



# Daily levels and rhythm in circulating corticosterone and insulin are altered with photostimulated seasonal states in night-migratory blackheaded buntings

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## ABSTRACT

The circadian rhythms are involved in the photostimulation of seasonal responses in migratory blackheaded buntings. Here, we investigated whether changes in daily levels and rhythm in corticosterone (cort) and insulin secretions were associated with transitions in the photoperiodic seasonal states. Buntings were exposed to short days to maintain the winter (photosensitive) non-migratory state, and to long days for varying durations to induce the premigratory, migratory (shown by migratory restlessness at night, *Zugunruhe*) and summer non-migratory (photorefractory) states. We monitored activity patterns, and measured plasma cort and insulin levels at six and four times, respectively, over 24 h in each seasonal state. Buntings were fattened and weighed heavier, and exhibited intense nighttime activity in the migratory state. The daytime activity patterns also showed seasonal differences, with a bimodal pattern with morning and evening activity bouts only in the summer non-migratory state. Further, the average baseline hormone levels were significantly higher in premigratory and migratory than in the winter non-migratory state. Both cort and insulin levels showed a significant daily rhythm, but with seasonal differences. Whereas, cort rhythm acrophases (estimated time of peak secretion over 24 h) were at night in the winter non-migratory, premigratory and migratory states, the insulin rhythm acrophases were found early in the day and night in winter and summer non-migratory states, respectively. These results suggest that changes in daily levels and rhythm in cort and insulin mediate changes in the physiology and behavior with photostimulated transition in seasonal states in migratory blackheaded buntings.

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## 1. Introduction

Migration in birds is an elegant example of the phenotypic flexibility, with migrants showing remarkable changes in the physiology and behavior with transition from the non-migratory to migratory state, and vice versa, in order to maximize fitness within the seasonally predictable photoperiod environment (Kumar et al., 2010). During the non-migratory state, night migratory songbirds are active during the day and roost quietly at night. By contrast, birds exhibit intense activity at night (nocturnal migratory restlessness, *Zugunruhe*) during the migratory state. Thus, daily activity patterns of migrating birds show alternation between the states of anabolism (rest at night) and catabolism (intense activity at night). The hormonal regulation of such contrasting daily shift in the physiology and behavior is still poorly understood, although a regulatory role of the corticosterone (cort) has been suggested; i.e. baseline cort levels are elevated during the catabolic or flight state to coordinate fuel usage and behavioral adaptations associated with the migratory flight (Falsone et al., 2009). Also, there occurs an

alteration in the diurnal pattern of plasma cort in parallel with behavioral shift from non-migratory to the migratory state. Plasma cort levels are increased towards the end of the night in non-migratory white crowned sparrows (*Zonotrichia leucophrys gambelii*) when they are preparing for the onset of the daytime activity (Breuner et al., 1999). By contrast, cort levels are increased at night during the photostimulated spring migratory state when white crowned sparrows show nighttime flight activity (Landys et al., 2004a; Ramenofsky et al., 2003, 2008). Similarly, high plasma cort levels at nights marked by *Zugunruhe*, and low levels during the day have been found in garden warblers (*Sylvia borin*; Schwabl et al., 1991) and dark-eyed juncos (*Junco hyemalis*; Ramenofsky et al., 1999). Elevated cort levels at night may assist promotion of stored lipid mobilization in order to meet energetic demands of an intense nighttime activity in night migratory birds (Dolnik and Blyumental, 1967; Landys et al., 2004b).

The pancreatic hormones also play a significant role in the metabolism. Particularly, a role of insulin has been suggested in the regulation of feeding and body mass in migratory birds (Kuenzel, 1972). Plasma insulin levels were found positively correlated with changes in food intake and body mass during the migratory season in garden warblers (Totzke et al., 1997; Totzke and Bairlein, 1998). Also, garden warblers showed

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insulin resistance during the period of migratory fattening; there was lower utilization, hence higher plasma levels of glucose suggesting inhibition of the glucose oxidation by high circulating fatty acid levels (Hintz, 2000; Totzke et al., 1997, 1998). Exogenous insulin suppressed the feeding and increased plasma free fatty acids (FFAs) levels in white crowned sparrows under short days (Boswell et al., 1995, 1997). Similarly, exogenous insulin increased FFA levels in domestic hens (*Gallus gallus domesticus*; Heald et al., 1965) and increased triglyceride levels in geese (*Anser anser*; Nir and Levy, 1973). However, when administered alone or with cort, insulin produced no effect on plasma triglycerides in European starlings (*Sturnus vulgaris*) exposed to short and long photoperiods (Remage-Healey and Romero, 2001). But, exogenous cort hastened plasma glucose recovery in insulin-induced hypoglycemic starlings during the day, but not at night, suggesting the role of cort and its interaction with insulin in the regulation of metabolic changes may vary with energetic demands throughout 24 h and also perhaps across seasons in birds (Remage-Healey and Romero, 2001).

Endogenous rhythms in interaction with environmental photoperiod regulate changes in the physiology and behavior associated with migration in songbirds. Previous studies have demonstrated the involvement of circadian rhythm in the photostimulation of spring body mass in seasonally migrant songbirds including the blackheaded bunting, *Emberiza melanocephala* (Kumar, 1988; Kumar et al., 2010; Tewary and Kumar, 1983). The circadian clock controls daily alteration during the daytime hopping and feeding behaviors, and the nighttime *Zugunruhe* in migratory birds (Bartell and Gwinner, 2005; Coppack et al., 2008; McMillan et al., 1970; Rani et al., 2006). Separate circadian oscillators appear to control the daytime and nighttime activities, and it is the phase relationship in the output from these two oscillators which determines the seasonal appearance of *Zugunruhe* (Kumar et al., 2010). Recent molecular studies have further shown the photoperiodic seasonal state dependence of the daily mRNA oscillations in circadian clock and photoperiodic genes in the blackheaded bunting (Mishra et al., 2017; Singh et al., 2015). Therefore, we hypothesized that alterations in 24-h levels and daily rhythm of cort and insulin secretions were associated with photostimulated transitions in the seasonal states. To test this, we continuously monitored activity patterns, and measured plasma cort and insulin levels at six and four times, respectively, over 24 h in blackheaded buntings photostimulated with the winter (photosensitive) non-migratory state under short days, and the premigratory, migratory (shown by *Zugunruhe*) and summer non-migratory (photorefractory) under long days. We predicted (i) high plasma cort and insulin levels in the premigratory and migratory states when blackheaded buntings prepare for migration and show *Zugunruhe*, respectively, and (ii) changes in 24-h hormone profiles and in cosine waveform of daily rhythm in plasma hormone levels in parallel with the photostimulated transition in seasonal states.

## 2. Materials and methods

### 2.1. Animals and experiment

The present study was conducted in accordance with guidelines of the Institutional Animal Ethics Committee (IAEC) at the Department of Zoology, University of Lucknow, Lucknow, India, on Palaearctic-Indian migratory blackheaded buntings (*E. melanocephala*). Buntings in captivity exhibit seasonal states under programmed photoperiods (Misra et al., 2004; Singh et al., 2015). Under non-stimulatory short days (e.g. 8 h light: 16 h darkness, 8L: 16D; SD), buntings maintain the photosensitive state with small reproductively inactive gonads. Under long days (e.g. 16L: 8D; LD), however, they sequentially undergo gonadal growth and maturation (photostimulated state) and subsequently enter into the photorefractory state (Kumar et al., 1993; Misra et al., 2004; Singh et al., 2015; Tewary and Kumar, 1982). In parallel, buntings under long days show photostimulated changes in the physiology and behavior associated with migration. They fatten and gain weight, exhibit

behavioral shifts from being day active to predominantly night active, and subsequently loose fat and cease to show nighttime activity (hence return to day activity; Misra et al., 2004; Singh et al., 2015). Thus, four seasonal states can be easily photostimulated in captive blackheaded buntings under artificial photoperiods (Kumar et al., 1993; Misra et al., 2004; Singh et al., 2015; Tewary and Kumar, 1982). These are: (i) winter non-migratory state when buntings are maintained under non-stimulatory short days and do not fatten and have small reproductively inactive gonads; (ii) vernal premigratory state during initial 1–2 weeks of long days when buntings initiate fattening and gonadal recrudescence but still are day active; (iii) vernal migratory state when buntings under long days fatten, show full gonadal maturation *Zugunruhe*; (iv) summer non-migratory state when following photostimulation buntings have undergone regression and become photorefractory under prolonged long day exposure.

For this study, birds were captured from overwintering flocks in late February and released in an outdoor aviary (size = 3 × 2.5 × 2.5 m) under natural day light and temperature conditions (NDL). At this time, buntings had small reproductively immature testes (testis volume, TV = 0.33–0.52 mm<sup>3</sup>) with no fat depots (body mass = ~25.0 g). After a week of acclimation, buntings were moved indoors and maintained in aviaries (2.2 × 1.8 × 2.8 m) under short days (SD, 8L: 16D) or long days (LD, 16L: 8D) at 22 ± 2 °C, until used in experiments several weeks later. Thus, at the beginning of the experiment, we had buntings in winter non-migratory state under SD and in summer non-migratory state under LD. Food and water were available ad libitum. Housing, feeding, and overall care and maintenance of birds have been described in our earlier publications (Singh et al., 2010; Singh et al., 2015).

In total, three groups of winter non-migratory (groups 1, 2 and 3; n = 42 birds per group) and a group of summer non-migratory buntings (group 4; n = 42) were singly housed in activity cages and maintained on SD and LD, respectively, as before, in light proof boxes and had no visual, tactile or acoustic contact with its neighbour. Groups 1 and 4 stayed on 8L and 16L photoperiods, respectively, until the end of the experiment. But, groups 2 and 3 birds were shifted to long days (16L:8D) by extending the time of light off for 7 days (group 2) or for the period (3.5 to 4.5 weeks) until each individual had shown 7 nights of *Zugunruhe* (the vernal migratory state). Thus, photostimulated birds showed a distinct seasonal state: group 1 – non-migratory (winter); group 2 – premigratory (vernal); group 3 – migratory (vernal); group 4 – non-migratory (summer, photorefractory).

### 2.2. Monitoring of phenotype measures and daily activity

Each bird was housed independently in an activity cage, furnished with two perches and mounted with a passive infrared motion sensor (DSC, LC100 PI Digital PIR detector, Canada). The PI sensor continuously detected general movements of a bird in its cage, which were collected in 5-min bins in a designated channel of the computerized data-logging system, as described in several previous publications (e.g. Singh et al., 2010, 2015). The Chronobiology Kit software program of Stanford Software Systems, Stanford, USA, collected, collated and analysed daily activity pattern of each individual. All birds were continuously monitored for the activity-rest pattern, and same individuals were bled for hormone assays. However, for the presentation and analyses of 24-h activity pattern, we considered activity in intervals of both 5 min and 1 h over 24 h from randomly chosen 7 birds from each group. From this, we also calculated total activity over 24 h as well as during the period of light and darkness each day, for which the activity over 24 h or for the period of light and darkness was first averaged for each individual over 7 successive days, and then mean (± SE) was calculated for the group. The activity of <5 counts per 5-min bin was considered as a quiet period, a modified criterion adopted from Watts et al. (2017).

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