

PHOTOPHASE AND TESTICULAR RECRUDESCENCE IN EUROPEAN STARLINGS

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In an elaborate sequence of experiments, Bissonnette (1930, 1931, 1937) demonstrated a positive correlation between testicular growth in European Starlings (*Sturnus vulgaris*) and seasonally increasing photoperiods occurring during the winter and spring months in north temperate zone latitudes. These results eventually led to the classification of the starling as a primary photoperiodic species (Farner and Lewis 1971). Berger (1947) reported that spontaneous testicular growth does not occur during the autumn months in temperate zone latitudes because natural photoperiods at this time are too short. Berger also documented that the refractoriness of the reproductive systems to long photoperiods immediately following a testicular cycle is naturally dispelled by late November. In a later study, Berger (1953) induced partial reproductive development in nonrefractory starlings held under stable photophases as short as 8.5 h per day. However, 8.5-h photoperiods did not allow complete testicular development to the spermatozoa-producing stage during the 20 weeks of treatment.

Recent data suggest that classifying the European Starling as a primary photoperiodic species may be somewhat misleading. (1) Although seasonal testicular metamorphosis in starlings under natural temperate zone photoperiods is correlated with increasing daily photophase durations, such photoperiod increases are unnecessary. Adult post-involution starlings held under fixed photoperiods ranging from 1 to 11 h subsequently reach histologically verified reproductive condition (an abundance of spermatozoa in the seminiferous tubules) despite the absence of daily photostimulation. (2) Photorefractory starlings chronically exposed to LD 10.5:13.5 and LD 11:13 achieve and maintain reproductive condition for at least 15 months (Schwab 1970). (3) Prolonged treatment under a semi-equatorial photoperiod (chronic LD 12:12) results in spontaneous testicular growth-involution cycles with an average 9.5-month interval between cycles (Schwab 1971, Rutledge 1974).

The present study was conducted in an attempt to refine our understanding of the photosexual response system in European Starlings, particularly the ways in which starlings appear to differ from many other photoperiodic avian species.

METHODS AND MATERIALS

Juvenile European Starlings were captured in central California and held in outdoor aviaries at Davis, California, for approximately 15 months before starting experimental treatments. During this period, all birds completed a testicular growth-involution cycle under the natural photoperiods at Lat. 38°N.

On 21 December, two 10-bird groups of adult male starlings were transferred from the outdoor aviary into light-tight photochambers, each internally illuminated by two 40-watt incandescent bulbs producing mid-chamber light intensities of about 540 lux. Chambers were ventilated with room-temperature air (23–28°C). Food (27% protein turkey pellets) and fresh water were provided ad libitum. One of the 10-bird groups was held until 19 June of the following year under a photoperiod regimen increasing two minutes per day. This daily rate of change approximates the average natural photoperiod increase from the winter to the summer solstice at Lat. 38°N and ultimately resulted in an increase from 9 to 15 h of light per day. The second 10-bird sample was maintained as above except that the photoperiod, rather than increasing each day, decreased at the rate of two minutes per day. Thus, birds in the second group ultimately experienced a photoperiod decrease from 9 to 3 h of daily light during the six-month experiment.

Measurements of the widths of the left testes of all birds were made at 20-day intervals following unilateral laparotomy, after the technique of Risser (1971). Standard histological preparation and examination of testicular tissue at various stages of development documents that testis width is a reliable indicator of spermatogenic condition in this species; spermatozoa are always present in the seminiferous tubules of testes with widths of 5.5 mm or greater (Schwab, unpubl. data).

RESULTS

Starlings held under the average rate of photoperiodic increase (2 min/day) characteristic of Lat. 38°N beginning 21 December and ending near the following summer solstice exhibited a testicular growth-involution cycle (Fig. 1) chronologically similar to that monitored in starlings held in outdoor aviaries under natural photoperiodic conditions (Schwab 1971). The testes of these birds achieved widths associated with com-

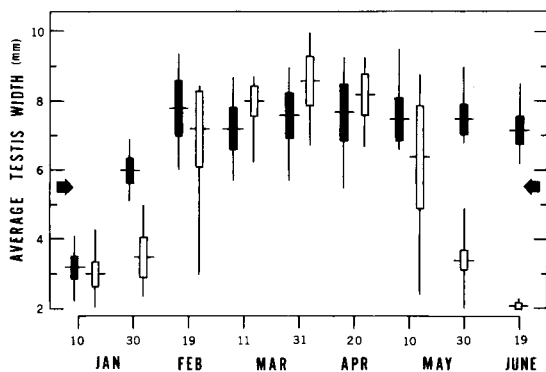


FIGURE 1. Mean left testis widths of adult European Starlings exposed to post-winter solstice photoperiods increasing from 9L to 15L at a rate of two minutes per day (open rectangles) compared with responses to photoperiods decreasing from 9L to 3L at a rate of two minutes per day (solid rectangles). Horizontal lines represent means of 10 birds, rectangles represent \pm two standard errors and vertical lines delineate the range of widths on each assay date (horizontal axis). Arrows at 5.5 mm indicate the testis width at or above which spermatogenesis is complete in this species.

plete spermatogenesis (5.5 mm) in an average of 52 days (SE = 3.0, range = 43–76). The average duration of spermatogenesis in birds under this light regimen was 91 days (SE = 4.8, range = 61–107).

Starlings maintained under decreasing photoperiods achieved spermatogenic testis widths significantly sooner ($P < 0.01$, Student's *t*-test, one-tailed) than those under the increasing photoperiod (Fig. 1). The average time to spermatogenesis for these birds was 37 days (SE = 1.6, range = 30–49). All birds in this group maintained spermatogenesis (testis widths above 5.5 mm) during the remainder of the study—a duration of time sufficient for complete testicular involution in the starlings held under increasing photoperiods (Fig. 1), as well as in those caged outdoors under naturally increasing winter and spring photoperiods at Lat. 38°N (Schwab and Rutledge 1973).

DISCUSSION

Under the seasonally varying photoperiods of temperate zone latitudes, male European Starlings exhibit characteristics typical of photoperiodic birds with respect to the control of various phases of the annual reproductive cycle (Schwab 1971). Testicular growth, initiated in January, is followed by a period of spermatogenesis extending through the spring months. Testes involute and enter a period of prolonged quiescence near the end of June. Between the fall equinox and the winter solstice, starlings grad-

ually regain the ability to begin testicular growth under daily photophase durations greater than those occurring naturally during the fall season.

Although photoperiods after the winter solstice undoubtedly play a role in an ecologically favorable chronology of the spermatogenic phase of starlings, they are unnecessary for the induction of testicular metamorphosis itself. All previously tested fixed photoperiods shorter in duration than the winter solstice photoperiod at Lat. 38°N (Schwab 1970, 1971, Schwab and Rutledge 1975, Schwab and Rutledge 1978), and the regimen of daily decreasing photoperiods presented herein, when applied following the winter solstice, produce testicular growth above the minimum widths associated with the production of spermatozoa. Because several of these light regimens are below the 9.5-h threshold proposed by Berger (1953), it has been necessary to remove this species from the list of birds for which minimum thresholds for reproductive maturation apparently exist (see Lofts and Murton 1968, Farner and Lewis 1971).

Several of the discussed photosexual responses of European Starlings conflict with the currently accepted photoperiodic control scheme initially proposed by Bünning (1936), later modified by Pittendrigh and Minis (1964), and adapted to avian reproduction by Hamner (1968). According to this external coincidence model, photoperiodic species have a period of time each day when they are most sensitive to light stimulation. When this internal "photosensitive phase" is temporally coincident with daylight portions of the 24-h day, organisms whose reproductive responses are controlled by photoperiod undergo gonadal metamorphosis. Presumably, naturally occurring autumn and winter photoperiods of the north temperate zone entrain the rhythm of photosensitivity, causing its movement into a position such that increasing spring photoperiods temporally coincide with the phase, initiating a reproductive response. Experimental results from several laboratories have confirmed the validity of this model for a variety of avian species (for an excellent review of these works see Gwinner 1975).

If the starling reproductive system required external light stimulation of an internal photosensitive phase for the induction of gonadal metamorphosis, responses to decreasing photoperiods would be difficult to explain. Assuming that a photosensitive phase is properly timed for photic stimula-

tion following the winter solstice, increasingly longer photoperiods should induce a faster reproductive response than daily photophases decreasing in length. Such was not the case. The daily decreasing light regimen actually induced or facilitated more rapid testicular growth than that occurring under naturally increasing photoperiods. Furthermore, these same decreasing photophases resulted in a substantial prolongation of the spermatogenic phase, whereas the naturally increasing photoperiods caused the completion of a testicular growth-involution cycle.

Farner et al. (1973) and Farner et al. (1977) have offered an explanation for similar, although not identical, results obtained with male House Sparrows (*Passer domesticus*). Previously, Threadgold (1960) and Middleton (1965) had demonstrated that photoperiods as short as one hour were sufficient to induce testicular recrudescence in sparrows whose testes had just begun to enlarge under natural late winter photoperiods. Results from Farner's laboratory indicate that these short photoperiods produce significant phase leads of locomotor activity rhythms. Thus, the circadian oscillator controlling activity (and presumably the photosensitive phase for reproductive stimulation) may be initiating the daily rhythm in such a fashion as to place the photosensitive phase within even the briefest period of illumination.

Although it is certainly possible that similar effects of short photoperiods may be responsible for testicular growth in starlings, it is not possible to apply the external coincidence model to the results documenting complete testicular recrudescence in starlings maintained in constant darkness (Rutledge and Schwab 1974). Male House Sparrows also achieve reproductive condition in the absence of light (Vaugien and Vaugien 1961), although experiments began after the initial stages of testis growth had commenced. Rutledge and Schwab (1974) proposed an internal coincidence model to explain the results obtained with starlings in constant darkness. Briefly stated, this model suggests that free-running circadian oscillations occurring in the absence of daily photostimulation (see Rutledge 1974) are, by some manner, conducive to the secretion of hypophyseal gonadotropins at levels sufficient to induce and maintain spermatogenesis.

Despite the fact that starlings are reproductively responsive in a classical manner to long-day photostimulation, it is entirely

possible that internal rather than external coincidence is operant in producing these results as well as the short-day responses presented herein. Pittendrigh (1960, 1972) has suggested that virtually all published results involving the photoperiodic induction of reproductive condition are explainable by invoking internal coincidence. Although it remains difficult to decipher the details implicit in such a control scheme, the possibility that internal oscillations—entrained, partially entrained, or free-running—are responsible for reproductive development should not be ruled out.

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LITERATURE CITED

- BERGER, W. J. 1947. On the relation of day length to the phases of testicular involution and inactivity of the spermatogenic cycle of the starling. *J. Exp. Zool.* 105:259-268.
- BERGER, W. J. 1953. The effect of photic and psychic stimuli on the reproductive cycle of the male Starling, *Sturnus vulgaris*. *J. Exp. Zool.* 124:227-239.
- BISSONNETTE, T. H. 1930. Studies on the sexual cycle in birds. I. Sexual maturity, its modification and possible control in the European Starling (*Sturnus vulgaris*). *Am. J. Anat.* 45:287-305.
- BISSONNETTE, T. H. 1931. Studies on the sexual cycle in birds. IV. Experimental modification of the sexual cycle in males of the European Starling (*Sturnus vulgaris*) by changes in daily period of illumination and of muscular work. *J. Exp. Zool.* 58:281-320.
- BISSONNETTE, T. H. 1937. Photoperiodicity in birds. *Wilson Bull.* 49:241-270.
- BÜNNING, E. 1936. Die endogene Tagesrhythmik als Grundlage der photoperiodische Reaktion. *Ber. Dtsch. Bot. Ges.* 54:590-607.
- FARNER, D. S., AND R. A. LEWIS. 1971. Photoperiodism and reproductive cycles in birds, p. 325-370. In A. C. Giese [ed.], *Photophysiology*, Vol. VI. Academic Press, New York.
- FARNER, D. S., R. A. LEWIS, AND T. DARDEN. 1973. Photostimulation of gonads in birds: the Bünning hypothesis and responses to very short photoperiods. *Int. Congr.: Le Soleil au Service de l'Homme*, Paris, B. 13:1-10.
- FARNER, D. S., R. S. DONHAM, R. A. LEWIS, P. W. MATTOCKS, AND T. R. DARDEN. 1977. The circadian component in the photoperiodic mechanism of the House Sparrow, *Passer domesticus*. *Physiol. Zool.* 50:247-268.
- GWINNER, E. 1975. Circadian and circannual rhythms in birds, p. 221-285. In D. S. Farner and J. R. King [eds.], *Avian biology*, Vol. V. Academic Press, New York.
- HAMNER, W. M. 1968. The photorefractory period of the House Finch. *Ecology* 49:211-227.
- LOFTS, B., AND R. K. MURTON. 1968. Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. *J. Zool. (Lond.)* 155:327-394.
- MIDDLETON, J. 1965. Testicular responses of House

- Sparrows and White-crowned Sparrows to short daily photoperiods with low intensities of light. *Physiol. Zool.* 28:255-266.
- PITTEDRIGH, C. S. 1960. Circadian rhythms and the circadian organization of living systems. *Cold Spring Harbor Symp. Quant. Biol.* 25:159-184.
- PITTEDRIGH, C. S. 1972. Circadian surfaces and the diversity of possible roles of circadian organization in photoperiodic induction. *Proc. Natl. Acad. Sci.* 69:2734-2737.
- PITTEDRIGH, C. S., AND D. H. MINIS. 1964. The entrainment of circadian oscillations by light and their role as photoperiodic clocks. *Am. Nat.* 98:261-294.
- RISSE, A. C. 1971. A technique for performing laparotomy on small birds. *Condor* 73:376-379.
- RUTLEDGE, J. T. 1974. Circannual rhythm of reproduction in male European Starlings (*Sturnus vulgaris*), p. 297-345. In E. T. Pengelley [ed.], *Circannual clocks*. Academic Press, New York.
- RUTLEDGE, J. T., AND R. G. SCHWAB. 1974. Testicular metamorphosis and prolongation of spermatogenesis in starlings (*Sturnus vulgaris*) in the absence of daily photostimulation. *J. Exp. Zool.* 187:71-76.
- SCHWAB, R. G. 1970. Light-induced prolongation of spermatogenesis in the European Starling, *Sturnus vulgaris*. *Condor* 72:466-470.
- SCHWAB, R. G. 1971. Circannual testicular periodicity in the European Starling in the absence of photoperiodic change, p. 428-447. In M. Menaker [ed.], *Biochronometry*. National Academy of Science, Wash., D.C.
- SCHWAB, R. G., AND J. T. RUTLEDGE. 1973. Effects of natural and artificial illumination on testicular metamorphosis in the European Starling (*Sturnus vulgaris*): Maturation, involution and photorefractory phases. *Int. Congr.: Le Soleil au Service de l'Homme*, Paris, B. 15:1-11.
- SCHWAB, R. G., AND J. T. RUTLEDGE. 1975. Stable daily light regimens as inductive factors of endogenous testicular cycles in the European Starling, *Sturnus vulgaris*. *Int. J. Biometeorol.* 19:219-231.
- SCHWAB, R. G., AND J. T. RUTLEDGE. 1978. Testicular metamorphosis rates in European Starlings maintained under short daily photophases. *Int. J. Biometeorol.* 22:116-122.
- THREADGOLD, L. T. 1960. Testicular response of the House Sparrow, *Passer domesticus*, to short photoperiods and low intensities. *Physiol. Zool.* 33:190-205.
- VAUGIEN, M., AND L. VAUGIEN. 1961. Le Moineau domestique peut développer son activité sexuelle et la maintenir dans l'obscurité complète. *C. R. Acad. Sci.* 253:2762-2764.
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Apparatus for Research on Animal Ultrasonic Signals.—J. A. Simmons, M. B. Fenton, W. R. Ferguson, M. Jutting, and J. Palin. 1979. *Life Sciences Misc. Pub.*, Royal Ontario Museum. 31 p. Paper cover. \$2.00. Available: R.O.M., 100 Queen's Park, Toronto, Canada M5S 2C6. This pamphlet describes ultrasonic sounds (10-150 kHz) and the apparatus and methods for studying them in the field. Instructions for choosing, building, and using instruments are given, but some knowledge of electronics is required. Examples given are of bats. Illustrated with schematic diagrams. List of references.

A Comparative Analysis of Acoustical Signals in Pied Woodpeckers (*Aves, Picoidea*).—Hans Winkler and Lester L. Short. 1978. *Bulletin of the American Museum of Natural History*, Vol. 160, Article 1. New York. 110 p. Paper cover. \$6.80. "There are few acoustical analyses of entire genera of birds, and [until now] none treating such communication in woodpeckers." This study describes in detail the vocal and instrumental sounds known for species of *Picoidea*. It then discusses the function, motivation, meaning, and homology of these signals. A short section considers the bearing of the acoustic analyses on the systematics of the genus. Illustrated with many fine tracings of sonagrams. An important monograph for those who study avian communication or woodpeckers.