

tion of using less number of sampling units (minimum of 25 pitfall traps) would suffice for studies evaluating the qualitative structure of the carabid community. For quantitative studies, higher number of sampling numbers (minimum of 35 pitfall traps) should be used for precise population estimates.

Obrtel¹⁴ suggested that 10–15 traps would be sufficient to capture all species of similar activity type in any part of the habitat – a recommendation based on studies at temperate situations. However, following such a procedure only six species could be recorded in the hitherto only study on carabid distribution in tropics, at forest sites of an area similar to the present study¹⁵ in the same locality. This shows the emergence of an incomplete picture of carabid community structure of the tropics from the previous study because of insufficient sampling numbers. The present study indicates the need for using more number of traps for establishing community distribution in carabids more precisely and also suggests the variation in sampling numbers to be adopted over geographic regions.

Differential responses to complete and corresponding skeleton photoperiods in male blackheaded bunting

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In male blackheaded bunting, we have investigated whether the action of the complete photoperiod (CP, single continuous long light pulse in a 24 h day) can be fully simulated by its corresponding skeleton photoperiod (SP, two short light pulses in a 24 h day). Birds were subjected to 12L:12D (CP) and 6L:5D:1L:12D (SP) daily or alternately interposed with constant darkness (12L:12D/DD, 6L:5D:1L:12D/DD) for a period of 21 weeks. There was a clear differential response to two photoperiods in the rate and magnitude of photoperiod-induced body fattening and gonadal growth. It appears that the action of a single long light pulse in the complete photoperiod, extending simultaneously to different phases, is different from that of two short light pulses in the skeleton photoperiod, falling discretely at two different phases of the circadian oscillator(s) regulating photoperiodic responses in the bunting.

It is believed that the action of single long light pulse in the complete photoperiod (CP) is fully simulated by two short light pulses in the skeleton photoperiod (SP) when the duration of a single long light pulse in CP equals the interval between the beginning of the first and the end of the second light pulse in SP. The data from experiments on some insect species (e.g. *Drosophila*, *Sarcophaga* and *Calliphora*) partially support the hypothesis. Simulation by SP of the responses induced by CP is almost perfect for all photoperiods up to 11 h, but not > 12 h; skeleton of a 13 h photoperiod causes unstable entrainment^{1,2}.

In photoperiodic vertebrates, the implication of simulation by SP of CP-induced responses is that the entrainment to two photoperiods of circadian rhythm of photoperiodic photosensitivity, which mediates physiological responses to light^{3–5}, is similar and, so, the phase of inducibility (photoinducible phase, Φ_i) remains in the same position in both photoperiodic situations. If that is true, exposure to CP and its corresponding SP which enable identical illumination of Φ_i should result in similar photoperiodic induction. However, this has not been examined precisely in any photoperiodic species so far. It is not known how exactly the CRPP responds to complete and skeleton photoperiods and how well the physiological responses induced by two kinds of pho-

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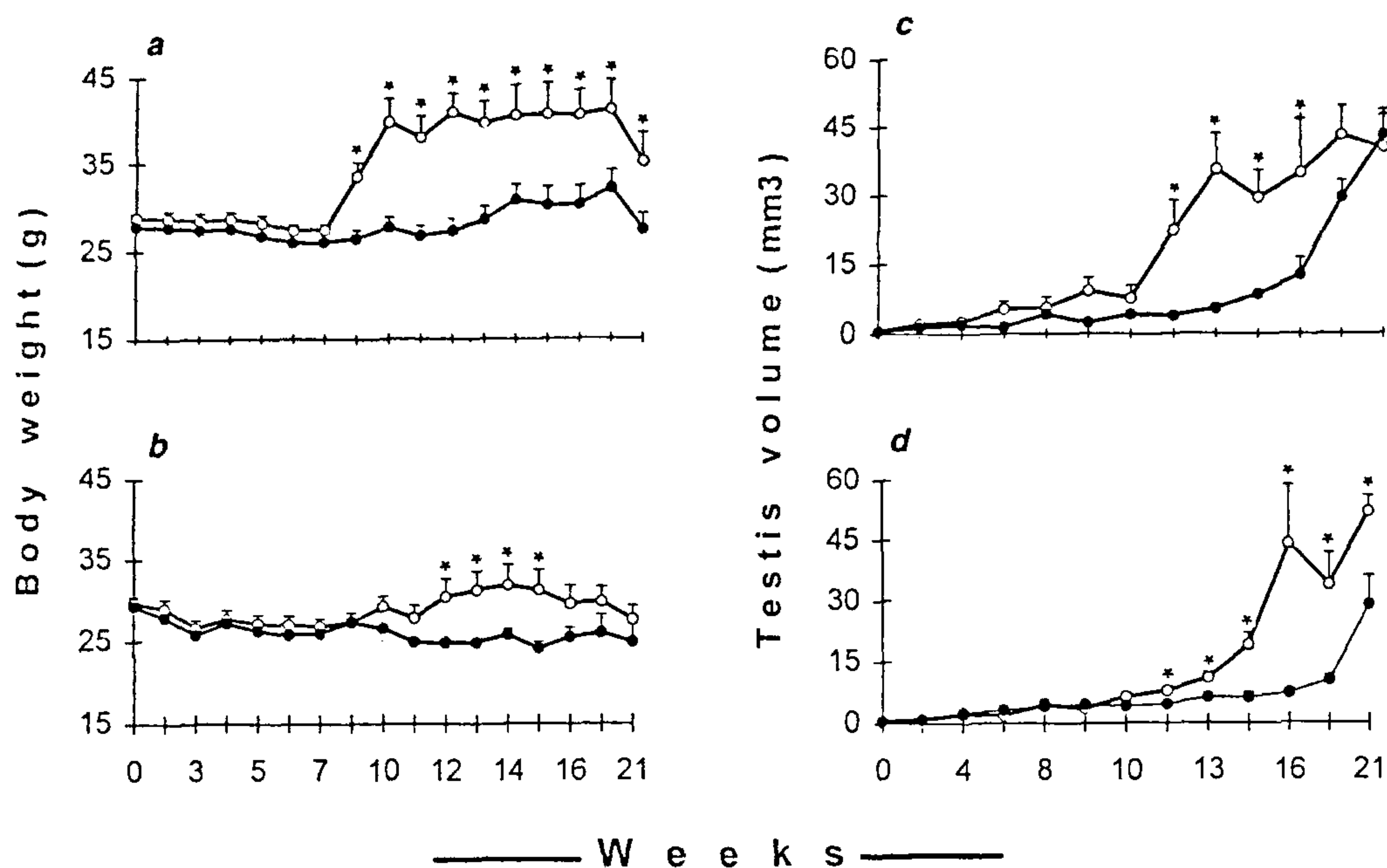


Figure 1. Photoperiodic responses (*a, b*, body fattening; *c, d*, testis growth) of photosensitive blackheaded bunting exposed to complete (12L:12D, open circles) and skeleton photoperiods (6L:5D:1L:12D, closed circles) when given daily (*a, c*) and alternatively (*b, d*) interposed constant darkness (12L:12D/DD or 6L:5D:1L:12D/DD). Birds were examined at the beginning and at the end of the experiments, and weekly/fortnightly in the treatment period of 21 weeks for recording the changes in body weight (after every week but weeks 1, 9, 17, 19 and 20) and testis size (after 2, 4, 7, 8, 9, 10, 11, 13, 15, 16 and 18 weeks). Each point symbol is the mean for 8–9 birds, and the vertical line on it indicates the standard error if it exceeds the limit of the point symbol. Asterisk indicates significance of difference ($P < 0.05$, Student's *t* test) in mean data between two photoperiods.

toperiods are comparable. In this study, we sought to determine in the highly photosensitive male blackheaded bunting (*Emberiza melanocephala*) if the responses to CP (single continuous long light pulse in a 24 h day) will be different from the corresponding SP (two short light pulses in a 24 h day), using fattening and gonadal growth as indices of the photoperiodic induction of CRPP.

The blackheaded bunting is a highly seasonal photosensitive migratory Emberizid finch, in which day length regulates seasonal responses^{6,7}. Long day length (≥ 12 h per day) stimulates a photoperiodic response (fattening and weight gain as well as gonadal growth and development), and short day length (≤ 11 h per day) is inhibitory or ineffective in stimulating a photoperiodic response⁶. This suggests that photoinducible phase (Φ_i) begins between hours 11 and 12 after the onset of light. Also, buntings subjected to 1 h light pulse introduced early (between 11 and 19 h after the beginning of the photophase) in the long night (e.g. in 6L:18D) behave as if they were exposed to a long day length^{8–10}.

In this paper, we have investigated relative inductive effects of CP 12L:12D and its corresponding SP

6L:5D:1L:12D, since in both photoperiods the duration of illumination of Φ_i will be similar. We also tested 'carry-over' inductive strength of two photoperiods when they were alternately interposed with one day of darkness (DD). The photoperiodic effects were examined at an intensity of 100 lux, a weakly inductive light intensity for this species¹¹, in order to exclude the possibility, if any, of the saturation effects of light on the photoperiodic response system in the bunting.

Groups of photosensitive birds ($n = 8$ to 10) were exposed to CP 12L:12D and SP 6L:5D:1L:12D when given daily and when given alternately interposed with one DD (12L:12D/DD and 6L:5D:1L:12D/DD); lights on beginning at 06:00 h. Artificial illumination in light-proof photoperiodic chambers housing a group of 4–5 birds provided fluorescent light at an intensity of 100 lux at perch level. All birds were provided food and water *ad libitum*. The birds were examined weekly/fortnightly (Figure 1) over a treatment period of 21 weeks. The body weight was recorded using a top pan balance to an accuracy of 0.1 g. The dimensions of left testis were recorded by laparotomy and testis volume (TV) was calculated from $4/3 \pi ab^2$, where *a* and *b* denote half of the long and short axes, respectively. The

data, plotted as mean \pm SE, were analysed using one- and two-way analysis of variance with repeated measures, followed by post-hoc tests if ANOVA indicated significance of difference. The mean of two groups on selected days was also compared using Student's *t*-test. Significance was taken at $P < 0.05$.

Both CP and SP caused a significant change in the body weight (CP- $F_{16,112} = 10.5$, $P < 0.0001$; SP- $F_{16,128} = 3.82$, $P < 0.0001$; 1-way RM ANOVA). But, there was a clear difference in the rate of stimulation between the two photoperiods ($F_{1,255} = 105.76$, $P < 0.0001$; 2-way ANOVA). A significant gain in weight ($P < 0.05$, Student-Newman-Keuls test) occurred by week 8 in CP, but by week 18 in SP (Figure 1a). Also, birds in CP fattened heavier ($P < 0.05$, Student *t*-test) than those in SP. When given alternately, response to both CP and SP was slow and inconsistent, but significant (CP/DD- $F_{16,128} = 2.59$, $P < 0.005$; SP/DD- $F_{16,112} = 2.56$, $P < 0.005$; 1-way RM ANOVA). Whereas in CP 5 of 9 birds fattened, in SP none of the eight gained weight, rather they lost ($P < 0.05$) weight from week 11 onwards (Figure 1b). A significant difference ($P < 0.05$, Student *t*-test; $F_{1,255} = 31.82$, $P < 0.0001$, 2-way ANOVA) in the rate and magnitude of fattening was clearly evident between the two photoperiods.

Testicular response was similar to body fattening. At the end of 2 weeks, 4 of 8 birds in CP, but only 2 of 9 in SP, showed slight initiation of testis growth. Testes continued to grow in size but the rate of growth was much slower in SP (Figure 1c). Interposition with DD delayed photostimulation of the testes, but the trend of response to the two photoperiods remained unchanged (cf. Figure 1c, d). Between two photoperiodic treatments, there was a significant difference in the inductiveness (CP vs SP: $F_{1,140} = 30.60$, $P < 0.0001$; CP/DD vs SP/DD: $F_{1,140} = 27.06$, $P < 0.0001$; 2-way ANOVA) and, because of the time taken for the photoperiodic stimulation, in the mean testis volume ($P < 0.05$; Student *t*-test).

This is the first report in which differential responses to CP and SP have clearly been shown in the photoperiodic situations where CP and SP enable comparable photostimulation of Φ_i . The results (Figure 1) indicate that differential photoperiodic effects may also be related to the response in question: lipogenesis and gametogenesis in bunting may be differentially stimulated. For instance, when interposed with DD, the stimulation of fat deposition, but not of testis recrudescence, under SP was drastically affected (Figure 1b, d). A similar

dissociation of fattening and gonadal responses was also observed when buntings were subjected to CP 13L:11D and corresponding SP 6L:6D:1L:11D; there was a differential stimulation of fattening, but not of testes, under the two photoperiods¹¹. It is likely that the way these photoperiods affect circadian oscillator(s) regulating liporegulatory functions is different than those regulating gonadotropic functions.

The present results are significant in showing that the action on the photoperiodic response system of SP is not identical to that of CP, as predicted by models based on external coincidence¹². Based on these results, however, we cannot explain clearly how the circadian photoperiodic system in the bunting responds differentially to CP and SP. Moreover, any explanation offered remains speculative for we do not know how CRPP responds to light, since it cannot be monitored directly. Assuming that CRPP responds to light as do other circadian rhythms (e.g. locomotor rhythms), it can be reasoned that the action of a single long light pulse in the complete photoperiod, extending simultaneously to different phases, is different from the two short light pulses in the skeleton photoperiod, falling discretely at two different phases of the circadian oscillator regulating photoperiodic responses in the bunting.

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