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Photorefractoriness in the black-headed bunting *Emberiza melanocephala:* Possible involvement of the thyroid glands

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Abstract. In the male black-headed bunting, *Emberiza melanocephala,* photostimulated testicular and/or body weight growth was followed by the regression. Transfer of photorefractory birds from 20L/4D to 23L/1D or from natural lighting (12-13 h) to 20L/4D failed to evoke testicular and/or body weight recrudescence. Thyroidectomy suppressed light-induced increase in the testes and resulted in early regression. Fully developed testes of breeding birds also regressed following thyroidectomy; an effect which was reversed by daily injections of 1 μg/bird of L-T_4. Treatment with L-T_4 at doses from 0·5-2·0 μg/bird/day/ 30 days had no effect on the testes of birds maintained on 12L/12D or following a shift from 12L/12D to 20L/4D. Photoinduced increase in body weight was inhibited by thyroidectomy; an effect which was reversed by treatment with L-T_4 at dose level 1 μg/bird/day. The extent to which thyroidectomy decreased body weight of birds depended upon the lipid reserves at the time of operation. It is suggested that in the male black-headed bunting (i) breeding is terminated by development of absolute-gonadal and metabolic-photorefractoriness and (ii) thyroid hormones are necessary for sustaining light-induced increase in the gonads and/or body weight and for their maintenance, but not for the development of photorefractory state.

Keywords. Thyroid; photorefractoriness; day-length; birds; breeding cycle.

1. Introduction

In many birds long day lengths induce rapid gonadal growth and increase in body weight. These responses are followed by development of photorefractoriness when gonads regress, body weight declines and further increase in day-length may (relatively refractory; Follett and Robinson 1980; Nicholls *et al* 1988) or may not (absolutely refractory; Thapliyal and Lal 1984; Sharp 1984; Nicholls *et al* 1988) evoke a second or additional response. For the sake of clarity, it is customary to distinguish photorefractoriness as 'gonadal' and 'metabolic' refractory states (Shank 1959; Thapliyal and Lal 1984). The former refers to the insensitivity of the neuroendocrine-gonadal axis and latter to the cessation in the response of the lipogenic mechanism(s) to photostimulation. Development of photorefractoriness is perhaps the most useful mechanism adapted by the species nesting during spring and summer months to help them terminate breeding at times when food resources in the natural environment are abundant, the day-length may still be increasing or may be more than the threshold level required initially for gonadal maturation (Singh and Chandola 1982; Wingfield *et al* 1983). Less is known of the metabolic photorefractoriness.

Physiological basis of photorefractoriness is poorly understood and may differ from species to species (Farner 1975; Sharp 1984; Lal and Thapliyal 1985; Nicholls *et al* 1988; Chandola-Saklani *et al* 1988a, b; 1990). Efforts made to unravel the physiological basis of photorefractoriness in birds implicate the importance of thyroid glands, in the development and maintenance of this mechanism in certain species for *e.g.* duck and teal (Assenmacher and Jallageas 1980), European starlings (Wieselthier and Van Tienhoven 1972; Nicholls *et al* 1988), and Japanese quail (Follett and Nicholls 1984), but not in others (Thapliyal and Lal 1984; Lal 1988; Thapliyal and Gupta 1989). Removal of the thyroid glands at appropriate sexual stage in the former type of birds, abolishes the onset of photorefractoriness (Nicholls *et al* 1988), while in the latter type, thyroidectomy may accelerate the onset of refractoriness (Lal 1988). Similarly, depending on the species, sex and reproductive stage, treatment with thyroid hormones in thyroidectomized and/or intact birds may or may not influence the developmental process of photorefractoriness (Nicholls *et al* 1988; Thapliyal and Gupta 1989). The purpose of the present experiment was to asses (i) nature of the 'gonadal' and 'metabolic' photorefractoriness, and (ii) possible involvement of the thyroid glands in the onset of photorefractory states-gonadal and metabolic-in the black-headed bunting *Emberiza melanocephala.*

2. Materials and methods

The black-headed bunting is a passerine migrant which visits India during October/ November and departs to its breeding grounds (west Asia-eastern Europe) (Ali and Ripley 1983) by late March to. mid April.

Birds were purchased from a local supplier in Varanasi, UP and were transported by plane to the lmphal valley of Manipur state. Birds were released in the outdoor aviary of the department which is fully exposed to fresh air and natural lighting.

A set of four experiments were performed.

Experiment I: Ten male buntings pretreated to constant 6L/18D day-length for 8 weeks, were individually weighed and laparotomized for measuring left testis size *in situ.* All the birds were transferred to light-proof box maintained on constant 20L/4D day-length (light on, 11 am; off, 7 am, light intensity at perch level–about 350 lux). After 4 months of photostimulation, day-length was increased from 20L/4D to constant 23L/1D for another two months. Monthly records on individual body weight and left testis size *in situ,* were maintained.

Experiment II: During the last week of January (quiescent phase), April (progressive phase), June (peak phase) and 2nd week of July (regression phase) 1991, 24 male birds were randomly selected and divided into 4 groups of 6 birds each. Birds of first two groups were surgically thyroidectomized (Lal 1988) and the remainder 2 groups were sham-operated. Immediately after surgery birds were exposed to constant 20L/4D day-length. The next day onwards, one group each of the thyroidectomized and sham-operated birds were treated with 1 μg of L-thyroxine (L-T_4; Sigma Chemical Company, USA) in 0·1 ml of slightly alkaline saline (pH 7·5). Control birds received 0·1 ml of the vehicle only. The dose of thyroxine was based on our earlier experience that this dose successfully reverses the effects of thyroidectomy on the gonads and body weight of the bunting under 20L/4D (Lal, unpublished). Treatment was continued until birds became photorefractory. Fortnightly observations were kept on individual body weight and left testis size *in situ.*

Experiment III: Male buntings pretreated to constant 12L/12D photoperiod for one month, were divided into 4 groups of 8 birds each. After keeping initial records on individual body weight and left testis size *in situ,* birds of 3 groups were treated separately with 0·5, 1·0 and 2·0 μg of L-T_4/bird/day in 0·1 ml of alkaline saline. Control birds received 0·1 ml of the vehicle only. After one month, injections were withdrawn and birds of all the groups were transferred to constant 20L/4D. Records on individual body weight and left-testis size *in situ,* were made before and one month after transfer to constant 20L/4D day-length.

Experiment IV: During the last week of January, 1991, intact and thyroidectomized male buntings were subjected to constant 20L/4D. Four months later when the birds became refractory, they were divided into 4 groups, 2 each of thyroidectomized and intact birds. One group each of the thyroidectomized and intact birds was treated separately with 1 μg/bird/day of L-T_4 in 0·1 ml of alkaline saline for a total period of one month. Control birds received 0·1 ml of the vehicle only. Records on individual body weight and left testis size *in situ,* were made at the beginning and at the end of the treatment.

Injections were made on alternate sides of breast and thigh muscles, daily between 11 to 11.30 am only.

Completion of thyroidectomy was ensured by delayed regeneration of sparse and colourless plumage which lacked barbules. At sacrifice, thyroid areas were also fixed in Bouin’s fluid and checked in serial sections for regenerated thyroid glands, but none were found.

Birds received food (Paddy, *Oryza sativa*) and water *ad libitum,* and remained in good health.

Testis volume was calculated by using the formula $4/3\ \pi\ ab^2$, where $\pi = 3{\cdot}14$, a = half of the long axis, and b = half of the short axis.

Data was analysed using one way analysis of variance (ANOVA; Snedecor 1961).

3. Results

3.1 *Effect of photostimulation on testicular and body weight cycles*

Testes of birds increased during first two months, started regressing in 3rd month and reached the minimum size by the 4th month of photostimulation by 20L/4D. Transfer of birds from 20L/4D to 23L/1D did not elicit testicular growth (figure 1). Photostimulated increase and/or decrease in body weight strictly followed the trend observed for the testes (figure 1).

3.2 *Effect of thyroidectomy and L-T_4 treatment during different sexual stages on light-induced testicular and body weight cycles*

Photostimulation during quiescent phase induced rapid testicular growth in sham-operated birds. Testes grew for the first 30 days, remained maintained for another 30 days and thereafter regressed, reaching their minimum by the 90th day of

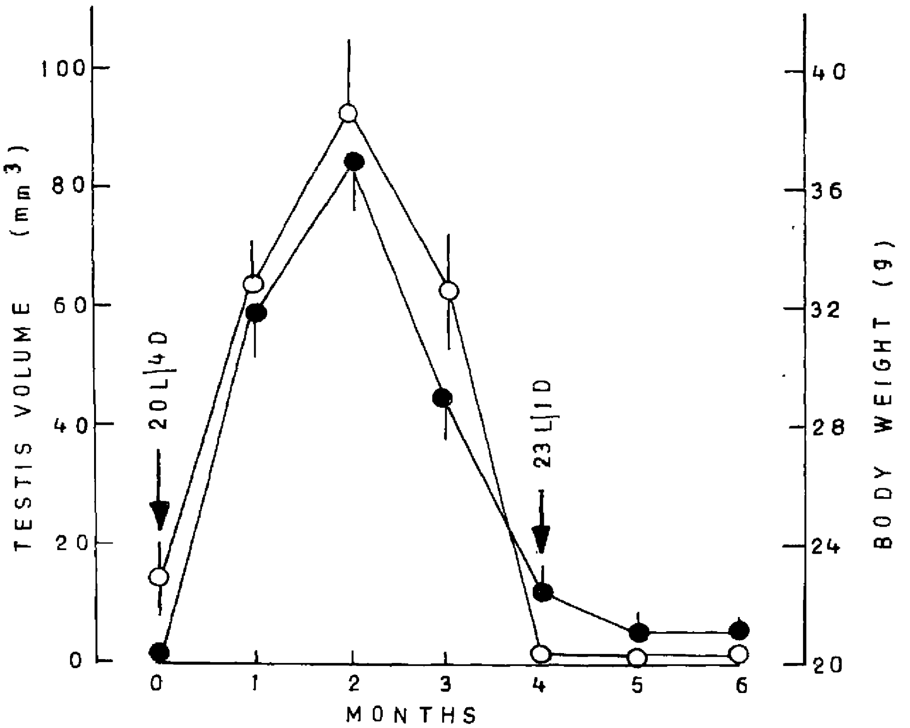

Figure 1. Testicular and Body weight response of the black-headed bunting following a shift from 6L/18D (8 weeks) to 20L/4D and from 20L/4D (4 months) to 23L/1D $n = 10$. (●) Testicular volume, (O) Body weight. Values are mean ± SE. Vertical bars represent the Standard errors of the mean value.

photostimulation. Thyroidectomy significantly suppressed ($P < 0{\cdot}001$) the amplitude of light-induced testicular growth. Testes grew partially during the first 30 days which was followed by regression and full involution occurred by 75th day of photostimulation (figure 2A). Between 15-60 days of light treatment, mean testicular volume of thyroidectomized birds was significantly low compared to sham-operated group (figure 2A). Treatment with L-T_4 fully reversed the effects of thyroidectomy on testicular growth, but had no effect on the testes of sham-operated birds (figure 2). With the only difference that onset of testicular regression was advanced, there was no qualitative difference in the light response of the birds following thyroidectomy and/or L-T_4 treatment during quiescent and progressive phases (figure 2 A, B). Light treatment alone or when combined with L-T_4 injection, failed to prevent testicular regression during peak and regression phases (figure 2 C, D). Except that development of metabolic photorefractoriness was advanced by a fortnight, the trend in photostimulated increase and/or decrease in body weight of sham-operated birds was comparable to that of the testes. Thyroidectomy during quiescent, progressive and peak phases accelerated the development of metabolic photorefractoriness but

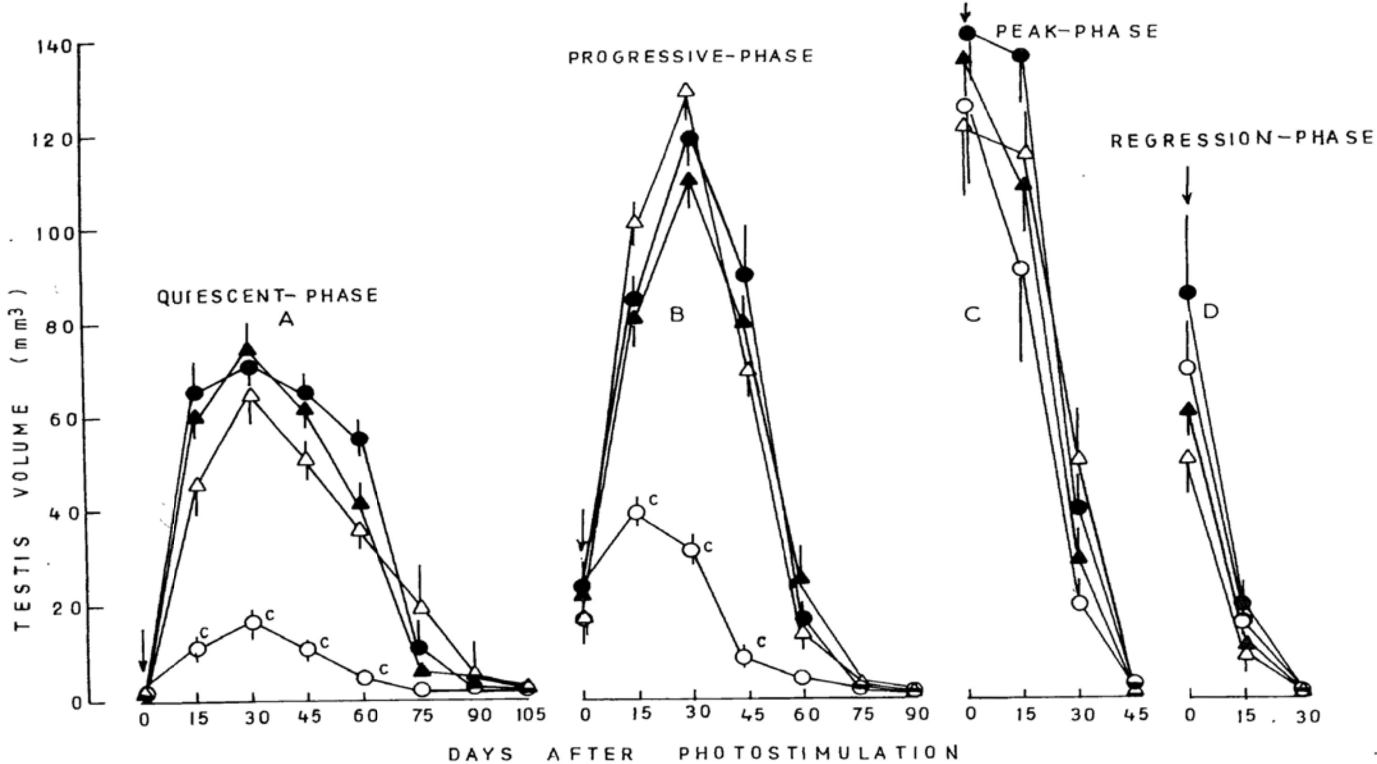

Figure 2. Effect of thyroidectomy (Thx) and L-T_4 (1 μg/bird/day) treatment on Testicular response of the black-headed buntings transferred from natural lighting to constant 20L/4D during different reproductive states.

(●) Sham + saline, (○) Thx + saline, (▲) sham + L-T_4, (Δ) Thx + L-T_4: $n = 6$ in each group. Values are mean ± SE. Arrows indicate to the point of photostimulation. Vertical bars represent the standard errors of the mean values.

A, B, C differ from the value of Sham ± Saline at $P < 0{\cdot}05$, $< 0{\cdot}01$ and $< 0{\cdot}001$ respectively (ANOVA).

had no effects on the decreasing weight of birds photostimulated during regression phase. Treatment with L-T_4 while repaired fully the decreased body weight of thyroidectomized birds photostimulated during quiescent, progressive and peak-phases, had no effect on the weight of birds thyroidectomized and exposed to 20L/4D during regression phase. Regardless, metabolic state, in sham-operated birds, L-T_4 had no effects on increasing and/or decreasing body weight (figure 3).

3.3 *Effect of photo stimulation by 20L/4D, on testicular and body weight growth of birds pretreated with L-T_4 under constant 12L/12D day-length*

Treatment with L-T_4 at dose levels 0·5-2 μg/bird/day/30 days had no significant effects on testicular volume and body weight. Testes and body weight of saline and L-T_4 treated birds grew to the same extent following transfer from 12L/12D to constant 20L/4D (figure 4).

3.4 *Effect of L-T_4 treatment on testes and body weight of photo refractory birds*

Treatment with L-T_4 at dose level 1 μg/bird/day/30 days in thyroidectomized and/or intact photorefractory birds on 20L/4D failed to exhibit testicular or body weight growth (table 1).

4. Discussion

Results indicate that transfer of photorefractory buntings from 20L/4D to 23L/1D did not evoke testicular and/or body weight growth. Obviously, unlike Japanese quail, *Coturnix cotumix japonica* (FoIlett and Robinson 1980; Nicholls *et al* 1988) and Indian weaver bird, *Ploceus philippinus* (Bisht and Chandolan-Saklani 1992); black-headed buntings exhibit absolute photorefractoriness. In the former species transfer of birds to day-lengths higher than under which they became refractory, stimulates gonadotrophic function; the latter species becomes refractory under day-lengths around 13 h, and photo-schedules higher than 15L/9D culminate into permanent dissipation of photorefractory state. The fact that transfer of buntings from natural lighting to constant 20L/4D during regression phase, failed to elicit testicular and/or body weight growth, lends support to the view that buntings exhibit absolute gonadal and metabolic photorefractoriness.

Thyroidectomy suppressed the amplitude of photoinduced testicular growth but a testicular cycle temporally similar to that of intact birds was apparent. A similar situation has been observed in the red-headed bunting, *Emberiza bruniceps* (Thapliyal and Lal 1984; Lal 1988). Further, although partially developed, testes of thyroidectomized birds began declining in advance of sham-operated buntings. This probably indicates to early development of photorefractoriness. Thyroidectomized buntings may become photorefractory earlier than sham-operated birds either due to suppressed synthesis and/or secretion of gonadotrophin-releasing hormone or to a reduction in responsiveness of the gonads to gonadotrophins. The latter possibility seems unlikely since treatments with gonadotrophins stimulates the gonads of thyroidectomized and sham-operated photorefractory buntings to the same extent

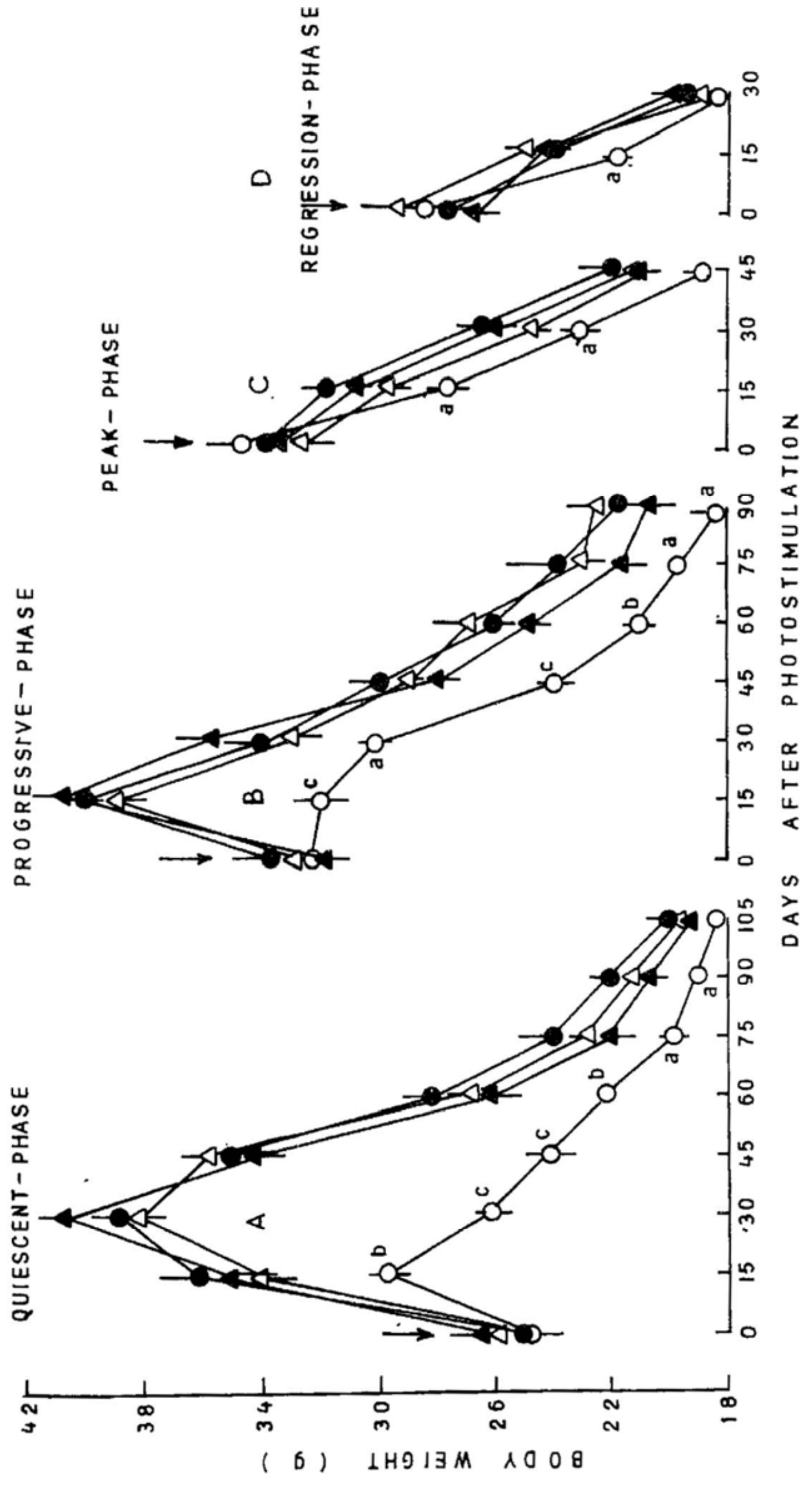

Figure 3. Effect of thyroidectomy (Thx) and L-T$_4$ (1 μg/bird/day) treatment on Body weight response of the black-headed buntings shifted from natural lighting to constant 20L/4D during different metabolic states. Other details as in figure 2.

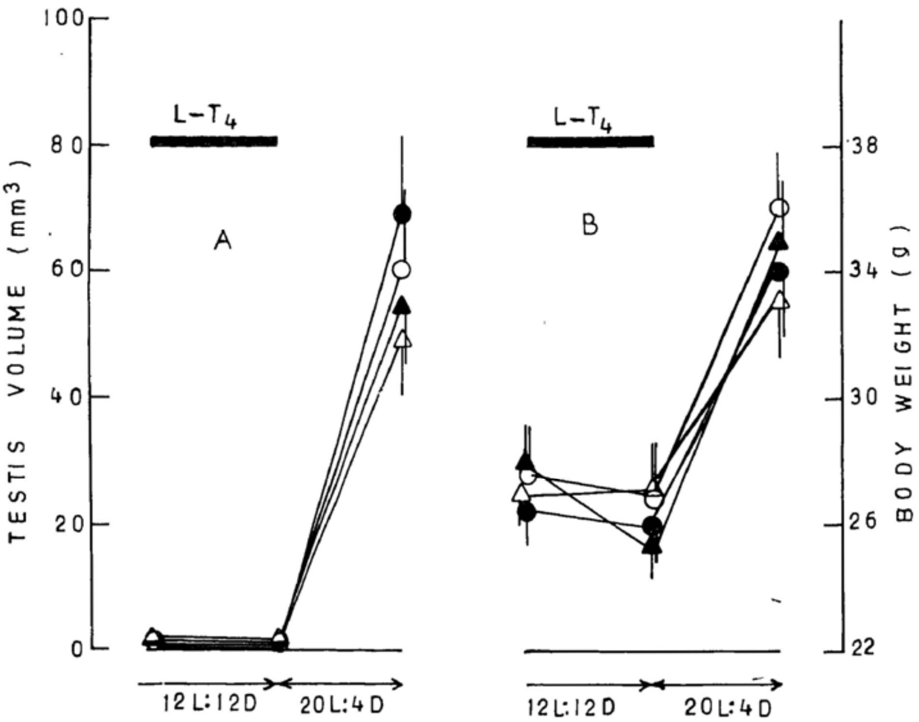

Figure 4. Effects of daily treatments with L-T_4 and repeated laparotomy on Testicular and Body weight response of the black-headed buntings maintained on 12L/12D and following a shift from 12L/12D to 20L/4D day-length.
(●) Saline, (O) 0·5 µg, (▲) 1 µg and 2µg, n= 5 in each group. Other details as in figure 1.

Table 1. Effect of daily treatment of saline or L-T4 (1 µg/bird) on the testes and body weight of the photorefractory. Black-headed buntings maintained on 20L/4D daylength.

Treatments	Testis volume (mm^3) Initial	Testis volume (mm^3) Final	Body weight (g) Initial	Body weight (g) Final
Sham + saline	1·25 ± 0·02	0·79 ± 0·01	22·38 ± 1·05	21·36 ± 1·38
Thx + saline	1·30 ± 0·12	0·99 ± 0·00	21·83 ± 2·10	20·85 ± 1·36
Sham + L-T_4	1·13 ± 0·03	1·01 ± 0·01	22·86 ± 1·55	21·20 ± 1·38
Thx + L-T_4	2·12 ± 1·01	1·15 ± 0·12	21·38 ± 1·03	22·10 ± 2·15

*Mean±SEM; n = 5; Sham = sham-operated; Thx = thyroidectomized.

(Thapliyal and Lal 1984; Lal P, unpublished data). Hypothalamic drive decreases towards the end of the breeding season, but this is not immediately reflected by a decrease in plasma levels of gonadotropins. If thyroidectomy exerts an inhibitory influence on hypothalamic drive, this, combined with photoinduced decrease in drive, might be expected to culminate into premature onset of photorefractory state.

The observation that treatment with L-T_4 in photorefractory buntings under 20L/4D failed to result in testicular growth, confirms that thyroidectomized birds did become photorefractory.

Fully developed testes of sham-operated buntings remained maintained at least for a fortnight but those of thyroidectomized birds underwent immediate regression and treatment with L-T_4 at dose level 1 μ*g* /bird/day for 30 days brought about full recovery. This probably indicates that unlike duck and teal (Assenmacher and Jallageas 1980), pied flycatcher (Silverin 1980), starling (Goldsmith and Nicholls 1984), spotted munia (Thapliyal 1978), Lal munia (Thapliyal 1981) and female weaver bird (Thapliyal and Bageshwar 1970) but similar to male weaver bird (Thapliyal and Garg 1969), red-vented bulbul (Lal and Thapliyal 1982a), house sparrow (Lal and Thapliyal 1982b) and red-headed bunting (Thapliyal and Lal 1984; Lal 1988), in the black-headed bunting, thyroid hormones are required for the maintenance of the testes. In the former group of birds, thyroidectomy renders birds sexually active and L-T_4 treatment precipitates gonadal involution, while in the latter group, thyroid hormones are essential for gonadal activity in breeding birds.

Treatment with daily doses of L-T_4 from 0·5-2·0 μg/bird for 30 days had no effects on the testes of buntings maintained on 12L/12D or after transfer to constant 20L/4D photo-schedule. This could be because in the black-headed buntings either the doses of L-T_4 employed were not enough to support testicular growth and development of photorefractoriness of birds require longer exposure to 12L/12D before they are treated with L-T_4. In the starlings, maintained on 12L/12D, L-T_4 accelerates gonadal growth and causes premature onset of photorefractoriness (Nicholls *et al* 1988).

Body weight of sham-operated birds increased following transfer to constant 20L/4D during quiescent and progressive phases, but not during regression phase. This confirms that similar to the neuroendocrine-gonadal axis, metabolic mechanisms do become photorefractory, and the nature of metabolic refractoriness is absolute.

Thyroidectomy curtailed photoinduced increase in body weight and daily dose of 1 μg/bird of L-T_4 reversed this effect. Obviously, presence of thyroid hormone(s) is necessary for light-induced increase in body weight. Remarkably, suppressive effect of thyroidectomy on body weight increased progressively with increase in weight and most steep decline occurred following thyroidectomy during peak phase. In the buntings, photoinduced gain in body weight is mainly due to multiplication of lipid reserves (Singh 1982). This would mean that effects of thyroid removal on body weight depends upon lipid deposited at the time of operation. Further, thyroidectomy depressed significantly the body weight of the buntings photostimulated during July (regression phase). This may be because thyroid hormones are required for slow mobilization of lipid reserves in incubating birds. Absence of thyroid hormones thus, may lead to suppressed synthesis and/or rapid mobilization of lipid reserves. Suppressed synthesis of free fatty acids by the liver cells has been observed in thyroidectomized chicken (Goodridge 1978) and red-headed bunting (Thapliyal 1980; Singh *et al* 1992).

Post-breeding decline in body weight and failure of long day-length and/or L-T_4 in preventing this decline while may denote the onset of metabolic photorefractoriness, also reveals that development of this process is independent of circulating levels of thyroid hormones. It remains to be established whether secretion of some lipogenic hormones which find synergism with thyroid and/or testicular hormones has stopped or output of some antilipogenic hormones is augmented which disappears under natural lighting during short winter days and, thus, rendering the lipogenic mechanism(s) sensitive to light.

In conclusion, in the black-headed bunting, in contrast with European starlings (Wieselthier and Van Tienhoven 1972; Goldsmith and Nicholls 1984), thyroid hormones may not be necessary for the development of photorefractory-gonadal and metabolic states. In the starling, thyroidectomy maintains the gonads permanently active and single dose of 50 μg of L-T_4, in thyroidectomized birds maintained on constant 18L/6D or 23L/1D, precipitates photorefractoriness (Nicholls *et al* 1988). The fact that testes and body weight of long-term thyroidectomized black-headed buntings kept on constant 20L/4D, did not develop following L-T_4 treatments, substantiates this view.

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