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Short-day experience is not a prerequisite for the termination of photorefractoriness in the reproductive cycle of baya weaver, *Ploceus philippinus*

MAHABIR BISHT and ASHA CHANDOLA-SAKLANI*
Reproductive and Wildlife Biology Unit, Post Box 45, Garhwal University, Srinagar Garhwal 246 174, India

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Abstract. In most photoperiodic avian forms (irrespective of temperate or tropical distribution) including the baya weaver, *Ploceus philippinus,* seasonal reproduction comes to an end due to the development of a photoperiodically controlled photorefractory phase when birds cease to respond to the stimulatory effect of long days. In the present paper photoperiodic control of the termination of photorefractory phase has been examined by studying the effect of short-day exposure lasting 4–6 months on long-day response of birds. Results indicate that unlike in other photoperiodic birds short-day exposure of winter is not a prerequisite for the termination of photorefractory phase in the reproductive cycle of baya weaver. Artificial long days on the other hand hasten the termination of this phase. Refractory phase in baya weaver, therefore, unlike that in temperate forms, is a temporary state resulting most likely from a sequel of physiological events triggered by long days of spring/summer which temporarily mask the photostimulatory response. Spontaneous termination of photorefractoriness in birds of tropical habitats may have a selective value imparting to the reproductive cycle the necessary elasticity for adaptation to diverse ecological conditions.

Keywords. Photorefractoriness; photoperiod; reproductive cycle; tropical baya.

1. Introduction

Adequate timing of termination of reproduction is as important as its timely onset in seasonal breeders. In temperate zone birds the long days of spring and summer induce gonadal recrudescence, and termination of breeding occurs as a result of the development of a post reproductive `photorefractoriness' which is dissipated by the short days of winter (Farner and Follett 1966, 1980). Until recently almost nothing was known about the mechanisms that terminate breeding in tropical birds. We have been investigating this problem in our laboratory with the help of a bird model, *viz.,* the baya weaver *Ploceus philippinus.*

In the baya weaver gonadal development is initiated in spring with increasing daylength and gonadal regression occurs during late summer when daylengths are still stimulatory. This indicates that birds become refractory in the presence of a daylength which was previously stimulatory (see reviews Chakravorty *et al* 1985; Chandola-Saklani *et al* 1983, 1985, 1990). Although earlier studies were suggestive of an absence of refractory phase in the baya weaver (Thapliyal and Saxena 1964), our experiments with monthly transfers to stimulatory daylength have detected a definite photorefractory period in the reproductive cycle (Chandola and Chakravorty 1982; Singh and Chandola 1982a; Chakravorty and Chandola-Saklani 1985; Chandola-Saklani *et al* 1988a). The refractory phase persists for 5–6 months

*Corresponding author.

(from July to December) and includes both relative and absolute components (Chandola-Saklani *et a!* 1988b; M Bisht and A Chandola-Saklani, unpublished results). It has also been demonstrated that the onset of the photorefractory phase is induced by the increasing daylength of spring and summer (Chakravorty and Chandola-Saklani 1985; Chandola-Saklani *et al* 1988b: M Bisht and A Chandola-Saklani, unpublished results). In this paper we present evidence that, unlike in other photoperiodic birds, exposure to short days of winter is not a prerequisite for the termination of refractory phase in baya weaver.

2. Materials and methods

In June 1985 birds were obtained from suppliers and maintained in an outdoor aviary. At Srinagar Garhwal (30° 13' N and 78° 48' E) the daylength at summer solstice is 14 h and at winter solstice 10 h. After a fortnight of acclimatization adult birds were sexed on the basis of sexual characters, *viz*., gonadotrophin-dependent yellow plumage and testosterone-dependent black beak (Thapliyal and Saxena 1964). Birds were laparotomized under ether anaesthesia and the long and short axes of the testis measured in *situ* and gonadal volume calculated. Initial records were made on testicular volume, plumage and beak colour. For the assessment of the latter two, birds were individually scored according to the following scale. Plumage: dull henny = 0, partial yellow = 50, complete yellow = 100; Beak: straw = 0, partial black = 50 and complete black = 100. During experimentation 4–5 birds were housed in wire cages with a single central perch. Birds were divided into two groups of 30 birds each. One group (G I) was maintained in natural daylength (NDL), in a bird room equipped with skylight (300 lux at perch level). The other group (G II) was maintained in the same room but light was restricted to eight hours (8L :16D) *i.e*., 2 h less than the shortest day experienced in nature. The photoperiodic response threshold in this bird lies between 11–12 h (Singh and Chandola 1981).

After complete gonadal regression had occurred (as evident from monthly laparotomies) in both 8L :16D and NDL conditions, 8–10 birds from each group were shifted in the month of October and again in December to photoperiodic chambers (1·20×0·75×0·60 m) equipped with flourescent tubes (300 lux at perch level) and automatic time switches adjusted for a 16L : 8D schedule. The remaining 8–10 birds in each group (G I and G II) served as NDL and 8L :16D controls respectively. The long-day responses of testes, plumage and beak colour were recorded for 3–4 subsequent months after these shifts.

All birds were fed a mixture of paddy, *Oryza sativa* and pearl millet, *Panicum frumentaceum* and water *ad libitum* and remained healthy. Quantitative data were analysed following standard `*t*' tests and ANOVA (Fisher 1963).

3. Results

Results are summarized in figure 1 and table 1. In 8L :16D gonadal regression occurred ($P < 0{\cdot}01$, June *vs* July) after shift from NDL (figure 1). By September all birds in this group had become sexually quiescent and remained as such till the termination of the experiment. The gonads of birds maintained in NDL regressed in August ($P < 0{\cdot}01$ July *vs* August) reaching a sexually inactive state by September

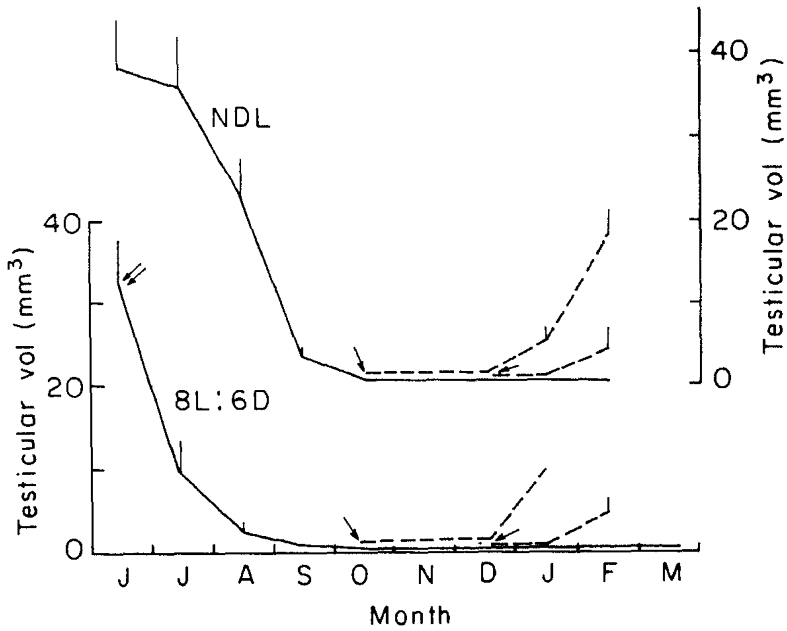

Figure 1. Effect of pre-exposure of short days on the termination of photorefraetoriness in baya weaver as indicated by gonadal status (⇙ transfer from natural daylength (NDL) to 8L: 16D, → transfer from NDL or 8L: 16D to 16L: 8D) Vertical bars indicate standard error of mean.

and thereafter remained as such. Birds which were shifted from both these groups to 16L : 8D in October showed first sign of gonadal recrudescence with appearance of one or both associated secondary sexual characters (yellow plumage and black beak) after 3 months of exposure, that is in January (table 1). Birds shifted from both these groups (constant 8L:16D and NDL) to 16L:8D in December showed gonadal recrudescence and appearance of yellow plumage after 2 months (in February). There was thus no difference in the long-day response of 8L:16D and NDL-held birds.

4. Discussion

It is clear from the present results that pre-exposure of short days of as long as 18 to 26 weeks did not advance the acquisition of the normal photoperiodic response in photorefractory birds. Termination of photorefractoriness in natural conditions in this bird is, therefore, not dependent on the winter daylengths. This is contrary to the classical type of photorefractoriness observed in other photoperiodic forms [*Zonotrichia leucophrys gambelii* (Wolfson 1958); *Z. atricapilla* and *Z. pugetensis* (Turek 1972); *Carpodacus mexicanus* (Hamner 1968); C. *erythrinus* (Kumar and Tewary 1982; Tewary and Dixit 1983); *Emberiza bruniceps* (Lal and Thapliyal 1985)] in which a short-day exposure of 2–6 weeks is a prerequisite for termination of photorefractoriness. In all these birds photorefractoriness can be eliminated by exposure to photoperiods less than those that stimulate maximal gonadal growth. Another striking difference is that in these forms long days maintain the state of photorefractoriness whereas in the baya weaver long days actually appear to hasten

Table 1. Effect of pre-exposure of short days on the termination of photorefractoriness in weaver birds as represented by secondary sex characters (gonadotrophin-dependent yellow plumage and testosterone-dependent black beak).

	Treatment		June	July	Aug.	Sept	Oct.	Nov.	Dec.	Jan.	Feb.
	NDL (control)	Plumage	91·66 ± 8·36	100·0 ± 0·0	60·00 ± 9·85	10·0	0·0	0·0	0·0	0·0	0·0
		Beak	83·33 ± 10·53	100·0 ± 0·0	60·00 ± 9·85	10·0	0·0	0·0	0·0	0·0	0·0
G I	NDL birds transferred to 16L:8D in October	Plumage	—	—	—	—	0·0	0·0	0·0	83.33 + 16·68	—
		Beak	—	—	—	—	0·0	0·0	0·0	0·0	—
	NDL birds transferred to 16L:8D in December	Plumage	—	—	—	—	—	—	0·0	0·0	50·0
		Beak	—	—	—	—	—	—	0·0	0·0	0·0
	8L:16D (control)	Plumage	100·0 ± 0·0	100·0 ± 0·0	50·0	0·0	0·0	0·0	0·0	0·0	0·0
		Beak	100·0 ± 0·0	100·0 ± 0·0	50·0	0·0	0·0	0·0	0·0	0·0	0·0
G II	8L:16D birds transferred to 16L:8D in October	Plumage	—	—	—	—	0·0	0·0	0·0	87·5 ± 12·5	—
		Beak	—	—	—	—	—	—	—	50·0	—
	8L:16D birds transferred to 16L:8D in December	Plumage	—	—	—	—	—	—	0·0	0·0	50·0
		Beak	—	—	—	—	—	—	0·0	0·0	0·0

Birds were individually scored according to the following—Plumage: dull henny = 0, partial yellow = 50, complete yellow = 100; Beak: straw = 0, partial black = 50 and complete black = 100.
Values are given as mean ± SE.

its termination. When birds were shifted to 16L :8D stimulatory daylength in October (irrespective of previous light exposure) gonads recrudesced 3 months later in January, and when shifted to this stimulatory regime in December, gonads took 2 months to recrudesce. Acquisition of photosensitivity by January may seem to account for this time difference in response. However, should this be the case, birds shifted to stimulatory daylength in December would have responded by January but they did not. Obviously, continued exposure to long days facilitated termination of refractoriness. Previous work (Singh and Chandola 1982b; Chandola-Saklani *et al* 1990; M Bisht and A Chandola-Saklani, unpublished results) support these findings.

It can be concluded that in baya weaver the onset of photorefractoriness is dependent on long-day exposure but the recovery of photosensitivity is a spontaneous phenomenon which can be accelerated by artificial long-days. It appears that in this bird light has a continually stimulatory role. Photorefractoriness is, therefore, a temporary state resulting from a sequel of physiological events, triggered by long days of spring/summer, which temporarily masks the photostimulatory response. Although hormones of the thyroid and pineal glands have been shown to have an antigonadotrophic effect in this bird (Chandola *et al* 1974; Balasubramanian and Saxena 1972), in our opinion testicular secretions (testosterone) may be of a greater importance since in addition to a negative feedback effect on the hypothalamo/hypophysial complex there is indirect evidence that these may affect photoresponsive centers in the CNS and hence may interfere with the photoresponse (Singh and Chandola 1982b; Chakravorty and Chandola-Saklani 1985).

Some tropical birds may have an absolute dependence on short days for the dissipation of photorefractoriness, for example *Carpodacus erythrinus* (Kumar and Tewary 1982). Recovery from photorefractoriness can occur spontaneously in tropical birds other than the baya weaver too [*e.g., Quelea quelea* (Lofts 1962)]. In our opinion this phenomenon reflects a relative independence from photoperiodic regulation and imparts to the reproductive cycle an elasticity for adaptation to the diverse ecological conditions of tropics.

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