Temperature alters the photoperiodically controlled phenologies linked with migration and reproduction in a night-migratory songbird

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We investigated the effects of temperature on photoperiodic induction of the phenologies linked with migration (body fattening and premigratory night-time restlessness, *Zugunruhe*) and reproduction (testicular maturation) in the migratory blackheaded bunting. Birds were exposed for four weeks to near-threshold photoperiods required to induce testicular growth (11.5 L:12.5 D and 12 L:12 D) or for 18 weeks to a long photoperiod (13 L:11 D) at 22°C or 27°C (low) and 35°C or 40°C (high) temperatures. A significant body fattening and half-maximal testicular growth occurred in birds under the 12 L, but not under the 11.5 L photoperiod. Further, one of six birds in both temperature groups on 11.5 L, and four and two of six birds, respectively, in low- and high-temperature groups on 12 L showed the *Zugunruhe*. Buntings on 13 L in both temperature groups showed complete growth-regression cycles in body fattening, *Zugunruhe* and testis maturation. In birds on 13 L, high temperature attenuated activity levels, delayed onset of *Zugunruhe* by about 12 days, reduced body fattening and slowed testicular maturation. The effect of temperature seems to be on the rate of photoperiodic induction rather than on the critical day length. It is suggested that a change in temperature could alter the timing of the development of phenologies linked with seasonal migration and reproduction in migratory songbirds.

Keywords: *Emberiza melanocephala*; migration; photoperiod; temperature

1. INTRODUCTION

Over a year, migratory songbirds exhibit well-defined life-history stages of spring (vernal) and autumn migrations, separated by reproduction and molt [1], programmed by circannual rhythms [2–4]. A circadian clock control of the processes underlying the development of the phenologies linked with seasonal migration (body fattening and premigratory night-time restlessness, *Zugunruhe*) and reproduction (gonadal maturation) is also suggested [5–7].

Most studies have focused on how day length (i.e. photoperiod) regulates clock-controlled seasonal body fattening, *Zugunruhe* and gonadal maturation in migratory songbirds [5,7–10]. This is in spite of the fact that in nature, the day length cycle is inseparable from the temperature cycle. Day is warmer than the night, and spring and summer months with long days are warmer than autumn and winter months with short days. Hence, the timing and duration of seasonal life-history stages, such as body fattening, *Zugunruhe* and gonadal maturation, may be regulated by both, day length and temperature cycles, and not by day length alone. In fact, an effect of temperature on seasonal reproduction has been shown in few birds. High temperature inhibits egg production and metabolizable energy intake in chickens (*Gallus gallus*) [11]. Also, temperature is reported to have a direct effect on the timing of egg-laying in great tits, *Parus major* [12].

However, the effects of ambient temperature on seasonal and metabolic traits can vary within and between the species. For instance, in migratory white-crowned sparrows (*Zonotrichia leucophrys gambelli*) exposed to long days, temperature affects fat deposition in females, but does not affect gonadal maturation in both sexes [13]. Similarly, temperature affects the timing of regression (refractoriness), but not of recrudescence, of gonads in the mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) [14], European starlings (*Sturnus vulgaris*) [15] and great tits (*P. major*) [16]. Interestingly, the effects of temperature on seasonal reproduction seem to be independent of the changes in the basal metabolic rate [17] or in prolactin levels [18], although there is evidence that high temperature affects the photoperiodic induction of prolactin secretion [19].

Thus, it can be reasoned that a drastic change in the ambient temperature would alter the timing and/or the duration of clock-controlled phenologies expressed at the daily and seasonal levels in migratory birds. Therefore, the present study aimed to investigate the effects of temperature on photoperiodic induction of the phenologies linked with migration (body fattening and *Zugunruhe*) and reproduction (testis growth—regression) in the black-headed bunting (*Emberiza melanocephala*). Buntings are a long distance, Palearctic–Indian, latitudinal migrant species, overwintering in India (see the electronic supplementary material for details). We hypothesized that: (i) Temperature will alter the responsiveness of buntings to the duration of day length. This was tested by exposing blackheaded buntings for four weeks to near-threshold

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photoperiods at low and high temperatures. (ii) Temperature will alter the timing and duration of photoperiod-induced seasonal phenologies (growth-regression cycles in body fattening, *Zugunruhe* and testes) in the blackheaded bunting. This was examined by exposing birds for 18 weeks to a long photoperiod at low and high temperatures.

2. MATERIAL AND METHODS

Three experiments were performed, separated by four weeks. Photosensitive male blackheaded buntings were subjected to artificial photoperiods at low and high temperatures that were 13°C apart. The photoperiods contained light hours shorter in duration than the daylight outdoors (sunrise to sunset), and the high temperature matched to the temperature outdoors, at the time of the experiment (details are in the electronic supplementary material).

The first two experiments examined whether temperature would alter the responsiveness of buntings to the duration of the day length. Experiment 1 began on 16 March 2008, when daylight and mid daytime outdoor temperature were approximately 12 h and 32°C, respectively. This was the time at least two weeks before the predicted onset of the spring migration, based on the measurement of *Zugunruhe* in the earlier study [20]. Birds ($n = 6$ per group) were exposed to 11.5 L:12.5 D at low (22°C) and high (35°C) temperatures for four weeks. Buntings are not photostimulated after exposure to 11.5 L for four weeks, but show full fat deposition and half-maximally enlarged testes by the end of eight weeks of exposure to 11.5 L [21]. Therefore, the prediction was that if temperature influences the rate of photoperiodic responses, then four weeks of exposure to 11.5 L would result in accelerated or slowed induction of body fattening, *Zugunruhe* and testicular maturation in one of the temperature groups. Because 11.5 L was non-inductive in both temperature groups, we re-examined our hypothesis in the experiment 2, by increasing the daily light period by 0.5 h. A 12 h light per day is weakly inductive when compared with longer days, e.g. 13 h light per day [21]. Beginning on 14 April 2008, when daylight and mid-daytime outdoor temperature were approximately 12.75 h and 39°C, respectively, birds ($n = 6$ per group) were exposed to 12 L:12 D at low (27°C) and high (40°C) temperatures for four weeks. The last experiment (experiment 3) investigated whether the timing and duration of the major life-history stages (viz., migration, reproduction and refractoriness) under long days differ between low- and high-temperature groups. It began on 17 May 2008, when daylight and mid-daytime outdoor temperature were approximately 13.5 h and 40°C, respectively. Birds ($n = 5$ or 6 per group) were exposed to 13 L:11 D at low (27°C) and high (40°C) temperatures for 18 weeks.

The effects of temperature on photoperiodic induction of the phenologies linked with migration and reproduction were assessed by recording fat deposition, changes in body mass, *Zugunruhe* and testicular volume. While the activity pattern over 24 h was considered to be a circadian rhythm response, the changes over several weeks in daily activity pattern, fat deposition, body mass and testis size (testicular volume, TV) were considered to reflect a seasonal (circannual) response. The methods of measurement of these phenologies are detailed in the electronic supplementary material.

The data were analysed by one-way analysis of variance (one-way ANOVA) with or without repeated measures, as

appropriate, followed by the post hoc Newman–Keuls test if the ANOVA indicated a significant difference. Student's *t*-test compared datasets of the same group at two time points (paired *t*-test) or of two groups at the same time point (unpaired *t*-test). Significance was taken at $p < 0.05$. The statistical analysis was performed using GraphPad Prism (v. 5.01) software program.

3. RESULTS

(a) *Effects of temperature on daily activity pattern and Zugunruhe*

In birds exposed to 11.5 h light per day, the pattern of daily activity significantly differed between the two temperature groups. In particular, activity during the day, but not at night, was significantly higher ($p = 0.0257$, *t*-test) in the low-temperature group than in the high-temperature group. Daytime activity had distinct morning (M, activity during 1.5 h after lights were on) and evening (E, activity during 1.5 h before lights were off) peaks in the low-temperature group with M activity being higher ($p < 0.05$, *t*-test) than E activity (figure 1b). In contrast, in the high-temperature group, while M activity was present, E activity was absent (figure 1a,b and electronic supplementary material, figure S1a–d). *Zugunruhe* was observed in one of six birds in each temperature group (electronic supplementary material, figure S1b,d).

In birds exposed to 12 h light per day, temperature had effects on activity similar to those seen in birds on 11.5 h (experiment 2, cf. figure 1d–f and electronic supplementary material, figure S1e–h), except that *Zugunruhe* was induced in four and two of six birds in the low- and high-temperature groups, respectively (cf. figure 1d,f and electronic supplementary material, figure S1e–h). However, temperature did not affect the timing of the occurrence of *Zugunruhe* in these birds.

In birds exposed to 13 L:11 D (experiment 3), there were temperature effects on both level and distribution of activity which changed with time (figure 2a–c and electronic supplementary material, figure S2). Birds in the low-temperature group had significantly higher ($p < 0.05$) daily activity than those in the high-temperature group (figure 2a–c,e). M activity was significantly higher ($p < 0.05$, *t*-test) than E activity (figure 2d). *Zugunruhe* was induced in all birds, but developed more slowly ($p = 0.0331$, *t*-test) in the high-temperature group (23.67 ± 4.39 days) than in the low-temperature group (11 ± 1.5 days; figure 2f). However, *Zugunruhe* persisted for similar durations in both the temperature groups (figure 2f and electronic supplementary material, figure S2).

(b) *Body fattening, weight gain and testicular growth*

Birds on 11.5 L did not fatten or show testicular recrudescence in either temperature groups (experiment 1; figure 3a–c). In birds on 12 L (experiment 2), however, a significant ($p < 0.05$; paired *t*-test) body fattening and weight gain occurred in the low-, but not high-temperature group (figure 3a,b). The testes were equally (half-maximally) enlarged in both the temperature groups on 12 L (figure 3c). After four weeks of exposure to 13 L (experiment 3), the birds fattened, gained weight and the testes showed full recrudescence, but these responses were attenuated in the high-temperature group compared with the low-temperature

Figure 1. Effects of temperature on daily activity rhythms in blackheaded buntings exposed to marginally photostimulatory photoperiods for four weeks of exposure: (a–c) 11.5 L:12.5 D and (d–f) 12 L:12 D. The response is plotted as activity (movement) counts (mean $\pm$ s.e.; $n = 6$ per group) for 21 days marked by horizontal lines on the right side of actograms in electronic supplementary material, figure S1. It is shown as changes in (i) daily activity profile (a,d), open circles, low temperature; closed circles, high temperature; (ii) time profile—morning and evening 1.5 h activity bouts (b,e); and (iii) total activity during day and night (c,f). Light–dark cycle in figures (a) and (d) is shown by a bar with time of light-on (open) and light-off (closed) in clock hours. An asterisk (*) at the point symbol indicates the significant difference ($p < 0.05$, unpaired Student's t -test) between two groups at the respective observation. Bars with identical alphabets, no difference; bars with different alphabets, $p < 0.05$ ($p < 0.05$, paired Student's t -test). Open bars, low temperature; closed bars, high temperature.

group ($p < 0.05$; Student's t -test) (figure 3a–f). Thus, after four weeks of exposure to 11.5, 12 and 13 L photoperiods, a significant difference was found in all the parameters among the low-temperature groups (fat score: $F_{2,14} = 9.947$, $p = 0.0021$; body mass: $F_{2,14} = 13.46$, $p = 0.0005$; TV: $F_{2,14} = 21.16$, $p < 0.0001$), but in only testicular growth among the high-temperature groups (fat score: $F_{2,14} = 2.846$, $p = 0.0918$; body mass: $F_{2,14} = 1.109$, $p = 0.3572$; TV: $F_{2,14} = 6.70$, $p = 0.0091$; cf. figure 3a–c, one-way ANOVA). Also, a significant difference ($p < 0.05$; Newman–Keuls test) was found in testicular response, but not in the body fattening and weight gain, between low-temperature groups at the end of four weeks of exposure to 12 and 13 L photoperiods (cf. figure 3a–c).

A significant growth-regression cycle in fat deposition, body mass and testes occurred in both the temperature groups on 13 L:11 D (low temperature—fat score: $F_{7,28} = 6.975$, $p < 0.0001$; body mass: $F_{9,36} = 6.354$, $p < 0.0001$; TV: $F_{4,16} = 18.17$, $p < 0.0001$; high temperature—fat score: $F_{6,42} = 13.15$, $p < 0.0001$; body mass: $F_{8,40} = 2.31$, $p = 0.0386$; TV: $F_{4,20} = 25.01$, $p < 0.0001$; one-way repeated-measures ANOVA; figure 3d–f). But, the rate of induction was slower in the high-temperature group than in the low-temperature group. Thus, there was at least four weeks delay in photostimulation of the body fattening and weight gain, and full testicular maturation in the high-temperature group when compared with the low temperature group (figure 3d–f). Also, there was significantly reduced ($p < 0.05$; Student's t -test) fat deposition and weight gain in the high-temperature group compared with the low-temperature group; in fact, birds in the high-temperature group did not fully fatten under the 13 L:11 D (figure 3d,e). In spite of late maturation

under 13 L, the testes regressed significantly faster ($p < 0.05$; Student's t -test) in the high-temperature group than in the low-temperature group (figure 3f).

4. DISCUSSION

The present study demonstrates the influence of temperature on photoperiodically controlled phenologies expressed at the daily (circadian) and seasonal (circannual) levels in the blackheaded bunting (cf. figures 1–3). In inductive photoperiods, there were significant differences between the two temperature groups in the amplitude and distribution of the daily activity (figures 1 and 2) as well as in the body fattening and testicular recrudescence (figure 3). High temperature attenuated the daily activity levels, and depressed the fat deposition and weight gain. Also under 13 L:11 D, *Zugunruhe* occurrence and testicular maturation were delayed in the high-temperature group compared with the low-temperature group (figures 2f and 3f and electronic supplementary material, figure S2). Further, a comparison of responses after four weeks of exposure to three photoperiods shows that (i) birds on 11.5 L were not photostimulated in either the temperature groups, and (ii) the rate of photoperiodic induction under 12 L and 13 L photoperiods was slower, resulting in reduced body fattening and delayed testicular maturation in the high-temperature group compared with the low-temperature group (cf. figures 1–3 and electronic supplementary material, figures S1 and S2). Thus, the effects of temperature seem to be on the rate of photoperiodic induction, rather on the critical day length. However, even the highest temperature used in this study did not override the inductive effects of the long photoperiod

Figure 2. Effects of temperature on daily activity rhythms in blackheaded buntings exposed to a long photoperiod (13 L:11 D) for 18 weeks. The response is plotted as activity (movement) counts (mean $\pm$ s.e.; $n = 6$ per group) at three times during the experiment, marked by horizontal lines on the right side of actograms in electronic supplementary material, figure S2. It is shown as changes in (i) daily activity profile (*a* at the beginning, *b* in the middle, *c* towards the end, 21 days each time), (ii) time profile—morning and evening 1.5 h activity bouts (*d*, mean $\pm$ s.e. for total 63 days), and (iii) total activity during day and night (*e*, mean $\pm$ s.e. for total 63 days). (*f*) The time of the onset of *zugunruhe* and the duration of its persistence are shown. The other details are as in figure 1. Open bars, low temperature; closed bars, high temperature; open circles, low temperature; closed circles, high temperature.

(13 L:11 D; figures 1–3; electronic supplementary material, figures S1 and S2). This is not surprising as blackheaded buntings have highly predictable migratory and breeding seasons, where day length is the most consistent environmental variable, and seem to use photoperiod as the primary cue for regulation of their seasonal timing [13,22].

The present results (figure 3) indicate the response-specific effects of temperature in the blackheaded bunting exposed to long days [14]. Temperature appears to have differential effects on the processes underlying the fat deposition and testicular recrudescence, as is evident by the response of the high-temperature group to the 13 L photoperiod (cf. figure 3*d–f*). Buntings in the high-temperature group on 13 L did not fully fatten and gain weight (figure 3*d,e*), but they attained full testicular maturation (figure 3*f*). This is not surprising as body fattening and testicular recrudescence in blackheaded buntings are reported to be the separate photoperiodic phenomena [5,20,21]. Our results (figure 3) further suggest that temperature affected both the timing and duration of a life-history stage in the blackheaded bunting.

When compared with the low-temperature group, the high-temperature group had a shortened reproductively active phase under the 13 L:11 D, caused by delayed maturation and advanced regression of the testes (figure 3*f*). The cycles of body fattening and weight gain in the high-temperature group were also shorter in duration than in the low-temperature group. It could therefore be deduced from these observations that consistently high temperatures in southern Europe during summer, resulting from global warming, would advance the termination of the breeding season of the blackheaded bunting, and possibly affect the initiation of their migration back to the wintering grounds in India.

Buntings were exposed to 11.5, 12 and 13 L photoperiods at about four-week intervals, beginning in mid-March (early spring). Therefore, one could argue that there is a progressive increase in the sensitivity of the underlying circannual rhythm in photoperiodic responsiveness during the period of current study (mid-March to mid-May), which may account for the faster and larger response to 12 or 13 L than to the 11.5 L photoperiod. We discount this, as results from our previous studies

Figure 3. Effects of temperature on induction of body fattening (fat score, top), body mass (middle) and testis growth (bottom) in blackheaded buntings ($n = 6$ per group) exposed to 11.5, 12 and 13 L photoperiods at 22°C or 27°C (low; open bar, open circle) and 35°C or 40°C (high; closed bar and circle) temperatures for four (11.5, 12 and 13 L; left panel, *a–c*) or 18 weeks (13 L; right panel, *d–f*). For comparison data for 13 L birds plotted in the left panel are taken from the right panel. The responses shown in (*a–c*) were statistically compared as follows. First, the response to each condition was assessed compared with the initial value using paired Student's *t*-test ($*p < 0.05$). Then, the effects of temperature in each photoperiod were determined by the comparison of responses between low- and high-temperature groups; $*p < 0.05$ (unpaired Student's *t*-test). Finally, one-way ANOVA compared the data from three photoperiods both in the low- and high-temperature groups; bars with identical alphabets, no difference; bars with different alphabets, $p < 0.05$ (Newman–Keuls post hoc test). An asterisk at the point symbol indicates significant difference ($p < 0.05$, unpaired Student's *t*-test) between two groups at the respective observation. Letter 'a' at the end of the line graph indicates a significant change within the group as determined by one-way ANOVA with repeated measures. Open bars, low temperature; closed bars, high temperature; open circles, low temperature; closed circles, high temperature.

on the blackheaded buntings do not suggest a change in the sensitivity to long days during the months of the year in which the current experiments were performed [5,20,21]. In a detailed study in which photosensitive blackheaded buntings were subjected to long days at monthly intervals for six months, beginning from mid-March, there were no significant difference in fat deposition and weight gain, and in testicular growth among groups that were exposed to 16 L:8 D in mid-March, mid-April and mid-May [21].

Our observations on the blackheaded buntings (figure 3) contrast with those on the white-crowned sparrows and European starlings in which the high temperature had been found to accelerate the rate of photoperiodic induction (figure 3) [14,15]. We do not know precise reasons for this, but will discuss a few possibilities. One possibility is that the

high temperatures used in our study acted as a stressor to photoperiodic induction, as blackheaded buntings do not experience such temperatures in the wild. We would not favour this however, as a 13°C temperature gradient we used in current experiments is close to that which buntings probably experience during their migratory and reproductive life-history stages [21]. Buntings start autumnal migration before temperature probably goes below 20°C, and start spring migration when temperature is about 30°C [20,23]. However, the depressive effects of the high temperature on photoperiodically controlled phenologies in the current study need to be viewed with caution in the context of what may happen in the natural world where usually, there are diel changes in the temperature.

The second possibility is that the response to temperature is influenced by the habitat of the species. In the song

sparrow (*Melospiza melodia morphna*), for example, the effect of temperature on the reproductive phenology (testis growth and cloacal protuberance) was relatively stronger in the mountain population (500–1200 m) than in the coastal population (3 m) [24]. However, this may not explain the difference in response to temperature between the blackheaded bunting and European starling. There is no report to suggest that during the breeding season, bunting's habitat is different from that of the starlings, as both species breed in southern Europe.

A third possibility is that the temperature cycles to which birds are exposed to in the year account for species differences in the temperature effects on the seasonal cycles. Clearly, the minimum and maximum daytime temperatures that blackheaded buntings experience are different from those that white-crowned sparrows and European starlings experience in the year.

Finally, one could ask about the adaptive significance of the role of temperature in photoperiodic induction of the seasonal phenologies in endotherms, e.g. birds. Is it advantageous for a photoperiodic species to evolve a second regulatory mechanism involving the environmental temperature? The present study answers this, as yes. Perhaps, the day length and temperature act in conjunction to synchronize biological clock-mediated processes that underlie daily and seasonal cycles in the migrant species in order to maximize their survival and the reproductive success [25]. Also, temperature influences the food availability, which has significant effects on the photoperiodic induction of the daily and seasonal responses [26]. Budki *et al.* [27] have reported that food deprivation during the non-breeding periods of the annual cycle affects the reproductive functions later in the year in the migratory redheaded buntings (*Emberiza bruniceps*). This implies that cues to which a species is exposed during a life-history stage possibly affect the events during the subsequent life-history stage [27]. Therefore, future studies should focus on investigating how the biological clock regulating daily and seasonal responses adjusts to sudden temperature changes in the environment.

The experiments reported herein were performed at the University of Lucknow, Lucknow, as per approval by the Institutional Ethics Committee.

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