

# PHOTOPERIODIC RESPONSES OF A SUBTROPICAL POPULATION OF THE FINCH (*ZONOTRICHIA CAPENSIS HYPOLEUCA*)

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The great majority of experimental studies of the control of annual cycles of birds has been restricted to populations that breed between latitudes 40 and 70° N. These studies, collectively, have demonstrated a strong role of the annual cycle in daylength in the regulation of the biological events (for review and analysis, see Farner and Lewis 1971; Lofts and Murton 1968). However, since the amplitude of the annual cycle in daylength decreases with latitude and becomes slight near the equator, many students have concluded that photoperiodic information is unlikely to be an effective timer at lower latitudes (e.g., Miller 1959a). There has thus been little investigation of the dependence, if any, of the annual cycle of low-latitude species on photoperiodic information. The few experimental investigations of low-latitude seasonal breeders that have been undertaken do not, however, effectively exclude some part of the cycle in daylength from the battery of information that controls the annual reproductive cycle. Furthermore, some investigations of low-latitude populations suggest that photoperiodic information (either in the sense of a "driver" or of a *Zeitgeber*) may be more involved than has hitherto been assumed (see especially Disney et al. 1961; Epple et al. 1971; Immelmann 1963; Thapliyal and Saxena 1964a, b; Thapliyal and Tewary 1964; Wolfson and Winchester 1959). Some insect systems can measure very small differences in photoperiod length, particularly those deviating around LD 12:12 (Adkisson and Roach 1971); pupal diapause is photoperiodically timed in the Red Locust (*Nomadacris septemfasciata*) at latitudes 7–9° S (Norris 1962). Starlings (*Sturnus vulgaris*) maintain a circennial cycle in testicular development when held on a chronic photoperiodic regime of LD 12:12; annual oscillations in daylength need not have an amplitude greater than 1 hr to make possible

the synchronization of photoperiodically timed gonadal cycles with the annual environmental cycle (Schwab 1971).

Two low-latitude populations of the Latin American species *Zonotrichia capensis* have been shown thus far to have photoperiodic gonadal responses: A Costa Rican population at about 10° N (Epple et al. 1971) and a Colombian population at 3.5° N (Miller 1959b, 1965). The present investigation contributes information on the photoperiodic responses of a low-latitude population (26.9° S) of *Z. capensis hypoleuca* that is resident at Horco Molle in the province of Tucumán in northwestern Argentina (King 1972a, b, 1973). This population is of interest because it breeds at the highest latitude of any population of *Z. capensis* for which there are now both field and experimental data on the annual cycle.

## MATERIALS AND METHODS

*Phase I* (simulation of the natural photocycle). Twelve adult male and five adult female *Zonotrichia capensis hypoleuca* arrived in Seattle (47.6° N) by air from Tucumán, Argentina (26.9° S), on 20 January 1970. All were in good condition; none were undergoing molt. All had identical histories since capture at Horco Molle in Tucumán, having been retained in an outdoor aviary at the latitude of capture since September 1969. The prior history of these birds was purposely withheld from the investigator charged with the conduct of *Phase I* treatment in order to eliminate bias in estimation of gonadal weights (see below). In Seattle, the birds were immediately placed two per cage (sexes separated) in canary breeding cages (41 × 26 × 22 cm) in a controlled environment chamber. The temperature and relative humidity were maintained constant at 20 (± 0.5)°C and 55 (± 5)%, respectively. Incandescent lamps provided a minimum light intensity of 400–440 lux in each cage. The initial photoperiod was identical to the current daylength (including civil twilight) in Tucumán: 14.09 hr of light per day (LD 14.09:9.51). During the ensuing 4.5 months, the photocycle was decreased (by decrements of 15 min at 8–16 day intervals) to simulate the natural photocycle at Tucumán. Following the experimental winter solstice, the birds were retained on LD 11.3:12.7 until 3 August, at which time *Phase II* of the treatment was initiated.

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*Phase II* (experimental photostimulation). On 3 August, four males and two females, selected randomly, were assigned to a constant photoperiod of LD 10:14 and the remaining eight males and three females were placed on a photoperiod of LD 20:4.

Throughout both phases, water, a mineral-enriched chick starter mash with vitamin supplement, and a seed mixture (white and yellow millets and canary seed) were freely available. Birds were weighed to the nearest 0.1 g at approximately weekly intervals. The progress of molt was assessed by the method of King (1972a) and of Morton et al. (1969), although in less detail. An exploratory laparotomy was performed on 30 June near the termination of molt to determine gonadal size and was repeated at the initiation of *Phase II* and at 20–30 day intervals during the ensuing 450 (LD 10:14 group) or 512 (LD 20:4 group) days. Gonadal weight (males) or stage (females) was thus visually estimated by comparison with a set of reference gonads. The average error of estimating testicular weight by this method is 20%. Ovarian weights are less reliably estimated by laparotomy; consequently, ovaries were assigned to four stages according to Lewis (1971). Briefly, *stage 0* is the fully regressed (or immature) ovary; no follicles are seen in gross aspect; and in *Z. capensis* the ovary weighs less than 6–7 mg. In *stage 1* the ovary contains follicles up to about 1 mm in diameter and weighs up to about 10–12 mg; the follicles are whitish or gray in color. In *stage 2*, the ovary is near the terminus of the previtellogenic or slow growth phase and contains follicles, the largest of which may be 2–2.5 mm in diameter; the larger follicles may have a yellowish tint; ovarian weight generally does not exceed 30–40 mg. The ovary, in *stage 3*, is fully developed with one or more large, yolky preovulatory follicles.

At the termination of the experiment, all surviving subjects were sacrificed and the histologically fixed weight of the gonads was determined by the method of Farner and Wilson (1957).

## RESULTS

The birds remained in good health; none died during the first 9 months, even though all had been subjected to exploratory laparotomy six times. The mortality rate during *Phase II* was 3.3% of the survivors per month. During *Phase I*, body weights steadily increased; during photostimulation (*Phase II*), body weights of the LD 20:4 group remained nearly constant while those of the LD 10:14 group increased moderately.

*Phase I* (simulated photocycle). The birds underwent a typical postnuptial molt. The pattern of molt was essentially as described by King (1972a) for this population, but the course of molt was slower. The molt began on 3 February (simultaneously with the natural population) and advanced to include all individuals by 22 April (ca. 3 weeks later than in the natural population). By 30 June, molt had terminated in half of our birds; at this time, the combined weight of the testes of each male was about 3 mg. Similarly, the ovaries were completely regressed (*stage 0*)

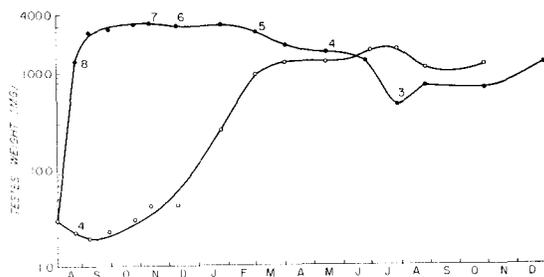


FIGURE 1. Combined testicular weights of adult *Zonotrichia capensis hypoleuca* in response to experimental photoperiods of LD 20:4 (upper curve) and LD 10:14 (lower curve). Numbers indicate birds remaining in the sample.

and were estimated to weigh less than about 6 mg in every case; no follicles were in evidence and the surface of the ovary was vesicular. Molt terminated in all individuals by 7 July, about 1 month later than the latest bird in the natural population.

*Phase II* (photostimulation). Testicular growth occurred in both groups but there was an initial lag in the response of the short-day group (fig. 1). In both groups, the growth appeared to be logarithmic up to a combined weight of about 100 mg. The estimated growth rates (expressed as "k"  $\pm$  estimated error of the sample mean) during the logarithmic phase (see Farner and Wilson 1957) were 0.08 ( $\pm$  0.01) and 0.01 ( $\pm$  0.003), respectively, for the LD 20:4 and LD 10:14 groups.

The average maximum combined weight of the testes of birds in the LD 20:4 group was more than 300 mg, which exceeded the mean maximum (ca. 200 mg) observed in the free-living population at Horco Molle (King 1973). In the free-living birds, individual testes weighing 100 mg or more produce sperm. This weight is reached in the natural population about 8 days before the first clutches are seen. Testicular weights above 100 mg were sustained in this experimental group for over 300 days, although there was a temporary decline in the combined testicular weights that persisted for about 4 months (fig. 1). The mean combined weight of the testes at the termination of the experiment was 155.9 mg ( $N = 3$ ). In the LD 10:14 group, the mean maximum weight of the testes was 178 mg; this value was reached after 357 days of treatment. Combined testes weights above 100 mg were maintained in this group for about 250 days. The terminal weights of the testes averaged 122.3 mg ( $N = 4$ ).

The ovaries in the LD 10:14 group developed to about stage I after nearly a year on this regime. At the termination of the ex-

periment, the ovaries of the two remaining females of this group weighed 11.8 and 11.3 mg (stage 1) and the oviducts weighed 6.2 and 26.1 mg, respectively. The ovaries of the LD 20:4 group grew more rapidly and reached a higher stage of development than did those of the former group. Stage 1 was reached after only 30 days of photostimulation and stage 2, after 8 months of the treatment. They remained at this stage for about 4–6 months. Vitellogenesis, but not full follicular maturation, occurred in these females. The largest follicles were ca. 2.5–3.0 mm in diameter; these were yolk-laden (stage 2) and were presumably at the threshold of the rapid phase of ovarian growth (King 1973). The ovarian weight at this time was judged to be approximately 50 mg. The ovary of the female remaining at the end of the experiment weighed 29.7 mg (stage 2).

During the first 150 days of photostimulation, there was no molt. Subsequently, we observed irregular, light (sometimes moderate) body molt in some birds of both treatment groups. There was an adventitious, irregular, usually unilateral wing molt in some individuals as well. In no case did the observed molt resemble a true postnuptial or annual type of molt.

## DISCUSSION

The annual cycle and biotope of the population of *Z. capensis hypoleuca* from which our experimental sample was drawn have been described by King (1972a, b, 1973). His observations suggest collectively that at least some of the proximate information that controls the time of initiation and termination of breeding precedes the actual conditions that support and perhaps trigger reproduction. It is thus not surprising that the accumulated information on *Z. capensis* from Horco Molle (King 1972a, 1973; the present investigation) strongly suggests that these birds employ some portion of the annual photocycle in the regulation of the annual reproductive cycle. In particular, the data suggest a photoperiodic component in the vernal phase of the reproductive cycle; and it would seem that the principal elements (i.e., molt and gonad cycle) of the annual physiological cycle retain adaptive phase relationships as a function of photoperiodic control. However, the culminating phases of gametogenesis and vitellogenesis are controlled by other information, especially that associated with the condition of the nesting substrate (King 1973).

## GNADAL GROWTH AND REGRESSION

Daylength (including civil twilight) at 26.9° S varies between 11.3 and 14.8 hr. The autumnal equinox, based on nautical day length plus civil twilight, occurs on about 26 April. The testicular growth rate of *Z. capensis hypoleuca* at Horco Molle (King 1973) was  $0.053 \pm 0.008$  days<sup>-1</sup> during the logarithmic growth phase. Measureable testicular growth in the free-living population begins in mid-August when the natural daylength (including civil twilight) exceeds about 12 hr; a combined testicular weight of 100 mg is reached in late September when the daylength is very nearly 13 hr. The nesting (fresh-egg) season extends from early October to mid-March (King 1973). Testicular regressions begins in late March when the daily photoperiod has decreased to about 12.6 hr.

The observed growth rate of the free-living population is similar to that expected from our *Phase II* experiments if testicular growth in the free-living birds is photoperiodically induced. Furthermore, the rate of testicular growth induced by LD 20:4 was similar to that seen in most photoperiodic species (Fanner and Lewis 1971) and was substantially greater and less variable than in *Z. capensis costaricensis* ("k" = ca. 0.05) in response to the same treatment (Epple et al. 1971).

## PHOTOREFRACTORINESS AND TERMINATION OF BREEDING

Most photoperiodic species develop a temporary postnuptial photorefractoriness at the end of the breeding season or show an analogous spontaneous gonadal involution when exposed to long-continued artificial photostimulation. At this time, the gonads rapidly regress and fail to grow in response to experimental photostimulation (Hamner 1968; Lofts and Murton 1968; Epple et al. 1971). If a photorefractory period exists in the *Z. capensis* from Tucumán exposed to the natural or a simulated natural photocycle, it must be very short (see also King 1973); the testes were maintained in a functional condition for 250–300 days on both LD 10:14 and LD 20:4. Testes of *Z. capensis* in the free-living population at Horco Molle do, however, undergo a postbreeding histological collapse as seen in the high latitude birds.

Since the gonads of our experimental birds regressed under the cycling daylengths of *Phase I* only to recrudescence under subsequent treatment with "short" (LD 10:14) or "long" (LD 20:4) constant photoperiods and to re-

main at high gonadal weights for a long period of time under these conditions, we infer either that these birds use the decrease in daylength as information in the termination of an active gonadal state, or that the gonadal cycle of regression (*Phase I*) and recrudescence (*Phase II*) represent a damped oscillation of a cycle that was initiated earlier and was entirely independent of the experimental photoperiod. Consonant with the former hypothesis is the fact that gonadal regression at Horco Molle (King 1973) begins after the summer solstice during the season of decreasing daylengths. Our hypothesis is further favored by the maintenance of testicular weights above 100 mg for at least 300 days under the constant photoperiod of LD 20:4 in *Phase II* of our study, and for at least 250 days on LD 10:14. Mean testicular weights remain above 100 mg in the free-living population at Horco Molle for somewhat under 200 days.

#### MOLT

In *Phase I* of our investigation, while on the simulated natural photoperiod of 26.9° S, all birds experienced a somewhat irregular, but essentially normal, postnuptial type of molt. This molt began in some individuals on 3 February, precisely on the schedule of the annual molt in the free-living population, and terminated approximately 1 month later in the sample than in the natural population. This is unusually good agreement in timing, especially in view of the stresses associated with airline transportation through 74° of latitude and in view of the imperfect (i.e., step changes) simulation of the natural photoperiod. The constant ambient temperature and relative humidity, and the presumed absence of annual environmental cues other than the photoperiodic cycle, strongly suggest that the postnuptial molt is induced either directly by the experimental photoperiodic regime or by some earlier event that induces and (or) entrains an endogenous physiological cycle that subsequently culminates in molt. If such an autonomous molt cycle exists, however, it was not expressed; whereas molt and gonadal function are compatible in free-living birds (King 1973), we failed to find anything resembling a complete or rhythmic molt in *Phase II*.

#### CONCLUSIONS

While our data indicate that the gonadal cycle of *Z. capensis hypoleuca* at 26.9° S is photoperiod-dependent and possibly under fairly strict photoperiodic control, the environmental factors that determine the precise time

of breeding are unknown and probably complex (King 1973). Conservatively, our data together with those of King (1973) show (1) that the factors that time the annual cycle are not entirely endogenous; predictive information is involved; (2) that control of the gonadal and molt cycles *could* be entirely exogenous, depending only on the actual oscillation in the photoperiod. There is, however, the suggestion of a long-period rhythm in gonadal weight (fig. 1); this should be explored further under appropriately controlled conditions.

From the results of this and other recent studies on various populations of *Z. capensis* (Epple et al. 1971; Miller 1959b, 1965), we must now conclude that it is probable that at least some relatively low-latitude populations of birds are capable of very fine discrimination of photoperiodic information, such that an approximately annual periodicity in testicular growth and collapse can be timed by the photoperiod.

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