronological comparison with gonadal responses in starlings under the programmed-light regimens.

TABLE 1. Testis width (mm) of European Starlings under chronic 10.5L-13.5D and 11L-13D light regimens; initial description of testis size in each programmed photoperiod indicates date exposure began.

	11L-13D				10.5L-13.5D				11L-13D			
Month	Day	n	$\bar{x} \pm$ SE	Range	Day	n	$\bar{x} \pm$ SE	Range	Day	n	$\bar{x} \pm$ SE	Range
1966												
Nov.	23	10	< 2.0	–								
Dec.	23	10	3.1 ± 0.4	2.1–6.2	22	10	< 2.0	–				
1967												
Jan.	23	10	7.5 ± 0.3	6.0–8.7	20	10	5.3 ± 0.6	2.7–9.4	19	10	2.2 ± 0.1	<2.0–2.9
Feb.	22	10	7.7 ± 0.1	7.0–8.3	20	10	7.1 ± 0.4	5.0–9.0	17	10	7.9 ± 0.3	6.8–9.0
Mar.	23	10	7.3 ± 0.2	6.5–8.4	22	10	7.2 ± 0.2	6.0–8.1	20	10	6.4 ± 0.2	5.0–7.5
Apr.	24	10	7.0 ± 0.2	6.0–7.8	21	10	7.5 ± 0.3	5.8–8.6	19	10	7.9 ± 0.2	6.9–8.8
May	23	10	6.8 ± 0.3	5.3–8.3	22	10	7.0 ± 0.3	5.4–8.5	19	10	6.8 ± 0.2	5.6–7.7
June	22	10	7.4 ± 0.2	6.3–8.8	20	10	6.4 ± 0.2	5.7–7.7	19	10	6.8 ± 0.4	4.1–8.7
July	21	10	6.6 ± 0.3	4.7–7.8	20	6	7.4 ± 0.3	6.0–8.5	18	10	6.7 ± 0.3	5.6–7.9
Aug.	23	10	5.7 ± 0.5	2.3–7.4	18	6	6.9 ± 0.4	4.5–7.8	23	10	7.2 ± 0.2	6.5–8.1
Sept.	20	10	6.0 ± 0.4	2.9–7.9	18	6	6.8 ± 0.2	6.3–7.4	20	10	6.6 ± 0.4	4.6–8.4
Oct.	23	10	6.8 ± 0.4	4.8–9.4	23	6	7.3 ± 0.2	6.2–7.8	19	10	6.7 ± 0.5	3.4–8.4
Nov.	22	10	6.4 ± 0.3	4.0–7.5	22	6	6.8 ± 0.2	6.0–7.4	20	10	6.7 ± 0.4	4.8–8.3
Dec.	21	10	6.0 ± 0.4	3.6–8.2	21	6	6.3 ± 0.2	5.7–6.7	19	10	6.1 ± 0.5	4.2–8.6
1968												
Jan.	23	8	6.2 ± 0.4	5.4–8.4	22	5	6.1 ± 0.7	4.0–8.0	19	9	7.0 ± 0.4	4.5–8.6
Feb.	23	7	6.3 ± 0.4	5.2–8.3	22	5	7.1 ± 0.5	6.0–8.5	19	8	7.2 ± 0.3	5.9–8.2
Mar.									19	6	7.0 ± 0.4	5.1–8.2
Apr.									19	6	6.7 ± 0.5	5.7–8.6
May									20	4	6.6 ± 1.0	5.0–9.0

TESTICULAR RESPONSES UNDER 10.5L-13.5D AND 11L-13D

Each programmed daily light regimen represents a photoperiod about 70 min longer than the natural daily photoperiod (sunrise to sunset) at the time the treatment began. It is well known that precocious gonadal development will be induced in photoperiodic birds by an artificially increased daily photoperiod applied just prior to the natural gonadal cycle. Hence, starlings initially exposed to chronic 11L-13D on 23 November 1966 achieved maximum gonadal size about two months before the controls. Starlings exposed to 10.5L-13.5D on 22 December 1966, and those exposed to 11L-13D on 19 January 1967, achieved maximum testicular size about one month before the controls (table 1, fig. 1). Initiating the treatments at various dates permitted testing for possible season-related differences in gonadal responses, but none were observed with respect to prolongation of spermatogenesis.

Most, though not all, individuals in the programmed-light regimens maintained testes well above the histologically-determined minimum size for spermatogenesis during the programmed-light treatment. Testicular widths of at least 26 starlings under the programmed-light regimens were measured each month between May and December 1967 (spanning approximately the portion of the natural testicular cycle from peak development through the involution and photorefractory phases). Seven starlings showed partial testicular involution during this period, which probably denotes cessation of spermatogenesis, though none achieved minimal testis width (2.0 mm or less). Subsequently, gonadal recrudescence and spermatogenesis occurred. There was no evidence that spermatogenesis ceased in any of the remaining 19 individuals during this period. Table 2 presents monthly testicular widths of 10 individuals, five exhibiting a partial gonadal involution and five showing no involution. These measurements are typical of the two different responses observed.

DISCUSSION

Figure 1 illustrates the salient finding, that spermatogenesis can be prolonged in European Starlings by manipulating the daily photoperiod. The average testicular size remained well above minimum size for spermatogenesis in all groups under chronic 10.5L-13.5D and 11L-13D, while other starlings under natural daylengths proceeded through two recrudescence-involution phases. Wolfson's report (1959, 1964) of a similar effect in juncos under 12L-12D is thus extended to another species, although there is species-specificity as to the particular daily photoperiods that prolong

TABLE 2. Testis width (mm) of individual starlings under chronic 10.5L-13.5D and 11L-13D photoperiods.[a]

Bird no.	Light regimen	Date regimen initiated	1967 May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Continuous spermatogenesis										
478	11L-13D	23 Nov. 1966	7.1	7.8	7.8	7.4	7.9	7.5	7.5	7.3
486	11L-13D	23 Nov. 1966	6.5	6.7	6.9	6.8	6.7	6.8	6.4	6.2
239	10.5L-13.5D	22 Dec. 1966	6.8	6.7	7.8	7.7	6.6	7.8	7.0	6.5
162	11L-13D	19 Jan. 1967	7.7	8.7	6.8	7.4	7.4	8.2	8.0	8.6
304	11L-13D	19 Jan. 1967	7.5	7.9	7.8	7.9	7.8	8.1	7.5	6.9
Partial involution										
423	11L-13D	23 Nov. 1966	6.3	7.2	*4.7*	*2.3*	2.9	7.4	7.4	5.6
435	11L-13D	23 Nov. 1966	8.3	8.2	5.9	*4.3*	5.6	9.4	7.5	8.2
236	10.5L-13.5D	22 Dec. 1966	7.0	5.8	7.4	*4.5*	6.6	7.6	6.6	6.6
358	11L-13D	19 Jan. 1967	6.6	7.7	5.7	6.5	*4.6*	*3.4*	*4.8*	6.5
523	11L-13D	19 Jan. 1967	7.0	*4.1*	5.6	7.4	7.7	7.0	7.0	7.0

[a] Widths of probable nonspermatogenic testes are italicized; measurement dates are presented in table 1. The duration includes the period of gonadal quiescence of starlings under natural daylengths.

spermatogenesis (spermatogenesis is not extended in starlings under 12L-12D).

Constant spermatogenesis in most individuals during a period of up to 15 months appears to conflict directly with Miller's (1954) hypothesis that gonadal cycles result from fatigue of the response mechanism, or from an inherent need for a period of gonadal quiescence. Even though 27 per cent of the animals did show a tendency for gonadal involution, phased chronologically with involution in starlings under natural daylengths, it was not complete and recrudescence occurred without a change in the daily photoperiod. It seems unlikely that a truly inherent biological necessity would be circumvented by a large majority of the animals held under chronic light regimens well within the photoperiodic range normally experienced by this species.

The partial testicular involution is probably not a function of the programmed-light regimens used here, or of the time that treatment began, since this phenomenon was observed in all three programmed-light regimens (table 2). The starlings used were of comparable but not precisely equal ages because of the 2–3 month hatching period at this latitude. It is plausible that the partial involution is a function of the animal's age, but additional experiment is needed to justify such a conclusion.

SUMMARY

Spermatogenesis was prolonged for up to 15 months in most European Starlings, *Sturnus vulgaris*, exposed to chronic daily photoperiods of 10.5 and 11 hr. However, about one fourth of the individuals exhibited a partial testicular involution that was phased chronologically with involution under natural daylengths. Testicular involution under the programmed daily photoperiods did not appear typical of that observed under natural daylengths, because the testis did not regress to minimal size and did not remain "quiescent" for the normal six-month period, and recrudescence occurred in the absence of photoperiodic change. Thus, the results support the concept that photoperiodic control of testicular involution in the European Starling is a function of the long daylengths. The daylengths, however, must be longer than those presently believed to cause involution and photorefractoriness in many other photoperiodic avian species.

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