PHOTOPERIODIC RESPONSES OF A SUBTROPICAL MIGRATORY FINCH, THE BLACK-HEADED BUNTING (*EMBERIZA MELANOCEPHALA*)

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ABSTRACT. – Groups of photosensitive male Black-headed Buntings (*Emberiza melanocephala*) were exposed to long (15L/9D) and short (8L/16D) daily photoregimes for a period of 120 days. Another group of buntings was simultaneously exposed to normal day lengths and served as a control. Birds were weighed and laparotomized at intervals of 30 days during the treatment period. The buntings exhibited photoperiodic responses similar to those of many north temperate birds from mid- and high latitudes. Long days caused complete gonadal development followed by rapid testicular regression and photorefractoriness, whereas short days inhibited testicular development. Premigratory fattening followed by metabolic photorefractoriness also developed in photostimulated birds.

Day length regulates the annual cycles of many species of birds (for reviews see Farner and Follett 1966, Lofts and Murton 1968, Farner and Lewis 1971). However, most of the abundant literature concerning avian photoperiodism pertains to mid- and high latitude forms. The variation in day length at low latitudes may in fact be too small to provide birds with reliable cues for the timing of seasonal events (Farner and Lewis 1971). Nonetheless, some tropical species are photoperiodic and exhibit testicular development if exposed to long daily photoperiods (Disney et al. 1961, Thapliyal and Saxena 1964a, Thapliyal and Tewary 1964, Epple et al. 1972, Lewis et al. 1974).

The Black-headed Bunting (Emberiza melanocephala) is a sexually dimorphic migratory finch found in the subtropics. It arrives in Varanasi, India (25°18'N, 83°01'E), in the fall (September/October), overwinters, and then returns to breeding grounds in southwestern Asia and eastern Europe (ca. 25-40°N) during the late spring (March/April;'Ali and Ripley 1974). It has distinct annual cycles of body weight, fat deposition, and gonadal size. In nature, buntings undergo gonadal recrudescence and gain weight during the summer (May/June) as day length increases, but their testes regress and weight diminishes in July, although the days are still quite long (unpubl. observ.). These data suggest that the Blackheaded Bunting is photoperiodic and has periods of reproductive and metabolic photorefractoriness in its annual cycles. We sought, therefore, to determine experimentally if the seasonal changes exhibited by this finch in the field were related to day length by exposing buntings to long and short daily photoperiods in the laboratory. The present experiments were designed to further our understanding of the environmental factors that control the annual cycles of birds residing at low latitudes, since so few of them have been studied.

MATERIALS AND METHODS

Adult male buntings were caught locally at Varanasi during fall 1978 and kept in an outdoor aviary. They were housed in small groups in wire-net cages ($50 \times 35 \times 30$ cm). In early December, two groups were brought indoors and allowed to acclimate to laboratory conditions for 15 days. Here, they were exposed to natural variations of photoperiod and temperature. Acclimated buntings were then put on a short daily photocycle consisting of 8 h light and 16 h dark (8L/16D; lights on beginning at 06:00) for eight weeks so that they would become photosensitive. Laparotomy at the end of this period showed that all birds had testes of minimal size (combined testicular weight = 5-8 mg); they also had little subcutaneous fat and weighed ca. 30 g.

One group of these birds (n = 8 initially) was then photostimulated with 15 h light daily (15L/9D; lights on beginning at 06:00) for the next 120 days. The other group (n = 7 initially)continued on 8L/16D. A third group of adults (n = 7 initially) having testes of minimal size (combined testicular weight = 5-8 mg) was also brought indoors and subjected to normal day lengths (NDL) for the same 120-day period. These birds received unrestricted natural light through the northeast-facing windows of the laboratory. A few birds died during the treatment period (see the group sizes in Table 1). The artificial light to which birds in the first two groups were exposed was provided by fluorescent tubes and had an intensity of ca. 400 lx at perch level. Food and water were always freely available. We did not regulate the temperature of the photoperiodic chambers closely, but it did not vary more than 2°C from the temperature of the bird room.

Birds were weighed and laparotomized at intervals of 30 days during the treatment period. The combined testicular weight of each was estimated visually by comparing the size of its testes in situ with a reference set of fixed gonads of known weight. (The error inherent in this method is ca. 20%.) Since the deposition of fat accounts for most of the weight gain of photostimulated passerines (King and Farner 1959, Helms et al. 1967), we assumed that variations in body weight reflected differences in the fat content of the birds in this experiment.

We performed statistical analyses on the data with simple *t*-tests, except when comparing the responses of a single group of birds as a function of time, in which case we used paired *t*-tests.

RESULTS

When photostimulated (15L/9D), buntings initially gained weight and exhibited testicular growth (days 30 and 60). Body and testicular weight then declined (day 90) and were minimal again on day 120 (Table 1, Fig. 1). In contrast, buntings on a short daily photoperiod (8L/16D) failed to exhibit testicular recrudescence (Fig. 1). Although fattening (increases in body weight) was not pronounced in these buntings, their average body weight on day 120 was significantly (P < 0.05) higher than at the beginning of the treatment period (Table 1). This weight gain was, however, relatively small compared with the increment that occurred in the NDL group in the same period (Table 1; NDL birds were experiencing day lengths of ca. 13 h on day 120).

Birds subjected to NDL did not exhibit a significant increases in body weight or testic-



FIGURE 1. Gonadal responses of *Emberiza melano-cephala* to long (15L/9D) and short (8L/16D) daily photoperiods, and to normal day lengths (NDL) at Varanasi, India, between February and June. The vertical lines associated with the symbols are standard errors.

ular size until 60 days of treatment (when day length was 12.36 h). Testes were still growing and body weight was still increasing when we terminated the study on day 120 (Table 1, Fig. 1).

DISCUSSION

Our data indicate that the Black-headed Bunting is photosensitive. Its photoperiodic responses are similar to those of many north temperate birds, i.e., mid- and high latitude forms: long days cause full gonadal development followed by rapid regression and photorefractoriness, whereas short days inhibit testicular development (responses of north temperate forms are reviewed by Farner and Follett 1966, Lofts and Murton 1968, and Dolnik 1976). Such findings may mean that buntings use the length of the daily photoperiod as a source of information for regulating their seasonal cycles, even though annual variations in day length at Varanasi are only about 3 h 8 min.

TABLE 1. Changes in the body weight of Black-headed Buntings during exposure to long (15L/9D) and short (8L/16D) daily photoperiods, and to the normal day lengths (NDL) of February through June at Varanasi, India.

Days of exposure	Photoperiods		
	15L/9D	8L/16D	NDL
0	29.25 ± 0.73 (8)	28.14 ± 0.40 (7)	28.28 ± 0.49 (7)
30	$a 41.87 \pm 0.81 (8)^{****}$	28.66 ± 0.49 (6)	$28.57 \pm 0.84(7)$
60	a 42.75 ± 1.66 (8)****	29.66 ± 1.69 (6)	$31.71 \pm 0.74 (7)^{***}$
90	$34.80 \pm 2.06(5)^{**}$	$31.20 \pm 1.65(5)$	$a 47.00 \pm 1.89 (6)^{****}$
120	29.75 ± 0.85 (4)	31.80 ± 1.56 (5)*	a 49.60 ± 1.20 (5)****

¹ Values in the table are $\bar{x} \pm$ SEM (*n*). Asterisks in each column indicate that the body weight differs from that on day 0 at a significance level of 0.05 (*), 0.02 (**), 0.01 (***), or 0.001 (****). The letter *a* on the left of a weight indicates that it differs significantly (*P* < 0.001) from the mean weight of the 8L/16D group on that day.

As is true of many other migratory birds (see King and Farner 1956, 1963; Farner 1960, 1964; King 1961; Dolnik 1975), premigratory activities such as fattening are also induced in buntings by long daily photoperiods (Table 1). Short daily photoperiods usually fail to induce such events in migratory forms, but a small significant (P < 0.05) increase in body weight occurred when our buntings were kept on 8L/ 16D for about six months (including the pretreatment days; Table 1). It is immensely interesting that these birds gained weight under conditions in which there was little (NDL) or no (8L/16D) photostimulation. Response to NDL and to long daily photoperiods suggests that weight gain is in part related to the length of the photocycle. However, the weight gain of birds exposed to short days suggests that fattening is also to some extent independent of day length. Perhaps Black-headed Buntings have a circannual rhythm in body weight; or, perhaps the change was related to room temperature which was not kept absolutely constant.

Buntings on 15L/9D fattened initially, but then lost weight beginning sometime after 60 days of photostimulation (Table 1). This suggests that they undergo metabolic refractoriness when photostimulated, as do mid- and high latitude migrants. Changes in the body weight of our birds coincided remarkably with changes in their testicular size (compare the data in Table 1 with those in Fig. 1). This may indicate that gonadal steroids modify the intensity of such premigratory activities as hyperphagia and fat deposition in Black-headed Buntings. Such effects have been reported occasionally in other passerines (e.g., see Morton and Mewaldt 1962, Weise 1967). However, castrated buntings also fatten considerably when they are photostimulated (Tewary and Kumar 1981).

Because the photoperiodic responses of so few tropical and subtropical passerines have been studied, it is still difficult to discern general patterns of photoperiodic response among them. To illustrate, some sedentary low-latitude forms, including Baya Weavers (Ploceus philippinus) and Rufous-collared Sparrows (Zonotrichia capensis), show testicular recrudescence in response to long daily photoperiods, but do not become photorefractory (Thapliyal and Saxena 1964a, Thapliyal and Tewary 1964, Lewis et al. 1974). In these cases, testicular activity ceases when the natural day length diminishes in autumn (but see Singh and Chandola 1981). However, other sedentary forms respond to long days in a more complex fashion. Black-headed Munias (Lonchura molucca) become reproductively active

when exposed to short or long daily photoperiods (Thapliyal and Saxena 1964b, Pandha and Thapliyal 1969). Spotted Munias (L. punctulata) respond to unnaturally short photoperiods, but long photocycles retard or inhibit gonadal development (Chandola et al. 1975). However, munias breed after the summer solstice and their testicular cycles appear to be regulated by environmental cues (e.g., monsoons) other than those associated with the photocycle. Yellow-vented Bulbuls (Pycnonotus goiavier), which are also sedentary, appear to time bouts of reproductive activity by seasonal changes in the food supply rather than day length (Fogden 1972). Red-billed Oueleas (Ouelea quelea) may also do this (Jones and Ward 1976), although they too are photoperiodic and exhibit a brief refractory period that dissipates spontaneously irrespective of photoperiodic conditions (Lofts 1962).

The photoperiodic responses of Blackheaded Buntings (Fig. 1) stand in contrast to those presented above, but resemble those of a related tropical *migrant*, the Red-headed Bunting (*Emberiza bruniceps*; Prasad 1980). Both of these species are photoperiodic and become refractory if retained on 15L/9D, responses typical of mid- and high latitude migrants in the north temperate zone. However, it remains to be determined if exposure to a short daily photoperiod is necessary to dissipate their refractory states, as it is in typical north temperate migrants.

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