ABSENCE OF A REFRACTORY PERIOD IN THE COMMON WEAVER BIRD

By J. P. THAPLIYAL and R. N. SAXENA

Light sensitive birds that breed seasonally in temperate zones or migratory birds that winter in the tropics (Engels, 1959) experience at the termination of the breeding season a refractory phase when gonads regress both in volume and activity, postnuptial cholesterol-positive lipids appear within the seminiferous tubules (Marshall, 1949), and increased light is unable to induce development of the gonads. The duration of this phase is known to differ among species of birds (see reviews by Burger, 1949; Wolfson, 1952*a*; Miller, 1954; Farner, 1959; Marshall, 1961). Short days (or long periods of darkness) shorten it (Damsté, 1947; Wolfson, 1952*b*, 1959*a*, 1959*b*, 1960; Miyazaki, 1934; Vaugien, 1952*a*, 1952*b*, 1954; Burger, 1947), and long days prolong it (Wolfson, 1952*b*; Miller, 1951, 1954; Vaugien, 1952*a*, 1952*b*; Burger, 1947). Further, while long days are capable of stimulating nonrefractory gonads to breeding condition, they are incapable of maintaining them in a continuous state of spermatogenesis (Burger, 1949; Wolfson, 1952*b*). Prolonged photostimulation, therefore, eventually leads to the refractory phase. Short days, or darkness of 12 hours or longer (Wolfson, 1952*a*), can alone make the bird again respond to photostimulation.

It is not known, however, whether tropical birds which have distinct breeding cycles, beginning in late spring or early summer, also experience refractoriness and show similar response to light. Therefore, an investigation of the refractory phase in local birds was undertaken at Varanasi, India (lat. 25° 18′ N, long. 83° 1′ E). The day length at Varanasi on June 21 is 13 hours and 34 minutes; on September 21 it is 12 hours and 4 minutes; and on December 21 it is 10 hours and 26 minutes.

This preliminary report deals with the effects of long days on the male Common Weaver Bird (*Ploceus philippinus*) in different phases of the annual cycle and suggests the absence of a refractory period.

METHODS

The Common Weaver Bird is a resident, seasonally dimorphic weaver finch found throughout the Indian Union (Ali, 1955). Females and juveniles the year around and males in the eclipse phase are fulvous-brown in color. At the approach of the breeding season in April, adult males undergo partial molt and assume a bright yellow and black nuptial plumage. Postnuptial molt in both sexes starts in August and is completed by September. The bill is straw colored in nonbreeding males, juveniles, and females, but in adult males the bill starts to darken by late April, turning black during the breeding season. The pigmentation of the plumage is regulated by the cycling hypophysis (Thapliyal and Saxena, 1961) and that of the bill by the testicular hormone (Saxena and Thapliyal, 1962).

The testis is of minimum size from November to February (fig. 1*a*) and attains maximum volume and activity by June. There is no change in size of testis in July, but by early August regression sets in and the minimum size is reached by November. Spermatozoa are present in the tubules during the breeding phase which extends from the latter half of June to the middle of August. Postnuptial, cholesterol-positive intratubular lipids, as have been reported for other birds (Marshall, 1954; 1959), appear in August and clear by February at which time the interstitium is cholesterol negative.

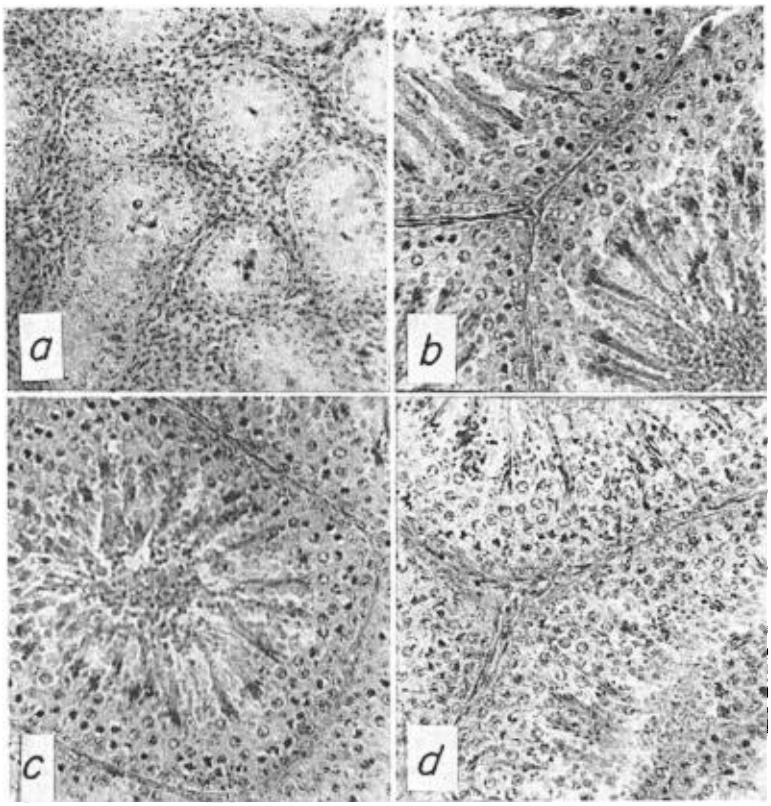

Fig. 1. Photomicrographs of testis of the Common Weaver Bird (*Ploceus philippinus*). *a*, in December (X 370); *b*, after three months of long-day treatment, beginning on November 21, 1961 (X 220); *c*, after a year of long-day treatment, beginning on December 21, 1961 (X 220); *d*, control weaver bird on June 21, 1962 (X 220).

Adult male birds utilized in this study were caught and their right sides were deplumed a fortnight before the beginning of the investigation. On the first day of the light treatment, the character of the regenerating feather follicles was noted and the left testis was measured *in situ*. A few birds were castrated and one testis from each of these was measured, fixed in Bouin's fluid, embedded in paraffin, sectioned at 7 μ, and stained with Harris' haematoxylin and eosin. The other testis was sectioned fresh on a freezing microtome and treated with Sudan IV for lipids; some sections were also given the Schultz test for cholesterol. Subsequently, on the same date every month, feathers of all the birds were plucked and stored, and the character of the regenerating feathers was noted. Some birds from each group were also opened every month and their left testis was measured *in situ*, and at least one bird from each group was castrated and the gonads treated as indicated. Birds of the November-December, 1961, experimental group were not so examined every month nor were the lipid contents of the gonads studied. These birds, however, have been deplumed regularly.

The controls and the experimental birds were maintained under similar conditions of food and water in captivity. Constant 15-hour days included five hours (5 to 7 a.m.

TABLE 1

RESPONSE OF WEAVER BIRDS IN GROUP–I SUBJECTED TO CONSTANT DAY LENGTHS OF 15 HOURS, BEGINNING NOVEMBER 21, 1961

Bird no.	Testis size in mm.	1961		1962									1963			
		Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	June	July	Sept.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
352	L	1.8	—	5.3	6.0*											
	B	1.0	—	4.0	4.0											
356	L	1.8	—	4.8	6.0	6.5	6.5	6.3	6.3	6.3	6.3	6 3	6.3	6.3	6.3	6.2
	B	1.0	—	3.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.2
Plumage		E	E	N	N	N	N	N	N	N	N	N	N	N	N	N
Bill		S	S	Base, S; tip, D	D	D	D	D	D	D	D	D	D	D	D	D

* Bird was castrated and testes fixed for examination.
Abbreviations are as follows: E, eclipse; N, nuptial; S, straw-colored; D, dark; L, maximum length; B, maximum breadth.

and 5 to 8 p.m.) of artificial illumination provided by a single 100-watt incandescent lamp, held at a distance of five feet from the base of the cages, and 10 hours of normal daylight. The controls, group-V, were maintained under natural conditions of light and day length. Group-I was subjected to 15 hours of daylight starting on November 21, 1961, group-II was exposed to 15-hour days starting on December 21, the shortest day in the year (sunrise to sunset—10 hours and 26 minutes), when the testis size is minimum, the bill is nonpigmented, and the plumage is typical of the nonbreeding period. Group-III was subjected to 15 hours of daylight starting on June 21, 1962, the longest day in the year (13 hours and 34 minutes of daylight), when the birds are at the peak of their reproductive activity. Group-IV was started on 15 hours of daylight on September 21, 1962 (length of day, 12 hours and 4 minutes). The control, group-V, was also started on June 21, 1962, and was used as a control for group-IV also.

OBSERVATIONS AND RESULTS

The response of the birds exposed to continuous 15-hour days in different periods of the gonadal cycle is presented in tables 1, 2, 3, and 4.

TABLE 2

RESPONSE OF WEAVER BIRDS IN GROUP–II SUBJECTED TO CONSTANT DAY LENGTHS OF 15 HOURS, BEGINNING DECEMBER 21, 1961

Bird no.	Testis size in mm.	1961	1962									1963			
		Dec.	Jan.	Feb.	Mar.	May	June	Aug.	Sept.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
LE2	L	1.5	—	3.5	5.8	5.8*									
	B	1.0	—	2.0	3.3	3.3									
LE8	L	1.9	—	4.2	5.0	5.2	5.2	5.4	5.4	5.4	5.4*				
	B	1.0	—	2.6	3.0	3.0	3.0	3.0	3.0	3.0	3.0				
LE6	L	1.7	—	3.1	5.8	5.8	5.6	5.6	5.6	5.7	5.7	5.7	5.7	5.7	5.3
	B	1.0	—	2.0	3.4	3.4	3.4	3.4	3.4	3.4	3.4	3.4	3.4	3.6	3.8
Plumage		E	E	N	N	N	N	N	N	N	N	N	N	N	N
Bill		S	S	Base, S; tip, D	D	D	D	D	D	D	D	D	D	D	D

* Bird was castrated and the testes fixed for examination.
For explanation of abbreviations see table 1.

Birds in group-I, started on a schedule of 15-hour days on November 21, 1961, when first examined after two months showed an increase in size of gonads and had, after regenerating eclipse plumage, assumed the nuptial plumage, indicating an activated hypophysis. The darkening bill at the same time suggested gonadal activity. The gonads developed to the maximum size by February when the seminiferous tubules were expanded and contained bunched spermatozoa (fig. 1*b*). This condition of maximum size of gonads, presence of nuptial plumage, and dark bill is being maintained by the surviving bird.

The response of birds in group-II was similar to that of birds in group-I. Under a 15-hour day the plumage changed to the nuptial type, and the gonads had started to

TABLE 3

RESPONSE OF WEAVER BIRDS IN GROUP–III SUBJECTED TO CONSTANT DAY LENGTHS OF 15 HOURS, BEGINNING JUNE 21, 1962

Bird no.	Testis size in mm.	1962							1963			
		June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
B12	L	5.0	5.0*									
	B	4.5	4.6									
B15	L	5.0	5.2	5.2*								
	B	3.6	3.6	3.6								
B5	L	4.5	4.5	—	5.0*							
	B	3.0	3.0	—	3.0							
B20	L	5.2	5.2	—	5.0*							
	B	4.6	4.4	—	3.0							
B7	L	5.5	—	5.5	—	5.5*						
	B	3.5	—	3.6	—	3.6						
B25	L	3.0	5.0	—	—	5.0**						
	B	2.0	3.0	—	—	3.0						
B1	L	5.2	—	5.2	—	5.9	5.9*					
	B	4.5	—	4.5	—	4.6	4.6					
B18	L	4.3	—	5.0	—	5.2	—	5.2*				
	B	2.2	—	2.8	—	3.6	—	3.6				
B14	L	4.2	—	4.9	—	6.9	—	6.9	6.9*			
	B	2.2	—	2.4	—	4.8	—	4.8	4.8			
B9	L	5.2	—	5.4	6.9	6.9	6.2	6.2	6.4	6.4*		
	B	4.6	—	4.6	5.0	5.0	5.0	5.0	5.0	5.0		
B22	L	5.5	5.5	—	5.5	—	5.8	5.8	5.8	5.8	5.8*	
	B	3.6	3.6	—	3.6	—	3.6	3.6	3.6	3.4	3.4	
B21	L	4.3	4.3	—	6.2	—	6.2	6.2	6.2	6.2	6.2*	
	B	3.0	3.0	—	4.6	—	4.6	4.6	4.6	4.6	4.6	
B6	L	5.0	—	5.0	—	5.6	—	5.6	5.6	5.6	5.6	5.8
	B	3.0	—	3.0	—	3.8	—	3.8	3.8	3.8	4.0	4.0
B13	L	5.3	—	5.6	—	5.8	5.8	5.8	6.0	6.0	6.0	6.0
	B	2.2	—	2.8	—	4.0	4.0	4.0	4.0	4.0	4.0	4.0
Plumage		N	N	N	N	N	N	N	N	N	N	N
Bill		D	D	D	D	D	D	D	D	D	D	D

* Bird was castrated and the testes fixed for examination.

** Bird died on October 5, 1962.

For explanation of abbreviations see table 1.

TABLE 4

RESPONSE OF WEAVER BIRDS IN GROUP–IV SUBJECTED TO CONSTANT DAY LENGTHS OF 15 HOURS, BEGINNING SEPTEMBER 21, 1962

Bird no.	Testis size in mm.	1962 Sept.	1962 Oct.	1962 Nov.	1962 Dec.	1963 Jan.	1963 Feb.	1963 Mar.	1963 Apr.
C5	L	3.0	1.6*						
	B	2.0	1.0						
C11	L	2.4	1.6	4.9*					
	B	1.8	1.0	3.8					
C21	L	2.0	1.5	4.6	6.2*				
	B	1.2	1.0	3.0	3.8				
C15	L	3.6	2.0	4.9	5.9	5.9*			
	B	2.4	1.5	3.0	3.6	3.6			
C2	L	1.8	1.8	3.8	5.2	5.2	5.2	5.2	5.3
	B	1.0	1.0	2.0	3.2	3.2	3.2	3.2	3.2
C18	L	3.5	1.7	3.2	5.7	5.7	5.7	5.7	5.7
	B	2.5	1.2	2.0	3.0	3.8	3.8	3.8	4.0
Plumage		E	E	N	N	N	N	N	N
Bill		Base, S; tip, D	Base, S; tip, D	Base, S; tip, D	D	D	D	D	D

* Bird was castrated and the testes fixed for examination.
Abbreviations explained in table 1.

increase in size by the second month. By the third month the maximum gonadal size was reached. One bird was castrated on May 21, 1962, and another on December 21, 1962, exactly 12 months after the start of the experiment, and in both cases the testes were found to be fully active and full of spermatozoa (fig. 1*c*). Bird no. LE6 maintained full reproductive condition for 22 months until it was sacrificed on December 21, 1963.

Group-III was started on a schedule of 15 hours of daylight on June 21, 1962, when wild weaver birds wear nuptial plumage and have a dark bill. At this time the testes are fully developed (fig. 1*d*). These birds, when subjected to 15-hour days, maintained their peak breeding condition (fig. 2*a*).

Group-IV was started on 15 hours of daylight on September 21, 1962, when the birds were undergoing postnuptial molt and were regenerating eclipse plumage, suggesting an inactive hypophysis. The gonads were small and were becoming smaller; the seminiferous tubules were collapsed (fig. 2*b*) and laden with postnuptial cholesterol-positive lipids (fig. 2*c*). In this group during the first month there was a decrease in the size of the testes and the plumage and bill also maintained their eclipse character, but by November 21, the gonads started recrudescing and the plumage and the bill pigmentation also changed, suggesting an activated adenohypophysial-gonadal axis. By December 21, the birds had attained breeding condition and are continuing to maintain it (fig. 2*d*).

The control group, maintained under natural conditions of light and day length starting on June 21, 1962, is behaving normally.

DISCUSSION

Tables 1, 2, and 4, showing positive response to a continuous 15-hour day, irrespective of the state of the gonad (fully regressed, tables 1, 2, or regressing, table 4), suggests the lack of a postnuptial refractory phase in this weaver bird. Under a continuous

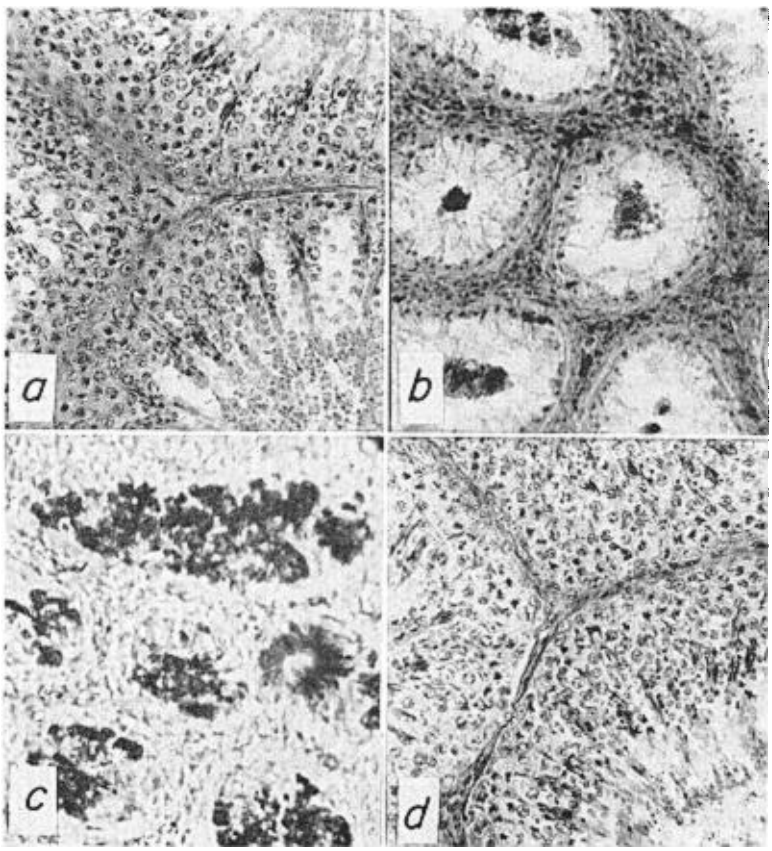

Fig. 2. Photomicrographs of the testis of the Common Weaver Bird. *a*, after six months of long-day treatment, beginning on June 21, 1962 (X 220), *b*, control weaver bird on September 21, 1962 (X 220); *c*, on September 21, 1962, showing cholesterol positive postnuptial lipids within the tubules (X 300); *d*, after three months of long-day treatment, beginning on September 21, 1962 (X 220).

15-hour day, the hypophysis of the Common Weaver Bird becomes active within one month, as indicated by the change in the character of the plumage; the gonads start developing by the second month and the bill also darkens. The peak breeding condition of maximal gonadal development, completely dark bill, and with free spermatozoa within the tubules is attained by the third month.

Further, the fact that the peak breeding condition is maintained once it is reached also indicates the absence of the refractory phase. The birds started on the 15-hour day treatment in November and December have now been in full sexual phase for over 15 months without showing any sign of regression or fatigue, and the birds started on this schedule in June, which were at the peak of their sexual activity when given the long-day treatment, are also maintaining their breeding condition. A bird of the temperate zone, on the other hand, cannot be maintained in a continuous state of breeding activity under continuous light treatment (Burger, 1949; Wolfson, 1952*b*).

The lipid contents of the seminiferous tubules of both the experimental and control birds have also been studied. Cholesterol-positive lipids appear within the tubules at the end of the breeding season and are dissipated when the hypophysis becomes active, either in the course of natural events or as a result of long-day treatment when gonads start recrudescing. In other birds investigated the dissipation of intratubular lipids and the development of gonads occurs only when either exogenous gonadotropic hormones are injected (Riley and Witschi, 1938; Miller, 1949; Vaugien, 1954, 1955; Lofts and Marshall, 1958) or after the natural recovery of the hypophysis from refractoriness, but it is never known to occur in the refractory birds in response to long-day treatment.

It is believed that the cause of refractoriness lies at the hypophysial or hypothalamic level which seems to suffer a seasonal fatigue and needs "rest" before it will respond again to light (Burger, 1949). The Common Weaver Bird, however, responds to light at all times and continues to do so as long as the treatment is maintained, suggesting that the response mechanism (the hypophysis or the hypothalamus) never develops "fatigue" and so need not be "rested."

TABLE 5

RESPONSE OF WEAVER BIRDS USED AS CONTROLS FOR PHOTOPERIOD EXPERIMENTS, BEGINNING JUNE 21, 1962

Bird no.	Testis size in mm.	1962							1963			
		June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
B64	L	5.5	5.5*									
	B	4.2	4.2									
B39	L	5.6	5.6	2.8*								
	B	3.8	3.8	1.9								
B60	L	5.2	—	4.3	2.5*							
	B	3.8	—	3.0	1.6							
B74	L	6.2	5.0	3.2	—	1.8*						
	B	4.0	3.5	2.2	—	1.4						
B83	L	5.8	5.8	3.5	2.2	2.0	1.7*					
	B	4.0	4.0	2.6	2.0	1.8	1.0					
B70	L	6.2	—	3.2	1.8	1.8	1.5	1.5*				
	B	4.3	—	2.2	1.6	1.6	1.2	1.2				
B71	L	4.8	4.8	—	2.6	1.7	—	1.7	1.7*			
	B	2.6	2.6	—	1.6	1.0	—	1.0	1.0			
B72	L	6.2	5.9	3.2	2.2	1.9	1.6	1.5	1.6	1.6	1.6	2.2
	B	4.2	4.0	2.8	1.6	1.5	1.0	1.0	1.0	1.0	1.2	1.8
B61	L	5.3	—	3.8	1.8	1.6	1.6	1.7	1.7	1.7	1.7	2.6
	B	3.8	—	2.6	1.4	1.2	1.2	1.2	1.3	1.3	1.3	2.0
B2	L	5.9	—	3.6	—	1.8	1.6	1.6	1.8	1.8	1.8	2.6
	B	3.6	—	2.8	—	1.2	1.0	1.0	1.0	1.0	1.3	1.8
B67	L	6.8	—	4.0	—	2.1	1.8	1.5	1.5	1.5	1.8	2.8
	B	4.5	—	3.0	—	1.6	1.2	1.0	1.0	1.0	1.2	2.0
Plumage		N	N	N	E	E	E	E	E	E	E	N
Bill		D	D	D	Base, S; tip, D	S	S	S	S	S	S	Base, S; tip, D

* Bird was castrated and the testes fixed for examination.
Abbreviations explained in table 1.

Long-day treatment for birds of group-III was begun on September 21, when the gonads had entered the postnuptial phase and the day length, although decreasing was still more than 12 hours. These birds also responded, and within two months the hypophysial-gonadal axis became active and by the third month full breeding condition had been reached. Thus, unlike the birds of the temperate zones, the response mechanism of the Common Weaver Bird is always easily activated by long days at any time during the postbreeding period, and a rest period of long nights is not necessary between two cycles. The Common Weaver Bird also seems to be the only species where continued long-day treatment does not cause refractoriness but actually maintains the bird in a continuous breeding state.

Marshall and Coombs (1957:579) did not find any refractory period in the female Rook (*Corvus frugilegus*). Brown and Rollo (1940) were able to maintain African weaver finches in an active breeding state for over a year. Wolfson (1952*b*) has also reported similar findings for a group of juncos treated with 20-hour photoperiods, beginning on April 6. Juncos started on long-day schedules on other dates, however, showed the usual pattern of response. Miller (1959) found no postjuvenal refractory period in equatorial Andean Sparrows (*Zonotrichia capensis*).

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SUMMARY

The Common Weaver Bird (*Ploceus philippinus*) does not experience any refractory period and can be maintained in a peak breeding condition continuously. It responds to long days (15 hours) during all phases of its breeding cycle. The cycle in nature probably ends not because the hypothalamus or hypophysis or gonad has become refractory but because the day length has fallen below the minimum required to maintain an active hypophysial-gonadal axis. Further experiments are in progress to study the behavior of this species of weaver bird under a schedule of short days and to determine the shortest day length at which this bird can be maintained in a continuously active breeding state.

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