Circadian basis for the photoperiodic response in the male blackheaded bunting (Emberiza melanocephala)

VINOD KUMAR and P D TEWARY*
Department of Zoology, Banaras Hindu University, Varanasi 221 005, India

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Abstract. Short day (6 hr light in a 24 hr cycle (LD 6 : 18)) inhibits growth and development of the testes in male blackheaded buntings, whereas the same (6 hr) nonstimulatory photoperiods in a 36 hr cycle (LD 6 : 30) induce complete testicular recrudescence and development. In another experiment of 24 hr cycles, using the same (6 hr) main photoperiod, testes were stimulated when the dark period was interrupted by light at 12 to 13 hr after the onset of basic photoperiod (LDLD 6 : 6 : 1 : 11). The results appear to conform to the tenets of the external coincidence model.

Keywords. Blackheaded bunting ; photoperiod ; circadian ; rhythm ; light : dark cycle ; external coincidence model.

1. Introduction

Since the pioneer studies of Hamner (1963) on house finches (Carpodacus mexicanus), the nature of the photoperiodic response mechanism(s) has been experimentally investigated in many photoperiodic birds (see reviews, Farner and Lewis 1971 ; Follett 1973 ; Farner 1975 ; Farner et al 1977 ; Turek 1978). The results from these experiments agree with the classical Büning hypothesis which mentions an endogenous circadian rhythm of sensitivity to light as the physiological basis for photoperiodism (Büning 1973). The validity of a circadian basis for photoperiodic time measurement in birds is generally tested by resonance and night-interruption experiments (see reviews, Follett 1973 ; Farner 1975 ; Turek 1978). Here, we report the results of night-interruption experiments designed to test the influence of an endogenous circadian rhythm in the photoperiodic time measurement of blackheaded buntings.

2. Materials and methods

Wild adult male blackheaded buntings (Emberiza melanocephala) were acclimatized to laboratory conditions for a fortnight. These acclimated birds were pretreated

* To whom correspondence should be made.
for 8 weeks with short days (LD 8 : 16) ensuring that they were photosensitive at the time of exposure to different light regimes. Three groups (numbered I, II and III) of birds then were marked individually and held under different programmed photoperiods (LD 6 : 18, LD 6 : 30 and LDLD 6 : 6 : 1 : 11, respectively) for a fixed period (see table 1) inside light-boxes. Food and water were freely available. The birds were lit by fluorescent tubes at an intensity of about 400 lux at perch level. The first experimental photophase was in phase with the pretreatment schedule and commenced at 06·00 hr. The birds were laparotomized at the beginning and end of experiments, and only during the main light phase of the cycle. Testicular growth was assessed as combined testicular weight \textit{in situ} and by comparing with the standard set of gonads of known weights. The error by this method is about (±) 20\%. The data from one bird of group III that died during the course of study were not included in our statistical analysis. The data were analysed using student’s ‘ \textit{t} ’ test.

3. Results and discussion

The results are presented in table 1. The birds either of group I (LD 6 : 18) or of II (LD 6 : 30) received equal photoperiods (6 hr) per cycle but only the birds of the latter group responded. Since the extended period of darkness could appear to initiate the gonadal recrudescence, in a separate experiment buntings were held in constant darkness (DD) for 100 days and found not to respond (unpublished results). Further, the birds of group III (LDLD 6 : 6 : 1 : 11) also responded although the total amount of darkness which these birds received per cycle (17 hr) was even less than the amount which birds of group I were experiencing (18 hr). The duration of light also cannot be a factor in initiation of the testicular growth in the buntings, since the total amount of light per cycle given in all the experiments (6 hr or 7 hr) was much shorter than the photoperiodic threshold for the species which lies at 11 to 12 hr light per day (Kumar and Tewary 1982). Further, it is to be noted that a light regimen consisting of 8 hr photoperiod (LD 8 : 16)

\begin{table}[h]
\centering
\begin{tabular}{|l|l|l|l|l|}
\hline
Group & Light regime & Light cycle & Days of treatment & Combined testicular weight (mg) \\
& (light : dark) & (in hr) & (in weeks) & Initial & Final \\
\hline
I & LD 6 : 18 & 24 & 5 & 9·5±1·68 (6) & 7·00±0·63 (6) \\
II & LD 6 : 30 & 36 & 5 & 8·0±0·00 (7) & 285·71±21·03 (7) \\
III & LDLD 6 : 6 : 1 : 11 & 24 & 6 & 7·5±0·50 (6) & 216·00±22·49 (5) \\
\hline
\end{tabular}
\caption{The gonadal responses of \textit{Emberiza melanoccephala} exposed to 3 different light regimes.}
\end{table}

\textit{Value in parenthesis gives the number of individuals}
for 6 months could not induce the testes of blackheaded buntings (Tewary and Kumar 1982).

It appears that neither the amount of light or dark nor the ratio of light to dark is the determining factor in stimulating the gonadal growth and development in blackheaded buntings. Our data agree with those obtained with similar experiments on other known photoperiodic birds (Hamner 1963, 1964; Follett 1973; Farner 1975; Tewary and Kumar 1981a, b; Chandola et al 1976). Such results may best be interpreted on the basis of an endogenous circadian rhythm involvement in the ‘photosensitivity’ of the hypothalamo/hypophyseal/gonadal system (Follett 1973; Farner 1975; Turek 1978). According to the external coincidence model, first developed by Büning (1973), a photoperiodic induction occurs if and only if photophase coincides (repeatedly, daily or otherwise) with the photosensitive phase (= photoinducible phase, subjective night) of the circadian rhythm. In the present experiments presumably the birds of group II received 6 hr light at alternate cycles, and of group III were receiving 1 hr light period daily in the photosensitive phase and a response was obtained in both the groups. In contrast, the birds of group I were receiving light periods (6 hr) daily only in the photoinsensitive phase (= non-photoinducible phase, subjective day), and hence photostimulation failed to occur.

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