PHOTOPERIODIC CONTROL OF THE MOLT CYCLE IN THE CHAFFINCH (*FRINGILLA COELEBS*)[1]

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ABSTRACT.—The molt cycle in Chaffinches (*Fringilla coelebs*) has a circannual periodicity under constant photoperiodic conditions (12:12LD, 20:4LD). The molt cycle and/or rate, however, can be modified by artificial alteration of daylength. The time of onset and completion of the postnuptial molt in Chaffinches under natural conditions is a remote expression of vernal photostimulation. The timing of the molt is initiated at the end of the unifactorial phase of photoperiodic control. The onset of molt is induced after a latent period and its termination after another period, i.e. the molt begins and ends spontaneously. Under natural conditions, daylength immediately before and during the molt does not control either the time of onset or of termination of molt. The additional control system increases the rate of the molt in its early phase under short days, whereas under long days it decreases the rate of molt in its late phase. This system may play an adaptive role in synchronizing the end of the molt among birds that begin molt at different times.

The postjuvenal molt begins and finishes spontaneously under control of a program of the individual development of juveniles. Short days increase the rate of molt and initiate earlier onset and completion, whereas long days decrease the rate of the molt and delay the times of onset and completion. Juvenile birds from late broods molt more rapidly than those from early broods. A combination of different programs and photoperiodic control of the molt synchronizes the termination of the molt in juveniles from early and late broods under natural conditions in summer and autumn. *Received 7 June 1977, accepted 22 August 1979.*

THE nature of the environmental information used in the control of the molt cycle and the mechanisms by which it exerts its effects remain controversial. A simple and direct photoperiodic control of the postnuptial molt appears doubtful, as most photoperiodic species, including the Chaffinch (*Fringilla coelebs*), are in a photorefractory phase from mid-summer until late autumn.

The function of this communication is an assessment of the relative role and interrelationships of daylength, as environmental information, and genetically fixed programs in the temporal regulation of molt. It is based primarily on experiments on and observations of adult and juvenile Chaffinches in captivity. The annual cycle of this species includes only a single molt, the postnuptial molt (Stresemann and Stresemann 1966), i.e. the prebasic molt of Humphrey and Parkes (1959).

METHODS

Adult and juvenile Chaffinches were obtained from the breeding population on Kurische Nehrung (55°N), USSR, on the Baltic Sea, a population that has been studied extensively in both laboratory and field. After capture the birds were placed in large outdoor aviaries at Rybachi, where they were maintained in good condition with a special diet (Gavrilov and Dolnik 1974) and water available *ad libitum* under natural conditions of daylength and ambient temperature. The experiments were conducted between 1966 and 1974. Some were conducted more than once in different years and the results combined.

The 193 adult birds used in the photoperiodic experiments were placed in chambers with selected
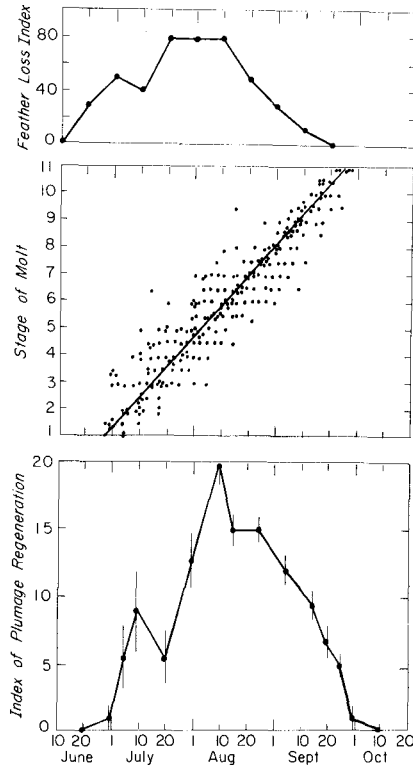
Fig. 1.   Numerical indices of molt in 35 adult Chaffinches under natural daylength.

artificial daylengths. Two experimental groups of 6-day old young were placed in chambers with constant artificial daylengths of 14 and 18 h, respectively, and were reared either by captive adults or by artificial means. Two additional groups of 6-day old birds, also reared artificially or by captive parents, were held for 3.5 yr on photoregimes of 12L:12D and 20L:4D, respectively.

Control groups of 35 adults and 50 juveniles were held under natural conditions for examination of the normal progress of the molt. The plumages of both experimental and control birds were dyed before the molt to facilitate distinction between old and new feathers. The experimental groups consisted of eight birds with dyed plumage, which were placed in individual cages on 1 June. The walls of these cages were made of white plastic and the floors of metal to assure the collection of all molted feathers.

Molted feathers were collected at 5-day intervals and separated into large (primary and secondary remiges), medium-sized (tertiary wing feathers and the larger feathers of the dorsal and ventral tracts), and small (smaller feathers of the dorsal and ventral tracts of the body and head feathers), and counted. The following formula, adapted from Lesher and Kendeigh (1941), was used to provide a mean *numerical index of feather loss,*

$$F = 10l + 5m + s$$

where F is the index of feather loss and l, m, and s represent the numbers of large, medium, and small feathers, respectively, lost during the 5-day interval. The numerical coefficients reflect the mean ratios of weights of the three groups of feathers. We have also employed a scheme for designation of the *progress of the molt of primary and secondary remiges* (Dolnik and Blyumental 1967) by the recognition of 11 stages, 1 being the onset and 11 the completion. In the course of natural molt the time interval between stages is constant so that graphic expression of the stages as a function of time is linear. If the rate of molt is greater, but constant, the slope is steeper; if the rate changes during the course of the molt, it is curvilinear.

The status of regeneration of feathers was designated as old (*o*), pins (*p*), brushes (*b*), and new (*n*) for four plumage areas—head, dorsal, ventral, and spinal.
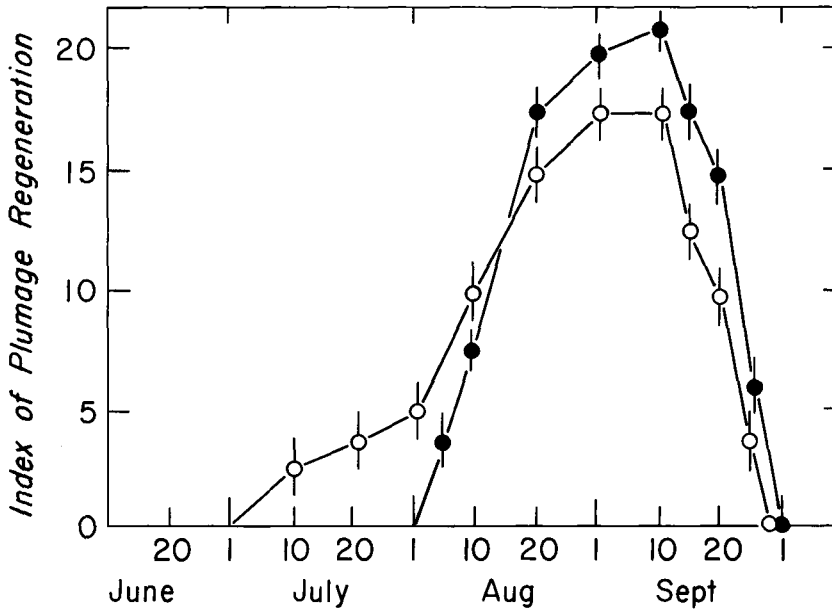
Fig. 2. The indices of plumage regeneration (*IPR*) in 50 juvenile Chaffinches from early (open circles) and late (dark circles) broods.

Intensity of regeneration of feathers for dorsal, ventral, wing, and head regions was recorded as "none," "light," "medium," or "heavy" with respect to each stage of feather replacement, i.e. old, pin, brush, or new feathers. We did not include tail feathers, because these were often lost in handling. In preliminary investigations we established the relative weights of the plumage of these regions in postnuptial molt to be as follows: head = 1, dorsal = 4, flight = 5, and ventral = 6. A number of molting birds were sacrificed; the feathers were removed, separated according to the above stages, and weighed. We found the following ratio for the visual categories of intensity of molt: "light" = 1, "medium" = 2, and "heavy" = 3. We estimate that the intensity of biosynthesis of pins is four times as great as for brushes. Stage brush includes here the entire period from the end of stage pin until the feather is completely grown, and is twice as long in duration as stage pin. We assume the coefficients of rate of synthesis to be 0 for old and new feathers, 1.0 for pins, and 0.25 for brushes. We transform the visual observations into a numerical *index of plumage regeneration (IPR)*,

$$IPR = \underbrace{1.0(1X_{ph} + 4X_{pd} + 5X_{pf} + 6X_{pv})}_{\text{for pins}} + \underbrace{0.25(1X_{bh} + 4X_{bd} + 5X_{bf} + 6X_{bv})}_{\text{for brushes}},$$

where 1.0 and 0.25 are coefficients of intensity of synthesis of pins and brushes, respectively; 1, 4, 5, 6 are the relative weights of feathers of head, dorsal, flight, and ventral regions, respectively; X is the degree of molt intensity (none, light, medium, heavy) expressed as numerical equivalents 0, 1, 2, 3, respectively; X_p and X_b are degrees of molt intensity for pins and brushes, respectively; h, d, f, v, indicate the degree of intensity for head, dorsal, flight, and ventral regions, respectively. The area under the curve of plumage regeneration as a function of time is proportional to the weight of feathers replaced and tends to remain constant regardless of the rate at which molt proceeds.

RESULTS

Molt of control birds.—The schedule of molt in adult Chaffinches is generally similar from year to year, with no differences between the sexes. Its onset occurs about 20 June. The first stage in the molt of wing feathers occurs on 27 ± 3.4 June
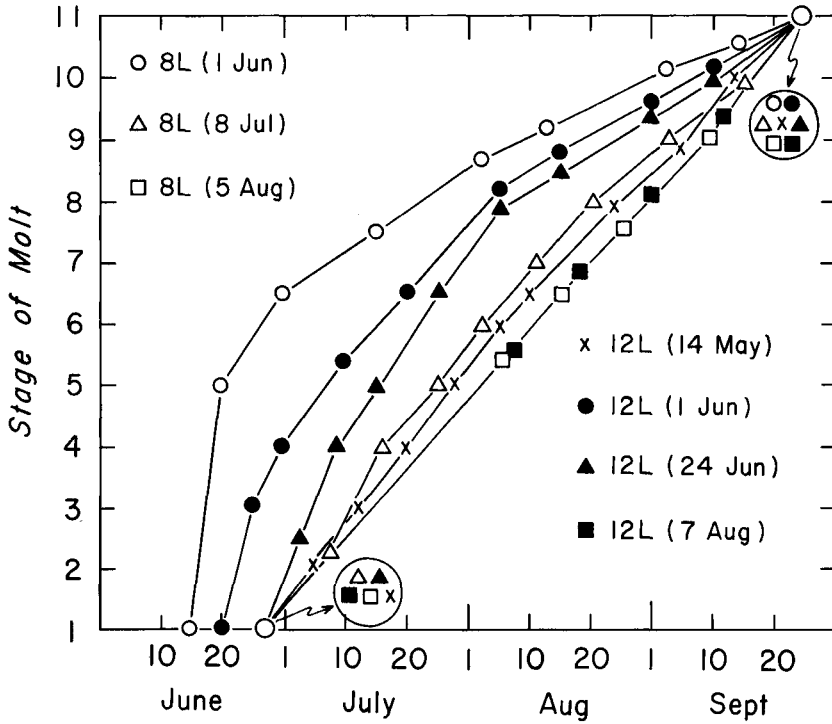
Fig. 3. The effect of short days (12L, 8L) on the rate of molt of primary and secondary remiges in adult Chaffinches. The molt of control birds under natural conditions is the straight line connecting the two large open circles. Dates in parentheses indicate the beginning of the experiments.

(Fig. 1), and the molt of these feathers is completed by 25 ± 1.2 September, i.e. about 90 days after onset. The replacement of the body plumage is completed by about 1 October.

Individual onset of the molt may occur within a range of 4 weeks, but the range of time of completion is only about 1 week, the time of molting being reduced by those individuals that begin late. The same holds in some other species with long molting periods, e.g. *Passer domesticus* (Zeidler 1966, Haukioja and Reponen 1968),

TABLE 1. Effects of short and long artificial days on the duration of the postnuptial molt in adult Chaffinches.[a]

Experimental day length (hours)	Number of birds	Onset of molt	Duration (days)
14 May (12)	10	27 ± 3 June	91 ± 2
1 June (12)	11	20 ± 4 June	98 ± 2
24 June (12)	10	27 ± 3 June	91 ± 1
7 August (12)	9	27 ± 3 June	91 ± 2
1 June (8)	8	15 ± 3 June	102 ± 2
8 July (8)	10	26 ± 3 June	92 ± 2
5 August (8)	6	27 ± 3 June	91 ± 2
1 June (20)	12	27 ± 4 June	128 ± 5
24 June (20)	11	27 ± 3 June	155 ± 5
8 July (20)	7	27 ± 4 June	158 ± 5
7 August (20)	10	26 ± 3 June	171 ± 5

[a] All groups were exposed to a natural day length from capture in late April until the beginning of the experiment. The exposure to experimental daylength continued until the completion of molt.
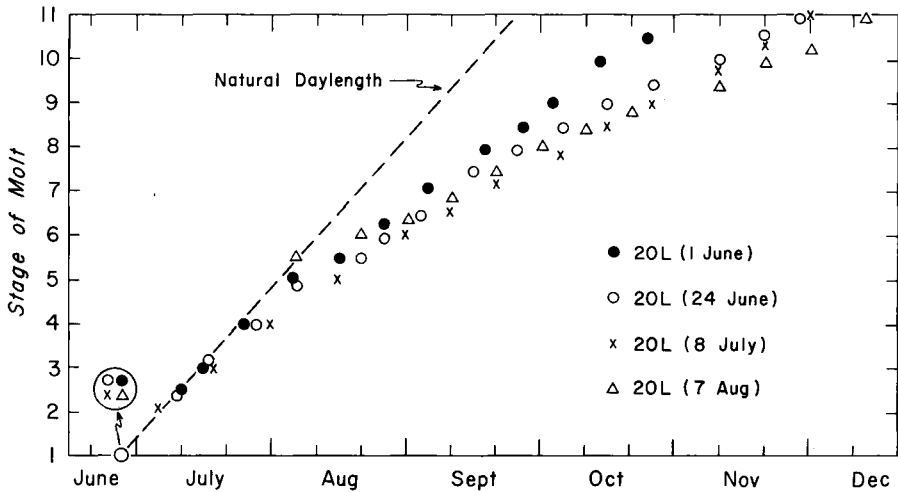
Fig. 4. The effect of long days (20 h) on the rate and time of completion of molt in adult Chaffinches.
For the explanation of symbols see Fig. 3.

P. montanus (Deckert 1962), *Pyrrhula pyrrhula* (Newton 1966), *Parus major* and
Fringilla coelebs (Dolnik and Blyumental 1967), but not in species that molt on a
more rapid schedule, e.g. *Phylloscopus trochilus* (Dolnik and Blyumental 1967,
Haukioja and Kalinainen 1968), *Carduelis flammea* (Evans 1966, Evans et al. 1967),
Zonotrichia leucophrys (Morton et al. 1969). The maximum index of feather regen-
eration occurs at stages 5–8 of the wing molt (1–25 August).

The postjuvenal molt is also completed by 1 October, even though the beginning
of molt differs greatly among individuals from early and late broods (Fig. 2).

Photoperiodic modification of the postnuptial molt.—At various times from Jan-
uary to August groups of adults were placed at constant daylengths of 20, 18, 16,
14, 12, and 8 h, respectively, all at an ambient temperature of 22°C. Each experi-
ment followed a different course. For example, 18L (20 January) + 12L (26 Feb-
ruary) means that the group was transferred from a natural daylength to 18L:6D on
20 January and then on 26 February transferred to 12L:12D. In all the groups, the
experiment was terminated at the end of the molt.

Effect of short days.—If the short photoperiod began 14 May, it did not modify
the schedule and rate of the molt. Between 1 and 24 June, reduction of daylength
to 12 or 8 h affected only slightly the normal duration (90 days) and termination of
the molt (Fig. 3, Table 1). If the short photoperiods began about 1 month (1 June)
before the usual time for the start of molt, they initiated an earlier onset, but if short
photoperiods began only a few days before the time of normal onset of molt, they
produced no change in schedule.

During June, short days accelerated the first part of the molt, but the rate of the
second part decreased, so that the times of completion on short and natural daily
photoperiods were similar. An accelerating effect of the short days has been dem-
onstrated in several species (Lesher and Kendeigh 1941, Voitkevitch 1962, Black-
more 1969). The exposure of Chaffinches to short days in the middle (July) and late
(August) stages of the molt did not modify its rate (Fig. 3).

TABLE 2. Effect of long days and the duration of the phase of natural photoperiodic control on the onset of molt in adult Chaffinches.[a]

Beginning of 20L:4D	Before (−) or after (+) natural photo-stimulation	Before (−) or after (+) unifactorial phase	Onset of molt	Duration of molt (days)	Onset of photo-stimulation to onset of molt (days)	Duration of unifactorial phase (days)	End of uni-factorial phase to end of molt (days)	n
20 January	−	−	24 ± 3 Mar.	89 ± 2	64 ± 3	17	47 ± 3	12
20 February	−	−	14 ± 3 Apr.	90 ± 3	63 ± 3	17	46 ± 3	10
26 February	±	−	2 ± 4 May	83 ± 2	65 ± 4	17	48 ± 4	6
30 April	+	−	12 ± 4 June	80 ± 3	112 ± 4	80	32 ± 4	6
14 May	+	+	29 ± 3 June	95 ± 3	129 ± 4	80	49 ± 3	5
1 June	+	+	27 ± 4 June	128 ± 5	127 ± 4	80	47 ± 4	12
24 June	+	+	27 ± 3 June	155 ± 5	127 ± 3	80	47 ± 3	11
Natural daylength			27 ± 3 June	91 ± 3	127 ± 3	80	47 ± 3	35

[a] It is presumed that natural daylength reaches a stimulatory level on 20 February and that the unifactorial phase of photoperiodic control terminates at about 11 May under natural conditions. In the first three experimental groups, the duration of the unifactorial phase was estimated from the increase in weight of the testes. (See footnote to Table 3.)
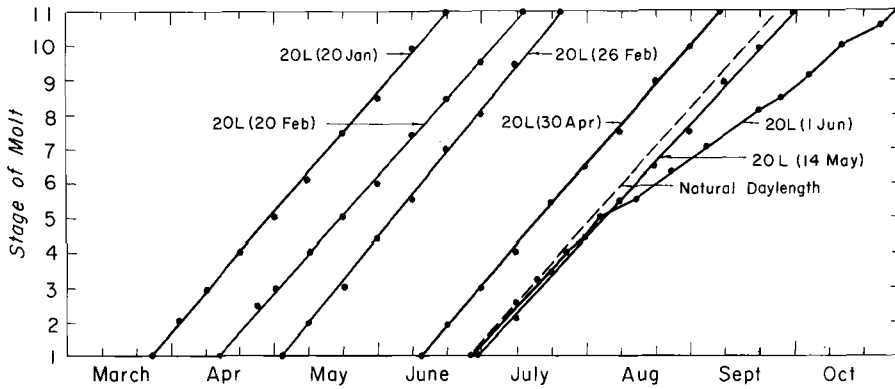
Fig. 5. The acceleration of the time of molt in adult Chaffinches by exposure to artificial long days in winter and spring.

Effect of long days.—The exposure to artificially long days (20L) during early or late June did not affect either the time of onset or the rate of the first part of the molt, but the rate of the latter part was decreased so that the molt was prolonged (Table 1, Fig. 4).

Discussion of these results necessitates the introduction of the concept of the unifactorial phase in photoperiodic control. The threshold of daylength for photoperiodic stimulation in the Chaffinch population studied is 10.4 h, which occurs at about 20 February (Dolnik 1963). From then until early May many physiological processes (e.g. migratory fattening and gonadal growth) are induced only by increased daylength. This is designated as the unifactorial period, in contrast to the following period in which additional environmental sources of information are used. The precise time of termination of the unifactorial phase is difficult to identify; perhaps it may not be precise. We can see, however, that increasing the daily photoperiod from 30 April (Table 2) advanced the date of onset of the molt but that a similar increase in daylength on 14 May or later was ineffective. We believe that the mean date of termination of the unifactorial phase for this population of the Chaffinch under natural conditions is about 11 May. Knowing that the rate of testicular growth is a function of daylength (P) during the unifactorial phase, its duration (t_u) for the population of Chaffinches used in our investigations can be estimated as:

TABLE 3. Effect of artificial long days beginning on 20 February and duration of the phase of unifactorial photoperiodic control on the onset of molt in adult Chaffinches.[a]

Length of artificial days (h)	Number of birds	Onset of molt	Duration of molt (days)	Duration of unifactorial phase (days)	End of unifactorial phase to onset of molt (days)
20	10	14 ± 3 April	90 ± 3	17	47 ± 3
18	5	23 ± 3 April	91 ± 2	22	51 ± 3
16	5	1 ± 4 May	84 ± 3	30	50 ± 4
14	5	17 ± 3 May	71 ± 3	46	51 ± 3

[a] The duration of unifactorial phase of photoperiodic control was calculated from the equation, $t_u = (\log W_t - \log W_o)/k$, in which W_o is the initial testicular weight, W_t is 200-mg testicular weight, $k = 0.0133 (p - 10.4 \text{ h})$ in days -1, and p is the duration of the experimental day in h (Dolnik 1963).
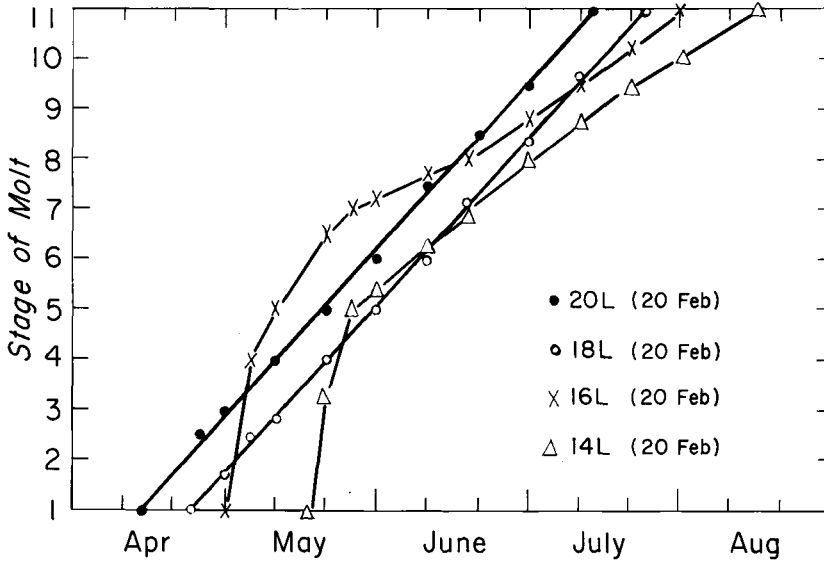
Fig. 6.   The effect of several long days on the time and rate of the molt in adult Chaffinches.

$$t_u = \frac{\log W_t - \log W_o}{0.0133(P - 10.4)},$$

where W_o and W_t are 1 and 200 mg, respectively. Although this is a useful method for estimation of the duration of the unifactorial period, we do not imply therewith that it is functionally dependent on the growth of the testes.

Effect of photostimulation in winter and spring.—When the exposure to long days was begun between January and 30 April, the time of onset and completion of molt were both accelerated, but its duration was similar to that of control birds (Table 2, Fig. 5). Change to long days 2 weeks later (14 May) changed neither the time of initiation of molt nor its duration. Acceleration of the time of molt by photostimulation in winter has also been demonstrated in the Indigo Bunting, *Passerina cyanea* (Emlen 1969).

Effect of artificial "long days" of various duration.—The time of onset and completion of the photoperiodically induced molt was found to be a function of the duration of the artificial day (Table 3). On 20L:4D and 18L:6D, the rate of molt was constant, but on 16L:8D and 14L:10D the rate of the first part of molt was found to accelerate (Fig. 6).

The effect of reduction of duration of daily photoperiod.—Change from 18L:6D to 12L:12D accelerated slightly the initiation of molt (Table 4), when the reduction was made 4–5 weeks after initiation of the 18L:6D experiment and 4–5 weeks before the molt began (26, 31 March, compared with 1, 2 April). When the reduction to 12L:12D was made later, it did not affect the time of onset of the molt. The reduction of daylength increased the rate of the first part of the molt but reduced the rate during the latter part (Fig. 7). The same pattern occurred in the experiments with the reduction of natural daylength before the onset of molt (Fig. 3).

Photoperiodic modification of postjuvenal molt.—Six-day old nestlings were divided in two groups. The first was subjected to a constant photoperiodic regime of

TABLE 4. Lack of influence of reduction of daylength on onset of molt in adult Chaffinches.

Daylength (h)	Beginning of treatment	Change to 12 h on:	Number of birds	Start of molt	Duration of molt (days)
18	20 Jan.		10	2 ± 3 April	91 ± 2
18	20 Jan.	19 Feb.	5	31 ± 3 March	93 ± 3
18	20 Jan.	26 Feb.	10	26 ± 2 March	93 ± 2
18	20 Jan.	15 Mar.	5	1 ± 3 April	90 ± 2
18	20 Jan.	1 Apr.	10	2 ± 3 April	88 ± 3
Natural photoperiod			35	27 ± 3 June	91 ± 2
12	14 May		10	27 ± 3 June	91 ± 2
12	1 June		11	20 ± 4 June	98 ± 2
12	24 June		10	27 ± 3 June	91 ± 1

18L:6D, the daylength on which this molt begins under natural conditions. The second group was subjected to constant 14L:10D, which is equivalent to the daylength at time of the completion of the molt under natural conditions. The experiment was performed thrice, with nestlings hatched in early (4 June), mid (29 June), and late (26 July) summer, respectively. The times of initiation and completion of molt of all birds subjected to 18L:6D and 14L:10D differed from those reared under natural daylengths (Table 5, Fig. 2). Short days (14L:10D) reduced the age of onset and completion of molt in all three groups, whereas long days (18L:6D) increased age of onset, age of completion, and duration of this molt (Table 5). Juvenile birds from early broods molted at a greater age than those from late broods under both 14L:10D and 18L:6D (Table 5). The rate of molt increased from early to late broods. Similar effects of daylength on the postjuvenal molt have been reported by Gwinner et al. (1972) for *Phylloscopus trochilus*.
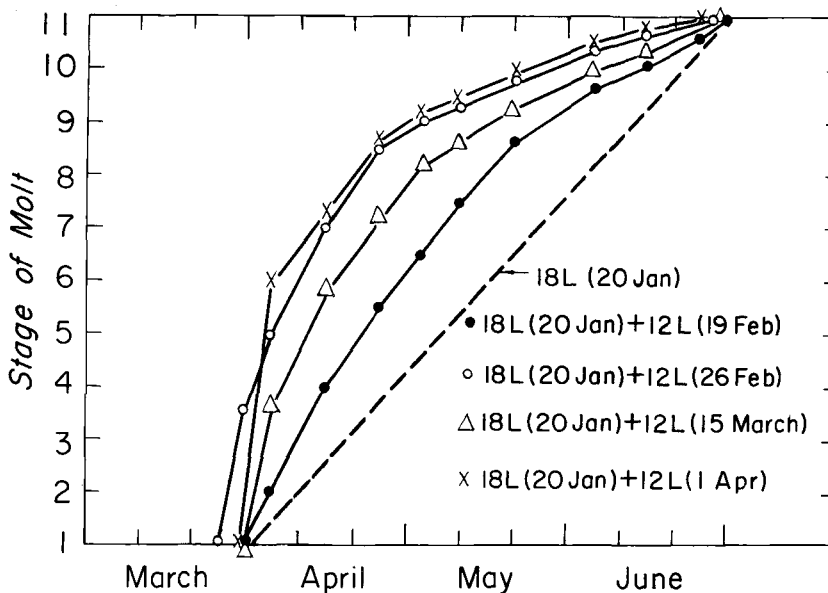

Fig. 7. Effects of reduction in daylength at different stages of photostimulation on the rate and time of onset of molt in adults. The abbreviations of the groups are given as long photoperiod (time of beginning of the exposure) + short photoperiod (time of change from long to short photoperiods).

TABLE 5. Effect of daylength and time of hatching on onset and duration of molt of fledgling Chaffinches.

Day-length (h)[a]	Num-ber of birds	Date of hatching	Onset of molt	Termination of molt	Age (days)		Duration of molt (days)
					Onset of molt	Termina-tion of molt	
14	8	4 June	5 ± 2 July	29 ± 1 Oct.	31 ± 2	127 ± 1	96 ± 2
14	10	29 June	24 ± 2 July	14 ± 1 Oct.	25 ± 2	107 ± 1	82 ± 2
14	6	26 July	14 ± 3 Aug.	27 ± 2 Sept.	19 ± 2	63 ± 2	44 ± 2
18	9	4 June	1 ± 4 Aug.	11 ± 5 Dec.	57 ± 4	190 ± 5	133 ± 5
18	12	29 June	23 ± 4 Aug.	1 ± 6 Dec.	55 ± 4	155 ± 6	100 ± 5
18	5	26 July	3 ± 3 Sept.	12 ± 6 Nov.	39 ± 3	119 ± 6	80 ± 5

[a] From six days of age.

Periodicity of molt under constant daylength.—The replacement of plumage was periodic under both short and long constant days (Table 6). The intervals between the postjuvenal and first postnuptial molts were 42–55 (49.5 ± 3.3) weeks and between the first and second postnuptial molts 39–57 (51.0 ± 6.5) under constant 20L:4D. Thus there was a periodicity in molt of ca. 1 yr.

A periodicity of molt was also observed in birds exposed to 12L:12D, but the time intervals between molts and its duration were longer: 81–87 (84 ± 2.1) weeks between first and second molts and 66–77 (66.5 ± 5.6) weeks between second and third molts. During second and third molts, there were many variations in the pattern of feather replacement. A circannual periodicity in molt under constant daylengths has also been reported for some species of Sylviidae by Berthold et al. (1972).

DISCUSSION

The replacement of feathers in Chaffinches is based on an endogenous program. The molt can repeat with circannual periodicity under constant photoperiods of 12L:12D–20L:4D. Both postjuvenal and postnuptial molts, however, are also under photoperiodic control.

The postjuvenal molt is included in a program of the individual development of Chaffinches. It can begin and terminate without photoperiodic induction. Daylength controls only time of molt, onset and completion, and its rate. The control is adaptive for birds living under natural conditions: short days accelerate the molt and long

TABLE 6. Circannual periodicity of the annual molt in Chaffinches under constant artificial daylengths.

	Duration of molt[a]						Period (weeks)	
	First		Second		Third			
Day-length	Onset	Comple-tion	Onset	Comple-tion	Onset	Comple-tion	1st–2nd	2nd–3rd
20	10 ± 1.5 (12)	22 ± 0.9 (12)	57 ± 2.8 (12)	71 ± 1.9 (12)	110 ± 5.1 (6)[b]	131 ± 1.9 (6)	47.2 ± 3.5 (12)	51.0 ± 6.5 (6)
12	4 ± 0.9 (10)	17 ± 1.1 (10)	87 ± 1.6 (10)	102 ± 3.1 (10)	154 ± 6.2 (4)[b]	166 ± 5.6 (4)	83.5 ± 2.2 (10)	65.8 ± 5.6 (4)

[a] In weeks from the time from hatching; mean ± SD, sample size in parentheses.
[b] Smaller sample size due to deaths between second and third molts.

days reduce its rate. The same system acts during the molt in adults as an additional control. Juveniles have adaptive differences in their programs of individual development between early and late broods. The program of late broods is faster. The difference in programs may be caused by the daylength of the first days after hatching or possibly induced in the egg before laying.

The photoperiodic control of the molt cycle in adult Chaffinches appears to have two stages or systems: (1) primary photoperiodic control by increasing daylength in early spring, and (2) additional controls during the premolt and molt period. The first system is initiated (or accelerated) by increasing daylength in spring, at the time of photoperiodic control also of the vernal migratory state and gonadal growth. In this period, the system begins a time program, and several days later the molt occurs spontaneously. A similar system controls the time of ending the molt. The timed program could hypothetically begin at various stages of photostimulation; for example, from the start of the photostimulation, from the beginning of the refractory phase, etc. But our experiments demonstrate that it begins at the end of the phase of unifactorial photoperiodic control (Tables 2 and 3).

Natural daylength increases to a threshold value in late February (ca. 20 February, see Dolnik 1963). The end of this unifactorial photoperiodic control is associated in male Chaffinches with a testicular weight of 200–250 mg. Caged birds under these conditions attain such testicular weight in early May, i.e. 70–80 days after the beginning of the photostimulation and 48–58 days before the onset of molt (20–27 June). In March and April, only daylength controls the rate of gonadal development, which can be calculated from empirical equations derived from experiments with a range of constant daylengths (Dolnik 1963). In early May the unifactorial photoperiodic control terminates, and other environmental factors become involved in controlling reproductive function, termination of the vernal migratory state, and breeding. By this time Chaffinches have returned to their breeding territories.

During the unifactorial phase, photoperiodic control synchronizes the annual cycles with the astronomical year. During the multifactorial phase, daylength still exerts an effect, but other factors now adjust the schedule of vernal and aestival functions to the environmental conditions on the breeding territory. In this second phase there may actually be a desynchronization between the annual cycle and the astronomical calendar. When we expose Chaffinches to long days before (20 January and 20 February) or during (26 February and 30 April) the unifactorial phase, the molt begins early, but when we expose birds after this phase (14 May and 1 June), the molt begins on the natural schedule.

In all of the experiments the times between the end of the unifactorial phase and onset of molt are similar, 47–51 days (Tables 2 and 3). This suggests that our hypothesis is more adequate than others (e.g. that molt starts at a fixed time after the beginning of photostimulation, after the beginning of photorefractory period, or after the reduction of daylength following the summer solstice).

The second control system is activated at the end of unifactorial control, 1 month before the onset of molt. Under natural conditions the effect of this system is absent on 14 May but present on 1 June (Table 1). This second system accelerates the time of start and the rate of molt if daylength is less than 18 h. The effect of daylength decreases and the effect of the second system increases inversely with the time interval between the beginning of decrease of daylength and the natural time for

onset of molt. Under natural conditions this decrease in daylength can accelerate the molt in late-molting birds. This system is similar to the system that controls the postjuvenal molt. This additional system of molt control by short days ceases at the end of the first part of molt. The latter part of the molt follows a standard time schedule. If the rate of molt during the first part is high, this system suppresses the rate, and the molt finishes at the standard time. If exposure to a constant long photoperiod is begun before 1 June, on the other hand, only the first system controls the rate and time of molt. But if daylength is experimentally increased to 20 h in June, July, or August, the system cannot control the latter part of the molt, and the rate of molt is decreased. We are unable to suggest a possible basis for this effect.

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