THE TEMPORAL RELATIONSHIP BETWEEN THE CYCLE OF TESTICULAR DEVELOPMENT AND MOLT IN THE WHITE-CROWNED SPARROW, *ZONOTRICHIA LEUCOPHRYS GAMBELII*

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Abstract.—Male White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) held on 12-h days for 46.5 months failed to develop a postnuptial-type molt, although they underwent 2–4 cycles of testicular growth and regression. At an estimated 47 days (range 43–59 days) after transfer to 18-h days, all began an essentially normal postnuptial molt of the primary remiges. The time elapsed between the loss of the first and ninth primary remiges was about 30 days, within normal range for this length of day. There was no identifiable relationship between size or rate of growth of the testes and the time of onset of the molt. These and other results indicate that there is a long-day (>12, <16 h) requirement for this molt. The hypotheses (1) that the role of long days in the induction of this molt is stimulatory, perhaps indirectly, or (2) that it entrains an endogenous circannual cycle involved in the control of molt are discussed in light of these results. *Received 6 July 1979, accepted 12 October 1979.*

THE temporal relationships among migration, molt, and reproductive effort and the selective forces that have resulted in the array of patterns of these functions in contemporary species of birds constitute one of the most fascinating aspects of modern avian biology. Although there are numerous and notable exceptions (e.g. Stresemann and Stresemann 1966, Payne 1972), it is nevertheless generally true that the annual reproductive effort and the postnuptial molt, the prebasic molt of Humphrey and Parkes (1959), are temporally separated (for reviews see Vaugien 1948, Assenmacher 1958, Pitelka 1958, Voitkevich 1962, Stresemann and Stresemann 1966, Payne 1972, Gavrilov and Dolnik 1974). Generally among small passerine species these functions occur during a segment of the annual cycle in which trophic resources are relatively abundant and environmental temperatures are mild. The temporal relationships among reproduction, postnuptial molt, and migration are especially interesting among small migratory species that breed at high latitudes. Commonly among these populations, such as those of the migratory races of *Zonotrichia leucophrys* (Blanchard 1941, Blanchard and Erickson 1949, King et al. 1966, DeWolfe 1967, Mewaldt et al. 1968, Morton et al. 1969, Lewis 1975) and the more southern populations of *Fringilla coelebs* (Blyumental and Dolnik 1966, Dolnik 1966), *F. montifringilla* (Dolnik 1967), *Carduelis flammea carbaret* (Evans 1966, Evans et al. 1967), *Acrocephalus arundinaceus orientalis* (Stresemann and Stresemann 1966, 1968a), *Luscinia luscinia* (Berger 1967), and *Sylvia communis communis* (Stresemann and Stresemann 1968a), the postnuptial molt occurs between the reproductive effort and the onset of late-summer or autumnal migration. In some individuals of *S. c. communis* the molt of the secondary remiges may not be completed before the onset of migration and is discontinued (Pimm 1973). In *Empidonax flaviventris*, most, but not all, individuals renew the three–five outer primary remiges before the onset of migration and then complete the wing molt on the wintering area in Central America (Phillips et al. 1966).

In some other small migratory passerine species, however, such as *Hirundo rus-*

tica rustica, with the exception of its southernmost breeding populations (Strese-
mann and Stresemann 1968b), *Sylvia borin* and *S. communis icterops* (Stresemann
and Stresemann 1968a), *Phylloscopus sibilatrix* and *P. borealis* (Stresemann and
Stresemann 1968a), *Carpodacus erythrinus* (Stresemann and Stresemann 1966), and
most North American tyrant flycatchers (Phillips et al. 1966), the postnuptial molt
occurs in the wintering area after the completion of the postbreeding migration.

   These temporal relationships among molt, migration, and reproductive effort ap-
parently reflect the evolution of mechanisms that control annual cycles so that func-
tions with high energy requirements are temporally separated (Kendeigh 1949, Far-
ner 1964, King 1974), presumably enhancing fitness. It seems probable that such
control systems have often evolved independently with development of migration
in individual species or populations (Farner 1950, 1964, 1975; King and Farner
1974; Menaker 1974). It is therefore not surprising that the reviews of Assenmacher
(1958), Voitkevich (1962), and Payne (1972) have failed to identify a common control
system for the annual molt. We agree with Payne (1972: 146) that ". . . if there is
a common scheme . . . for control of molt, no one has come close to finding it."

   The temporal separation of the reproductive effort and molt, which is widespread
among small passerine species, has led to hypotheses that the control systems for
these two functions are closely integrated, so that molt begins essentially automat-
ically with the regression of the gonads (Farner 1964, King et al. 1966, Farner and
Follett 1966, Farner and Lewis 1971), perhaps because of the removal of an inhib-
itory effect of sex hormones (Vaugien 1955, Assenmacher 1958, Wagner and Müller
1963, Mewaldt et al. 1968, Payne 1972) that thereby permits the molt to proceed,
possibly under the influence of thyroid hormones (Voitkevich 1962, Wagner and
Müller 1963, Dobrynina 1974).

   We communicate herein results that were obtained as byproducts of two experi-
ments designed primarily for other purposes and hence not optimally suited to the
purposes of this report. Nevertheless, these results, coupled with field observations
and data already in the literature, indicate that there is not necessarily a fixed phase
relationship between the onset of testicular growth or regression of the testes and
the onset of postnuptial molt. They argue against a simple relationship between the
systems that control the timing of gonadal and molt cycles, although they suggest
strongly that the endocrine activity of the gonads may delay the onset of photore-
fractoriness as well as that of the postnuptial molt.

   The White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) in the first ex-
periment reported herein were from an investigation in which the effects of constant
artificial day lengths of different durations were compared during long periods of
exposure. The survivors of a group subjected to 12L:12D constitute Group A. The
birds in the second experiment (Group B) had been used in an experiment on the
plasma level of luteinizing hormone as a function of day length and represent the
survivors among those exposed to 12L:12D.

METHODS

   Group A.—A group of 56 first-yr male *Zonotrichia leucophrys gambelii* was captured in Kittitas
County, Washington, between 20 and 30 September 1971 and held in outdoor aviaries until 20 January
1972, when the birds were placed 2 per cage in small cages (41 × 26 × 27 cm) in a controlled environment
room with a photoperiodic regime of 12 h of light (at least 400 lux at the floor of the cages) per day.
Temperature and relative humidity were maintained at 20 ± 0.5°C and 55 ± 5%, respectively. Food
(Purina Chick Startena) and water were available *ad libitum.* At approximately monthly intervals,

TABLE 1. Observations on molt and testes in male *Zonotrichia leucophrys gambelii* (Group A) subjected to 12L:12D for 46.5 months, during which there was no postnuptial-type molt, and then transferred to 18L:6D.

Bird number	Testicular cycles during 45 months on 12L:12D	Estimated weight of testes in mg		Number of primary remiges missing or being replaced[a]				
		Day -2[a]	Day 26[a]	26	64	73	81	92
1638	4	2	80	0[b]	4	5	8	9
0900	3	20	300	0	6	8	9	9
1265	3 (?4)	2	300	0	5	7	8	9
0853	4	10	30	0	6	9	9	9
3228	—[c]	20	300	0	5	6	8	9
2097	—[c]	—[d]	30	0	4	4	5[e]	9
1141	4	30	25	0	5	7	8	9
1313	4 (?5)	10	12	0	6	7	9	9
1334	4	15	20	0	6	8	9	9
3263	1[b]	—	—	0	4[e]	5	6	9

[a] Days of 18L:6D.
[b] P_4 growing on left wing; no primary remiges missing on right wing.
[c] In cages for recording motor activity, insufficient laparotomies.
[d] Testes could not be seen in laparotomy; certainly smaller than 10 mg.
[e] Diseased foot removed.

observations were made on the plumage and testicular size. The estimation of the testicular weight was made by laparotomy and by visual comparison of the exposed left testis with a graded series of fixed testes of known weight. Because the right and left testes are usually similar in size, a reasonably accurate estimate can be made rapidly. As a monitor of the health of the birds and to provide information on possible cycles in body weight, the birds were weighed to the nearest 0.1 g at biweekly intervals. In the course of the 46.5 months these birds, after an initial, apparently normal testicular development and regression, underwent "cycles" in testicular size with progressively smaller amplitudes and periods (Table 1). Although there were very occasional unilateral adventitial losses of individual primary and secondary remiges in a few birds during the 46.5 months on constant 12-h days, no member of the group developed a postnuptial-type molt of these feathers. On 5 December 1976 the 16 survivors were transferred from 12L:12D to 18L:6D, other conditions remaining unchanged. Plumage was examined at about weekly intervals from day 64 through day 92 of 18L:6D, after which the experiment was terminated. At this time all 10 survivors had replaced all primary remiges. By interpolation, the day of loss of primary remiges was estimated with a range of possible error of ±2 days. Construction of a schedule of loss of primary remiges prior to day 64 is described below. Laparotomies were performed after 26 days to estimate weights of testes.

In retrospect, it is clear that this secondary experiment was not ideally planned and that we failed to obtain an optimal set of observations. Despite these shortcomings, the results have implications concerning the relationships between the controls of testicular function and molt.

Group B.—This group of eight first-yr males, selected randomly from 94 captured with mist nets in October 1977 in Kittitas County, Washington, was held in outdoor aviaries until 22 November, when they were transferred into individual small cages in a constant-condition chamber with a photoregime of 8L:16D under the same conditions of light intensity, temperature, and availability of food and water as described for Group A. On 15 December laparotomies were performed to estimate weights of testes. The photoregime was changed to 12L:12D on 19 December. Thereafter, laparotomies were performed at intervals of about 2 months. On 29 October 1978, no molt having occurred, the photoregime was shifted to 18L:6D; laparotomies were performed on the three survivors after 16 and 34 days; plumages were inspected for molt at least semiweekly until the 9th primary remix was lost (80–92days). Days of loss of primary remiges were estimated by interpolation, generally with a range of possible error of ±1 day, only infrequently ±2 days.

RESULTS AND DISCUSSION

Of the 56 birds subjected originally to 12L:12D, there were 16 that survived the entire 46.5 months, an annual survival rate of about 70%, a rate somewhat greater than our estimate of about 55% for birds that survive the postjuvenal molt in natural
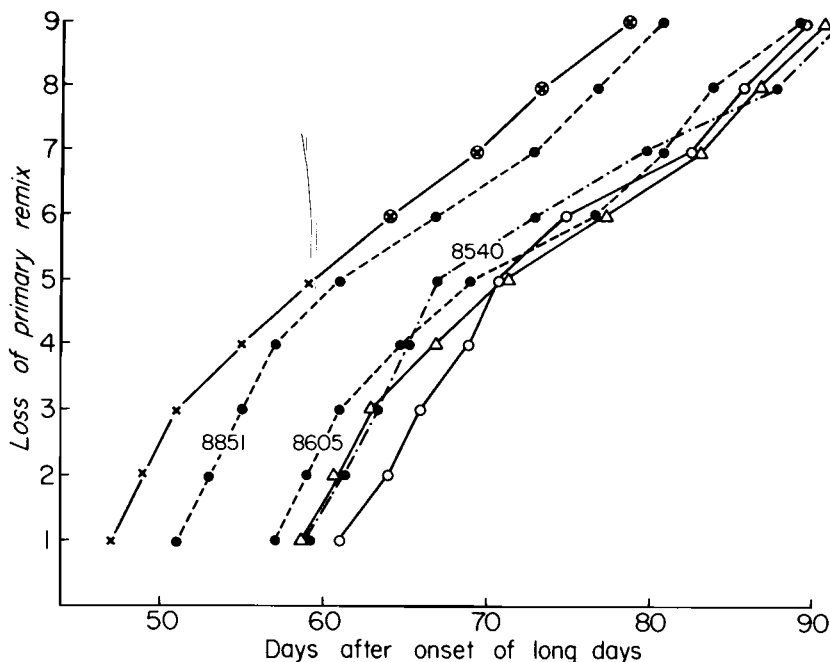
Fig. 1. Schedule of loss of primary remiges as a function of time after onset of constant long days. ⊗ = Group A observed (means), × = Group A extrapolated (means), △ = 18L:6D (means), (D. S. Farner, R. S. Donham, M. C. Moore unpubl. results). ○ = 20L:4D (means) (D. S. Farner, R. S. Donham, M. C. Moore unpubl. results), ● = Group B (individuals with band numbers).

populations. The 16 survivors constitute Group A of this article. Six birds of this group died after the onset of 18L:6D but before the termination of the experiment on day 92 of 18L:6D. One died before day 26, at which time none of the survivors had begun to molt. Four, which had not begun to molt on day 26, died between days 26 and 64. Unfortunately, we have no information on their plumages after day 26. The 6th bird that failed to survive to day 92 was found dead on day 81; the first 5 primary remiges had been dropped and were being replaced in a pattern consistent with the surviving 10 birds. The observations on these 10 survivors are summarized in Table 1.

With the exception of the reversal of order of loss of two in each of two birds, the sequences of the observed losses of the primary remiges were normal. There are unfortunately, however, some problems of interpretation of our observations, as by mischance the first observations were recorded only after primary remiges 1–4 to 1–6 had already been dropped (Table 1). In an attempt to compensate for this, we have compared (Fig. 1) the schedule of molt of 5–9 or 6–9 of these birds with a group of 7 that had been changed from a photoregime of 8L:16D to 18L:6D (D. S. Farner, R. S. Donham, M. C. Moore unpubl. obs.), 4 groups subjected to 16L:8D by Chilgren (1978), and 3 birds (Group B) that had been subjected to 12L:12D for 10 months without molt and then changed to 18L:6D (Tables 2–4, Fig. 1).

If we then assume that the entire schedule of loss of primary remiges in Group A was similar to those shifted from 8L:16D to 18L:6D and to those of Group B (D. S. Farner, R. S. Donham, M. C. Moore unpubl. results; Table 3), the mean time of loss of the first for Group A from the time of the shift from 12L:12D to 18L:6D

TABLE 2. Day of loss of primary remiges 6–9 after onset of 18L:6D.

Primary remex number	Prior photoregime		
	12L:12D, 46.5 months ($n = 10$)[a]	12L:12D, 10.5 months ($n = 3$)[b]	8L:16D ($n = 7$)[c]
6	64, 65	67, 72, 76	77 (69–81)
7	69 (65–76)	71, 79, 80	82 (75–91)
8	73 (68–77)	77, 82, 89	87 (79–94)
9	78 (75–82)	80, 90, 92	92 (86–95)

[a] Group A. Means, ranges in parentheses. Two birds, 2097 and 3263, are excluded from the means and ranges. Each had developed an infected foot, subsequently removed by surgery, before the loss of primary remex 6, which occurred at about days 83 and 79, respectively; loss of number 9 occurred on days 93 and 91. Primary remiges were molted in normal order and at approximately normal intervals. Four birds dropped primary remex 6 before day 64, making it necessary to estimate the day of loss by extrapolation. Two different schemes of extrapolation give slightly different means. Days of loss of other primary remiges were estimated by interpolation, which involves a possible error of ±2 days.
[b] Group B. Individual data. Five of the initial 8 birds in this group died before the onset of molt among the 3 survivors.
[c] Means, ranges in parentheses (D. S. Farner, R. S. Donham, M. C. Moore unpubl. obs.).

would have been day 47 (SE = ±4 days) (Fig. 1). Although we assume that the schedule of loss and replacement of primary remiges in Group A was normal, or nearly so, it is to be emphasized that molt of these feathers could not have begun earlier than day 27, because all feathers were still in place on day 26 (Table 1), or later than about day 55, because by day 64 all 10 birds had lost at least the first 4 primary remiges (Table 1, Fig. 1). The mean day of loss of the first primary remix in a group that was shifted from 8L:16D to 18L:6D was 59 ± 2 (D. S. Farner, R. S. Donham, M. C. Moore unpubl. obs.; Fig. 1, Table 4). It therefore seems possible that molt in Group A may have begun somewhat earlier than in the birds shifted from 8L:16D to 18L:6D (Fig. 1, Table 4). This is supported by a direct comparison of the schedules of the losses of primary remiges 6–9 (Fig. 1, Table 2).

It is of interest to compare the intervals between losses of primary remiges 1 and 9 among groups A (estimated), B, the group cited above that was shifted from 8L:16D to 18L:6D, a group shifted from 8L:16D to 20L:4D (D. S. Farner, R. S. Donham, M. C. Moore unpubl. obs.), and 2 groups caged under otherwise natural conditions at 65°N at Fairbanks, Alaska (Table 4). Thus, although it is not critical to the major argument advanced in this article, it seems highly probable that the sequence and rate of the molt of primary remiges in Group A was essentially normal and that the prolonged treatment with 12L:12D may have somehow caused an earlier onset of molt after the shift to long days. More important, the data recorded

TABLE 3. Observations on molt and testes in three *Zonotrichia leucophrys gambelii*, Group B, subjected to 12L:12D for 10.5 months, during which there was no postnuptial-type molt, and then transferred to 18L:6D.[a]

Bird number	Estimated weight of testes in mg				Time in days from onset of 18L:6D to loss of primary remex 1	Interval between loss of primary remiges 1 and 9 (days)
	At beginning of 12L:12D	Maximum observed on 12L:12D[b]	At time of transfer to 18L:6D	Maximum observed on 18L:6D[b]		
8540	1.0	40 (166)	20	200 (16)	58	33
8605	1.0	350 (242)	60	>300 (16)	56	33
8851	1.0	50 (205)	12	>300 (34)	51	30

[a] Five of the initial 8 birds died before the onset of molt among the 3 survivors.
[b] Day of observation in parentheses.

TABLE 4. Photoperiodic induction of postnuptial molt in *Zonotrichia leucophrys gambelii*.

Photoregime	n	Onset of photoregime to loss of primary remex 1 (days)[a]	Interval between loss of primary remiges 1 and 9 (days)[a]	Source
18L:6D[b]	10	47 (est.)	30 (est.)	Group A
18L:6D	7	59 (54–62)	32 (29–36)	D. S. Farner, R. S. Donham, M. C. Moore unpubl. obs.
18L:6D[c]	3	(51–58)	(30–33)	Group B
16L:8D	17	70	26	Adapted from Chilgren (1978)
20L:4D	6	55	—	Adapted from Chilgren (1978)
20L:4D	8	61 (58–64)	29 (25–37)	D. S. Farner, R. S. Donham, M. C. Moore unpubl. obs.
Natural, Fairbanks, Alaska	7	—	29	Adapted from Chilgren (1978)
Natural, Fairbanks, Alaska	17	—	26	Morton et al. (1969)

[a] Range is given in parentheses.
[b] Before the beginning of treatment with 18L:6D, these birds had been held on 12L:12D for 46.5 months during which no postnuptial-type molt occurred.
[c] As above, except that exposure to 12L:12D was for 10.5 months without the development of a postnuptial-type molt.

in Table 1 and Table 3 collectively suggest to us that there is no regular relationship between testicular weight, or change in testicular weight, at the time of onset of 18L:6D and the onset of molt. The latter appears to have proceeded independently of the level of testicular development. This suggestion is consistent with the failure of molt to occur during the 46.5 months on 12L:12D despite "cycles" in testicular size.

The results reported herein appear to us to demonstrate clearly (1) that the development of the postnuptial molt in *Zonotrichia leucophrys gambelii* has a long-day requirement, i.e. greater than 12 h but less than 16 h (see results from Chilgren 1978, in Table 4); and (2) that the development of this molt is not closely associated with the stage of testicular development at the onset of long-day (>12 h) treatment and therefore that the control scheme is not intimately related to that of at least the gametogenic function of the testes.

That there is a long-day requirement is clear from the failure of any of the original 56 birds in Group A, 16 of which survived the 45 months of 12L:12D, to undergo a postnuptial-type molt of the primary remiges. This is consistent with the results of Chilgren (1978), who found that no such molt occurred after 95 days of 12L:12D, the observations of the birds in Group B, and the observations of Wolfson (1958) of *Zonotrichia albicollis*. King (1968) has already demonstrated in *Z. l. gambelii* that no molt occurs under 8L:16D, which is consistent with our less systematic observations (D. S. Farner and many others unpubl. obs.). Because postnuptial molt occurs in birds subjected to day lengths of 16 h or more, including LL (Chilgren 1978; D. S. Farner, R. S. Donham, M. C. Moore unpubl. obs.), the "threshold" for its induction must lie between 12 and 16 h per day, which seems to be consistent with the observations of Wolfson (1954, 1958) of *Junco hyemalis, Z. albicollis,* and *Z. l. leucophrys* and of Dolnik and Gavrilov (1972) and Noskov (1977) of *Fringilla coelebs coelebs.*

Our observations of *Zonotrichia leucophrys gambelii* suggest that induction of gonadal development and postnuptial molt are both obligately dependent on long days but that the former is not a component of the system that induces the latter (see also Wolfson 1954). On the other hand, they are by no means inconsistent with a hypothesis that gonadal hormones cause delay of the onset of photorefractoriness and the postnuptial molt induced by long days (e.g. Wolfson 1958, Farner 1964). Support for this latter hypothesis can be derived from several studies of *Zonotrichia leucophrys*: (1) the repeated occurrence of a postnuptial-like molt in castrated *Z. l. gambelii* (P. W. Mattocks, Jr. unpubl. obs.) with no detectable plasma testosterone (McCreery and Farner 1979) but which become photorefractory at about the same time as intact males under natural conditions at Seattle (Mattocks et al. 1976); (2) the delay in onset of the overt effects of photorefractoriness and the postnuptial molt in renesting *Z. l. gambelii* in Alaska (Wingfield and Farner 1979); (3) the early development of photorefractoriness and molt in nonbreeding *Z. l. gambelii* (Wingfield and Farner 1979); (4) the delay of postnuptial molt in photostimulated male *Z. l. gambelii* with implants of testosterone (J. C. Wingfield and K. S. Matt unpubl. obs.; also R. S. Donham and P. W. Mattocks, Jr. unpubl. obs.); (5) the interruption of postnuptial molt in late-season resumption of reproductive function in *Z. l. nuttalli* (Mewaldt and King 1978); and (6) the consistent correlation between the onset of molt and a decline in the plasma level of testosterone in natural breeding populations of *Z. l. gambelii* and *Z. l. pugetensis* (Wingfield and Farner 1978a, b; 1979).

An apparently similar suspension of postnuptial molt has been reported for lowland subtropical populations of *Zonotrichia capensis hypoleuca* (King 1972, 1973). In this race, at least in the vicinity of Tucumán, the onset of the molt may occur while the testes are still capable of spermatogenesis (King 1973, 1976), doubtless a reflection of climatic conditions in which a complete temporal separation of gonadal function and molt is not critical. Unfortunately, the plasma levels of androgens at the onset of molt have not been ascertained for this race.

The concept of a close functional relationship between photorefractoriness and molt was at least implied as early as 30 yr ago by Vaugien (1948) and is consistent with observations of Kobayashi (e.g. 1954, 1957) of domestic canaries, and of Wolfson (e.g. 1958) of *Junco hyemalis* and *Zonotrichia albicollis*. More recently Dolnik (e.g. 1975, 1976) has suggested, on the basis of extensive studies of the breeding population of *Fringilla coelebs coelebs* at Kurische Nehrung, that the postnuptial molt is induced by long days and that it begins after a fixed interval (47–51 days) following the termination of the unifactorial phase of photostimulation as indicated by the end of logarithmic growth of the gonads. Although Dolnik (1974) has described this as an hourglass function, the physiologic implications of this suggestion are unclear; he does not assume a direct functional dependence of the onset of molt on the growth of the gonads. In a series of seven groups of male *Zonotrichia leucophrys gambelii*, each held on constant daily photoregimes ranging from 16L:8D to continuous light, we (D. S. Farner, R. S. Donham, and M. C. Moore unpubl. obs.) have also found a nearly constant, although shorter, interval of 30–34 days between the end of the logarithmic growth phase of the testes and onset of postnuptial molt of the primary remiges. Because the onset of the postnuptial molt begins coincidentally with, or more probably shortly after, the beginning of photorefractoriness, however, one may hypothesize that the former is functionally dependent on the latter. Such a hypothesis, however, requires more rigid examination by carefully controlled experiments. Such are now in progress in our laboratory.

A hypothesis of a causal relationship between photorefractoriness and the onset of the postnuptial molt as applied here to temperate taxa of *Zonotrichia* is not inconsistent with the beginning of this molt while the testes are at least gametogenically active in near-equatorial populations of *Z. capensis* (Miller 1961, Wolf 1969, King 1972), because photorefractoriness appears not to be characteristic of these races (Miller 1965, Epple et al. 1972, Lewis et al. 1974). This can be rationalized by the assumption that, as the low-latitude races of *Z. capensis* evolved from a mid-latitude, North American ancestor (Chapman 1940), natural selection operated to eliminate the photorefractory component, thereby enhancing fitness in areas in which seasonal differences are smaller and not reliably predicted by day length (King 1976).

Because we have no previous information on the responses of testes at various stages of development and regression in *Zonotrichia leucophrys gambelii* held first on 12L:12D and then shifted to long days, and because we unfortunately made no observations on the size of testes in Group A after day 26 of 18L:6D, we do not know which, and indeed if any, of the birds were photorefractory at the time of transfer to 18L:6D. Of the 14 for which we have estimated testicular weights on days −2 and +26, at least some testicular growth occurred in 8; no definite conclusions can be drawn concerning the remaining 6, including 1141, 1313, 1334 and 3263 in Table 1. Because of the age of the birds and their long confinement under unnatural conditions, one cannot assume that failure to respond to 18L:6D is necessarily indicative of true photorefractoriness. The three birds in Group B (Table 3) had clearly not become photorefractory after 10.5 months on 12L:12D. It is therefore possible that this photoperiodic regime does not induce photorefractoriness, a conclusion reached earlier by Wolfson (1958) for *Z. albicollis*. This would be consistent with the observed fluctuations in testicular size observed during the 46.5 months of 12L:12D (Group A), if one were to make the reasonable assumption that they reflect negative feedback from the testis on the secretion of FSH. Because photoregimes of 12L:12D have been frequently employed in the demonstration of apparently endogenous circannual rhythms (e.g. Berthold et al. 1972a, b; Dolnik 1974; Gwinner 1975, 1977a, b; Schwab 1971), it is both curious and unfortunate that the development of photorefractoriness has received almost no attention. Further investigations of the effect of exposure of *Z. l. gambelii* to 12L:12D are needed, because we cannot preclude the possibility that some birds in Group A became photorefractory under this regime. Such investigations are now in progress. Should any birds be proven to have become photorefractory under 12L:12D, hypotheses that implicate photorefractoriness in a simple and direct role in the induction of the postnuptial molt must be modified or adandoned.

Of the hypotheses that have emerged concerning the basic role of day length in the control of annual cycles in birds, we comment here on two: (1) Day length functions as predictive environmental information in the sense of a *driver* (e.g. Farner 1964, 1970, 1975; King and Farner 1974; Vaugien 1948; Wolfson 1959, 1966). (2) Day length functions only as a *Zeitgeber* for endogenous, self-sustaining circannual cycles (e.g. Aschoff 1955; Dolnik 1974; Gwinner 1977a, b). The first hypothesis has been developed primarily from the aspect of the neuroendocrine and endocrine components of the control system and their properties, as observed under experimental and natural conditions. The second is based extensively on formal analyses of the cycles as periodic phenomena in birds held under constant, light-dark cycles. Discussions concerning the relative merits and the extent of applicability among the

species of birds of these two hypotheses may well be clouded by multiple evolution-
ary origins of control systems with superficially similar characteristics (e.g. Farner
1950, 1964, 1975; Farner and Lewis, 1971; Menaker 1974; Farner et al. 1977), and
possibly because of the difficulty in discrimination, in at least some species, between
truly endogenous self-sustaining rhythms and annual periodicities based on control
systems with natural circannual periods but without self-sustainment (Farner and
Lewis 1973, King and Farner 1974).

The results described herein present some difficulties for both hypotheses.

Day length as driving information.—For this hypothesis, the idea of a chain of
long-day induced physiological events, including the development of endocrinolog-
ically and gametogenically active gonads, of photorefractoriness, of a postnuptial
molt with an onset that is adjustable to the termination of the reproductive effort,
and of a migration thereafter now appears excessively simple.

This hypothetical scheme, however, can be revised by specifying gonadal devel-
opment as an independent long-day effect with no role in the postreproductive events
other than the delaying effects of elevated plasma levels of sex hormones on the
onset of photorefractoriness and postnuptial molt. As noted above, the additional
hypothesis that photorefractoriness is causal to, or necessary for, the induction of
postnuptial molt is heuristically useful. Methods with which these revised hypotheses
can be tested are now available as are methods for the examination of the suggestions
or implications (e.g. Woitkewitsch and Nowikow 1936, Woitkewitsch 1940, Novi-
kov 1947, Vaugien 1948, Höhn 1950, Kobayashi 1954, Assenmacher 1958, Voit-
kevich 1962, Wagner and Müller 1963, Dobrynina 1974 and many others) that the
postnuptial (photorefractory) period is accompanied by an increase in the secretion
of thyroid hormone that, in turn, induces the molt. A definitive hypothesis must
take into account also an apparently increasing sensitivity of the feather follicles as
a function of time after the molt (e.g. Tanabe and Kasuragi 1962, Wagner and
Müller 1963).

Day length as Zeitgeber.—For various reasons we find it difficult to apply this
hypothesis to the control of annual cycles of *Zonotrichia leucophrys* for which the
evidence suggests that the control systems have intrinsic labile circannual periods
but lack the capability of generation of self-sustained rhythms (King and Farner
1974; Farner 1975; Farner and Follett 1979; D. S. Farner, R. S. Donham, R. A.
Lewis unpubl. obs.). Nevertheless, it is of heuristic value to examine the results
presented herein from the aspect of the possible role of day length as a *Zeitgeber*.
We are inclined to interpret the fluctuations in testicular size in 12L:12D, which are
generally characterized by progressively decreasing amplitudes and periods, as re-
flections of a negative feedback system with a natural circannual period in the
control system activated by the change in photoregime from 8L:16D to 12L:12D.
For the purpose of this discussion of the possible role of day length as a simple
Zeitgeber, however, we ignore the conspicuous damping of amplitude and progres-
sive shortening of period and assume that the fluctuations reflect the operation of
self-sustained circannual rhythm. In order to account for the lack of molt during
46.5 months of 12L:12D but in the presence of "testicular cycles," the hypothesis
seems to require the assumption of at least two normally coupled oscillators, either
mutually or with a common oscillator, one in the molt-control system and one in
the testis-control system. The data of Gwinner and Dorka (1976) and Gwinner
(1977c) on the relationships of the molt and testicular cycles of *Sturnus vulgaris*

subjected to "annual" photocycles of natural amplitude but of varying periods are interpretable by the assumption of the existence of two such coupled oscillators with a labile phase difference. But one must then assume further that the molt oscillator either ceases under 12L:12D or that this photoregime somehow fails to provide "permissive conditions" for its overt expression. If one assumes the former, one must then also provide an explanation of the variety of phase-angle differences between it and the testis oscillator when it is reactivated by 18L:6D. If one assumes the latter, which would seem the more probable from the aspect of the hypothesis, one is nevertheless also confronted with the necessity of an explanation of the lack, among individuals, of a constant phase-angle difference between molt and testicular development after the shift from 12L:12D to 18L:6D. Consideration must be given to the possibility that the oscillators that control the cycles of testicular development and molt are either loosely coupled or not coupled, and that active gonads, or the central function responsible for active gonads, inhibit the expression of molt.

We do not argue that these and other problems constitute a basis for outright rejection of a *Zeitgeber* hypothesis of the role of day length in the annual cycles of *Zonotrichia leucophrys*. Our application of the Law of Parsimony, however, suggests that the driver hypothesis, as modified above, provides the simpler rationalization of the results. Because, as already noted, there is growing evidence that suggests multiple evolutionary origins of the control systems of annual cycles in birds, we restrict this conclusion to *Zonotrichia leucophrys*. We also recognize the possibility that the difference between the two hypotheses may not be as great as it now appears.

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