

PHYSIOLOGICAL PREPARATION FOR AUTUMNAL MIGRATION IN WHITE-CROWNED SPARROWS

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ABSTRACT.—Termination of breeding, the development of photorefractoriness, subsequent postnuptial molt, and fat deposition precede autumnal migration in White-crowned Sparrows (*Zonotrichia leucophrys*). The timing of these post-reproductive functions differs from that of analogous vernal functions because they are neither synchronous within the population nor uniformly coincident with environmental stimuli. We hypothesize that the expressions of autumnal functions are internally coupled and that they result from a separate process initiated by the increasing vernal daylength. Our data concerning the effect of various photoregimes on testicular regression, postnuptial molt and fat deposition of *Z. l. gambelii* are consistent with the following generalizations: (1) on daylengths that exceed 16 h these processes begin after 40–60 days of photostimulation, inversely related to daylength; (2) transfer of photostimulated (20L 4D) males to an intermediate daylength of 12 h near the end of the testicular growth phase blocks the expression of autumnal functions, although their expression is not blocked if the birds are photorefractory when transferred; (3) males transferred from 12L 12D to 20L 4D in various stages of testicular development begin postnuptial molt after a fixed number of days regardless of the stage of testicular development at the time of transfer; (4) rates of postnuptial molt and fat deposition are inversely related to the daylength to which the birds are exposed when these functions occur, which may explain the acceleration of preparation for autumnal migration in late-starting individuals. Therefore, the systems that control autumnal processes appear not only to be independent of those that regulate analogous vernal processes, but also appear to rely more on internal coupling to integrate these functions than do the latter.

The physiological preparation that precedes migration usually involves several functions that require coordination—activation (spring) or inactivation (autumn) of the reproductive system, hyperphagia, and fat deposition, and usually at least a partial molt (Stresemann and Stresemann 1966, Farner and Lewis 1971, Murton and Westwood 1977, Wingfield and Farner 1980). These processes occur in a species-specific order and are temporally separated in small avian forms, although the extent of separation varies among species (Stresemann and Stresemann 1966, Payne 1972, Farner et al. 1980).

Although the mechanisms that ensure that these functions occur at the proper time and in the proper sequence have been extensively studied in the migratory races of the White-crowned Sparrow (*Zonotrichia leucophrys*), they remain only partially understood. Differences in preparation for vernal and autumnal migration under natural conditions suggest that different control mechanisms are employed in

these two seasons. Preparation for spring migration is synchronized within a population of *Z. leucophrys* wintering at a given latitude because it appears to be initiated in direct response to increasing daylength (Farner and Wilson 1957, King 1961, King and Farner 1965, Mewaldt and King 1978b). In contrast, preparation for autumnal migration is less synchronous within populations because it does not begin until the birds finish nesting. If a clutch or brood is lost, a pair may renest and delay onset of postnuptial molt, although there is a compensatory acceleration of the molt (Wingfield and Farner 1979). In addition, the decreasing daylength of late summer and autumn differs from lengthening days of spring as predictive information for fall migration (King 1963). Because of (1) lack of synchrony among individuals with the same environmental information and (2) individual differences in rate of preparation due to renesting, it seems likely that this sparrow relies on external information to coordinate its post-repro-

ductive functions somewhat less than it does for vernal functions (King and Farner 1963, Farner 1964, Farner and Follett 1979).

Differences in the expression of vernal and autumnal processes in the laboratory also suggest that White-crowned Sparrows rely more heavily on internal coupling in the fall than in the spring. The occurrence, relative timing, and sequence of each vernal function can be altered by photoperiodic manipulations (Farner and Mewaldt 1955, King and Farner 1963, Mattocks 1976). Autumnal functions, however, are expressed in the laboratory in the natural sequence after photosensitive birds have been exposed to an apparently fixed number (45–50) of long days of constant duration (King 1963, Farner 1964, Farner et al. 1980). Thus, although autumnal functions are induced by long days, they appear to differ from vernal functions in the sense that the order in which they occur cannot apparently be altered or interrupted with photoperiodic manipulations.

Four specific, complementary hypotheses have been proposed to explain how internal and external information are integrated when *Z. leucophrys* prepares for autumnal migration: (1) The expression of autumnal functions may be an autonomous process that is initiated by increasing vernal daylength and sustained by long days, and that culminates in the latent induction of late summer and autumnal functions (King 1963). This latent or remote effect of photostimulation may be independent of the induction of vernal functions (Wolfson 1958, Chilgren 1978, Farner et al. 1980). (2) The apparent inseparability of autumnal functions (e.g., Farner et al. 1980) suggests that they are induced by a single process as a working unit. (3) The high circulating levels of sex steroid hormones in late-breeding individuals may delay initiation of postreproductive functions (Payne 1972, Wingfield and Farner 1979). (4) The accelerated expression of autumnal functions in these late-starting individuals may be a direct response to shortening days (Berthold et al. 1970, Payne 1972, Gavrillov and Dolnik 1974, Rymkevich 1976, Noskov 1977, Dolnik 1980, Dolnik and Gavrillov 1980, Wingfield et al. 1980).

The results of several laboratory experiments on *Z. leucophrys* (K. S. Matt, M. C. Moore, J. C. Wingfield, and P. W. Mattocks, unpubl.) and observations under natural conditions (Wingfield and Farner 1979) are consistent with hypothesis 3. We report here the results of three laboratory experiments on *Z. l. gambelii*, the migratory race that breeds in Alaska, which support the other three hypotheses. In Experiment I, sparrows were trans-

ferred from 8L 16D to long days of various lengths to test (1) the prediction of hypothesis 1 that gonadal regression and postnuptial molt always occur as delayed effects of photostimulation on daylengths above a critical threshold and (2) the prediction of hypothesis 4 that the rate of molt is an inverse function of daylength. In Experiments II and III, we exploited the effects of intermediate daylengths, such as 12L 12D, which in *Z. l. gambelii* induce the expression of vernal, but not autumnal functions (Wolfson 1958, Chilgren 1978, Farner et al. 1980). In Experiment II, groups of males were transferred to 12L 12D before or after the onset of photorefractoriness, but before the beginning of postnuptial molt, in order to test (1) the prediction of hypothesis 2 that birds molt and fatten after they become refractory, regardless of photoperiodic manipulations, and (2) the prediction of hypothesis 4 that shorter days accelerate molt and fattening. In Experiment III, birds were transferred from 12L 12D to long days at various stages of gonadal development in order to test the prediction of hypothesis 1 that the onset of autumnal functions depends on the number of long days to which the birds are exposed, irrespective of the stage of gonadal development at the time of transfer.

MATERIALS AND METHODS

GENERAL

White-crowned Sparrows (*Z. l. gambelii*) were captured from wintering flocks in Yakima County, Washington (46°N, 120°W). Their sex was determined by laparotomy. They were placed initially in outdoor aviaries in Seattle and subsequently transferred to controlled-environment chambers where they were held two per cage (41 × 26 × 22 cm) at 22°C and 55% relative humidity. Fluorescent lamps provided at least 400 lux of illumination at floor level of each cage. Food (chick starter mash) and water were provided ad libitum.

Testicular weights were estimated visually during laparotomy by comparing the size of the left testis with a series of fixed testes of known weight. Birds were weighed periodically and examined for postnuptial molt (the "prebasic molt" of Humphrey and Parkes 1959) every three days. Each primary remex on the left wing was recorded as either old, missing, in pin, in sheath, or as a fully grown new feather. "Onset of molt" is defined as the day when the first primary remex was shed, and "duration of molt of primary remiges" as the number of days between the shedding of the first (P1) and last (P9) primary remiges.

We used nonparametric statistics in the

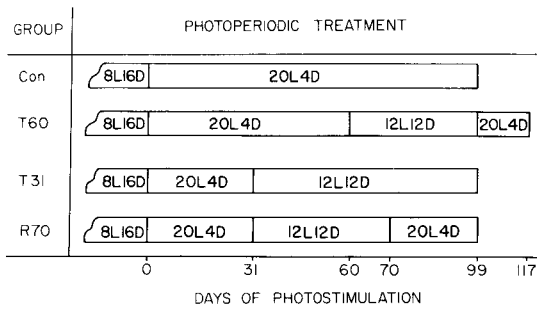


FIGURE 1. Photoperiodic treatment of the groups of *Z. l. gambelii* in Experiment II. Sample sizes: Con—five males, four females; T60—five males; T31—six males; R70—five males. Death of two control (Con) males on day 84 and two T60 males on day 79 reduced sizes of these groups thereafter.

analysis of gonadal weight and molt because our techniques produced data that were grouped into discontinuous classes. Kruskal-Wallis test, sign test, or Wilcoxon rank-sum test were also used when appropriate. However, we used linear regression and correlation analysis for means in Experiment I. Since data on the body weight satisfy the assumptions of parametric statistics, we used analysis of variance, paired *t*-test, or Student's *t*-test as appropriate.

EXPERIMENT I

This was a continuation of the experiment reported by Farner et al. (1981) in which photosensitive first-year males were held initially on a nonstimulatory photoregime (8L 16D) and later transferred to 12L 12D, 16L 8D, 18L 6D, 20L 4D, 22L 2D, 23L 1D, 23.5L 0.5D, or continuous light (LL), or were maintained on 8L 16D as controls. Data on molt and testicular development, but not on body weight, were collected at regular intervals. The loga-

arithmic testicular growth-rate constants, *k*, that appear in Table 1 were reported previously (Farner et al. 1981), but are reiterated here in a different context.

EXPERIMENT II

Adult *Z. l. gambelii* of both sexes were captured in December 1978, moved indoors on 1 February 1979 and maintained on 8L 16D. Photostimulation (20L 4D) began on 5 March 1979. Subsequent treatments of the different groups are depicted in Figure 1. One group was transferred from 20L 4D to 12L 12D after the testes had attained near-maximal size, but before testicular regression or photorefractoriness had begun. Half of these birds (Group T31, transferred on day 31) were maintained on 12L 12D thereafter to determine if molt occurred, and the remainder (Group R70, retransferred to 20L 4D on day 70) were subsequently returned to long days to test for photosensitivity. Another group (T60, transferred on day 60) was transferred to 12L 12D after testicular regression had begun and, after a period of 12L 12D identical in duration to that received by Group R70, were returned to long days to test for photosensitivity. Controls were maintained on 20L 4D for the entire experiment.

We determined testicular size, molt of primary remiges, and body weights of males at regular intervals during the experiment. Female controls were not laparotomized and only data on their molt are included in this paper.

EXPERIMENT III

First-year male *Z. l. gambelii* were captured in October and November 1978 and moved indoors on 5 December 1978, where they were held on 8L 16D. All were transferred to 12L 12D on 22 December 1978 and either main-

TABLE 1. The effect of daylength on testicular growth and on the onset and duration of postnuptial molt of primary remiges in *Z. l. gambelii* (Experiment I). Values in the table are $\bar{x} \pm SE (n)$ unless otherwise noted.

Photoregime	k^a (days ⁻¹)	Combined testicular weight on day 64 ^b (mg)	Molt of primary remiges	
			Onset ^c (days)	Duration (days)
8L:16D	0.008 ± 0.0050 (8)	—	—	—
12L:12D	0.009 ± 0.0046 (7)	—	—	—
16L:8D	0.062 ± 0.0027 (8)	164 ± 47.0 (8)	66.3 ± 2.00 (8)	28.8 ± 3.54 (8)
18L:6D	0.074 ± 0.0099 (8)	56 ± 42.0 (8)	60.0 ± 1.57 (7)	31.6 ± 1.48 (7)
20L:4D	0.079 ± 0.0074 (8)	41 ± 16.5 (8)	60.0 ± 1.37 (6)	31.3 ± 2.35 (6)
22L:2D	0.088 ± 0.0095 (8)	12 ± 2.9 (8)	56.9 ± 1.17 (8)	29.8 ± 1.31 (8)
23L:1D	0.085 ± 0.0072 (10)	32 ± 19.2 (10)	60.9 ± 0.99 (7)	36.4 ± 1.39 (7)
23.5L:0.5D	0.082 ± 0.0068 (14)	21 ± 12.4 (14)	60.2 ± 1.05 (11)	36.8 ± 2.17 (11)
LL	0.090 ± 0.0060 (14)	16 ± 8.2 (14)	58.2 ± 0.70 (11)	36.9 ± 2.70 (10)

^a Testicular growth-rate constant; values in this column are $\bar{x} \pm 95\%$ confidence limits, calculated from estimated testicular weights on day 18, 19, or 20.

^b Reported only for those photoregimes in which birds achieved maximum testicular weight on or before day 64 of treatment. Maxima in birds on the other photoregimes were reached after day 64 and consequently testicular weights on that day cannot be used to compare rates of testicular regression in those groups.

^c Days after the birds were transferred from 8L 16D to each experimental photoregime.

tained on this photoregimen (controls) or subsequently changed to 20L 4D at various stages of the testicular cycle. Past experience (e.g., Farner et al. 1980, 1981) had demonstrated that the testicular growth of White-crowned Sparrows on 12L 12D is very slow and highly variable among individuals. Therefore, it would have been meaningless to transfer birds to long daily photoperiods on a specific date because they would be heterogeneous with respect to stage of gonadal development. Hence, we randomly assigned them to five groups, each member of which was laparotomized at 10- to 40-day intervals and transferred whenever it reached a predesignated stage of testicular development. Males in Group ELP were transferred near the end on the logarithmic phase of testicular growth (testes weights about 200 mg, cf. Farner and Wilson 1957); those in Group MTW were transferred when their testes attained maximum weights (300–400 mg); those in Group MTR were transferred midway through testicular regression (testes about 50 mg); and those in Group ETR were transferred at the end of testicular regression (testes less than 10 mg). Blood samples and body weights were also taken at this time.

During their initial treatment with 12L 12D, subjects were also examined for body molt and the percentage of contour feathers growing in each feather tract was estimated. These values were first multiplied by the fraction of the total body-feather mass in that tract (which we determined by weighing plucked feathers from each tract of a male sparrow) and then summed for each individual to estimate the percentage of growing body feathers.

RESULTS

EXPERIMENT I: TRANSFER TO VARIOUS DAY LENGTHS

No molt of primary remiges occurred on either 8L 16D or 12L 12D, but on all day lengths greater than 16 h these feathers were molted in normal sequence. The following analysis is confined to those photoperiods that induced postnuptial molt. Both onset and duration of molt of primary remiges were significantly different among the groups subjected to the various daylengths ($P < 0.02$ for both, Table 1). Mean onset of molt of primary remiges was earlier on longer days (in a linear regression, $r^2 = 0.47$, $P < 0.05$, 7 df) and mean duration of molt decreased on shorter days ($r^2 = 0.66$, $P < 0.05$, 7 df). The groups also differed in the dates when primary molt ended ($P < 0.02$), but there was no linear relationship between mean termination date and daylength ($r^2 = 0.06$, $P > 0.50$, 7 df). In other words, the birds

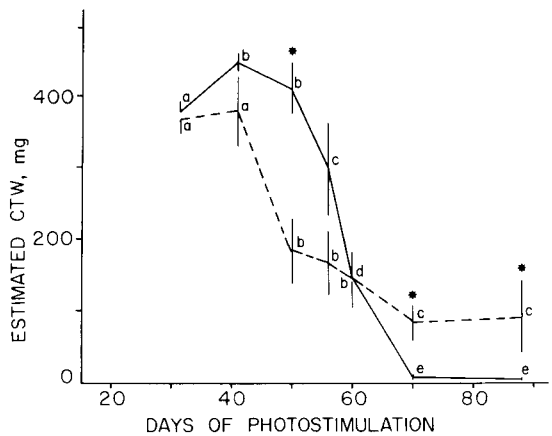


FIGURE 2. Changes in the testicular weight of male *Z. l. gambelii* retained on 20L 4D (solid line) or transferred to 12L 12D on day 31 of photostimulation (broken line) in Experiment II. Consecutive points with different superscripts are statistically different ($P < 0.01$). Asterisks indicate days on which treatment groups differed significantly. Values are $\bar{x} \pm SE$.

terminated molt more uniformly than they began it.

The groups also differed significantly in the testicular growth-rate constant, k , ($P < 0.001$, Table 1). Mean values for k were an approximately linear function of duration of photoperiod ($r^2 = 0.85$, $P < 0.001$, 7 df) for this range of daylengths (although this is not true for the entire range of daylengths; see Farner and Wilson 1957, Farner et al. 1981). The estimated combined testis weight (CTW) on day 64, after all groups had begun testicular regression, which we used as an index of the rate of testicular regression, was also significantly different among these groups ($P < 0.01$, Table 1). Mean values were a negative function of daylength (in a log-linear regression of means, $r^2 = 0.78$, $P < 0.01$, 7 df). This indicates that birds on longer days had smaller testes on day 64 and therefore their testes must have either regressed more rapidly, regressed sooner, or both.

We performed correlation analyses to determine the relationships among these variables, i.e., to determine whether systems controlling them respond independently to daylength. Correlations between k and log CTW on day 64 or onset of molt ($r^2 = 0.93$ and 0.79 , respectively) explained more of the variance than did correlations between the latter two variables and daylength. This indicates that variations in k were duplicated in log CTW on day 64 and onset of molt, suggesting further that the control systems for these three variables were responding to changes in daylength by the same mechanism. However, onset of molt was even more closely correlated with log CTW ($r^2 =$

0.85) than with k , i.e., birds that maintained enlarged testes longer also molted later. Surprisingly, duration of molt was not significantly correlated with k ($r^2 = 0.35$, $P > 0.20$), although both are approximately linear functions of daylength.

EXPERIMENT II: TRANSFER FROM 20L 4D TO 12L 12D

Gonadal cycles. Testicular weight did not differ significantly between controls and Group T60; consequently, these data are combined in Figure 2. Similarly, data from groups T31 and R70 are combined in the figure through day 70, because treatment was identical to that point; data for Group R70 after day 70 are not depicted and are reported separately below.

Combined testes weights were nearly maximal in all males on day 31 (cf. Farner and Wilson 1957, Lewis 1975b, Lam and Farner 1976). Those of controls and Group T60 continued to increase until day 41 and then decreased sharply between days 50 and 56 as photorefractoriness developed. In contrast, subjects transferred to 12L 12D on day 31 did not show further significant increases in CTW, although on day 41 it was not significantly less than the CTW of the control group ($P > 0.05$). After day 41, the testis weights of birds on 12L 12D initially decreased more rapidly than those of controls (significantly less on day 50, $P < 0.01$), but later decreased more slowly so that they were significantly higher than control weights on days 70 and 80 ($P < 0.01$ and 0.02 , respectively; Fig. 2). However, there was great individual variation among these birds on the latter two sample dates (extremes 3–250 mg).

Test for photorefractoriness. Birds in group R70 that were transferred to 12L 12D after 31 days of 20L 4D either were not photorefractory when transferred or had their photorefractoriness ended by this photoregime because CTW of all of them increased after their return to 20L 4D on day 70: from 30–200 mg on day 70 to 500 mg 18 days later. We think the latter explanation is unlikely since the three survivors of Group T60 that were returned to 20L 4D on day 99 with small testes (2, 3, and 5 mg) still had small testes 18 days later (2, 2, and 3 mg, respectively). This indicates that birds transferred to 12L 12D on day 60 were photorefractory and were still in this state 39 days later. We assume, therefore, that similar treatment did not terminate refractoriness in Group R70. Thus, it appears that the birds transferred to 12L 12D on day 31 underwent testicular development and regression, but did not become photorefractory.

Postnuptial molt. Onset of molt was the same in male and female controls (day 59–70 and

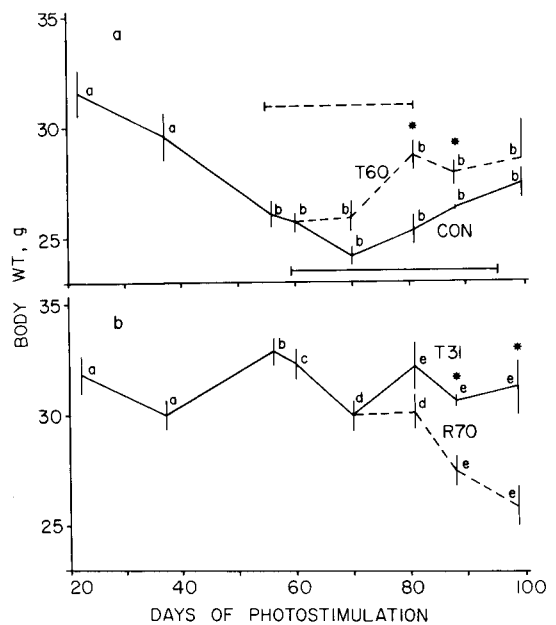


FIGURE 3. Changes in the body weight of male *Z. l. gambelii* in Experiment II. Upper panel (a): males held initially on 20L 4D and then transferred to 12L 12D on day 60 (broken line) or retained on 20L 4D (solid line). Horizontal lines indicate range for duration of molt of primary remiges. Lower panel (b): males transferred from 20L 4D to 12L 12D on day 31 and either retained on 12L 12D (solid line) or transferred back to 20L 4D on day 70 (broken line). Subscripts and asterisks have the same meanings as in Figure 2. Values are $\bar{x} \pm SE$.

day 59–73, respectively, $P > 0.50$). Duration of molt was also the same in the two sexes (22–29 days in males and 22–26 days in females, $P > 0.50$). Therefore, these data are pooled in the comparisons that follow (cf. Morton et al. 1969, Lewis 1975a, Chilgren 1978).

All males in Group T60 molted the primary remiges in the normal sequence (cf. Morton et al. 1969) when exposed to 12L 12D. The onset of this molt (day 57–66; one bird began to molt before transfer) was not statistically different from that of the controls ($P > 0.50$), but its duration was significantly less than in the controls on 20L 4D (6–15 days vs. 22–29 days, respectively, $P < 0.001$). Individuals in both groups began molting in the same order that they began testicular regression ($P < 0.05$, Kendall's coefficient of rank correlation).

None of the birds in groups T31 and R70 molted after the transfer to 12L 12D, even though by day 70 seven of 11 had CTW below 50 mg, the threshold assumed to be permissive for molt (Morton et al. 1969, Lewis 1975a). In other words, those transferred before photorefractoriness began (Groups T31 and R70) did not molt on 12L 12D, in contrast to those transferred after they became refractory (Group T60).

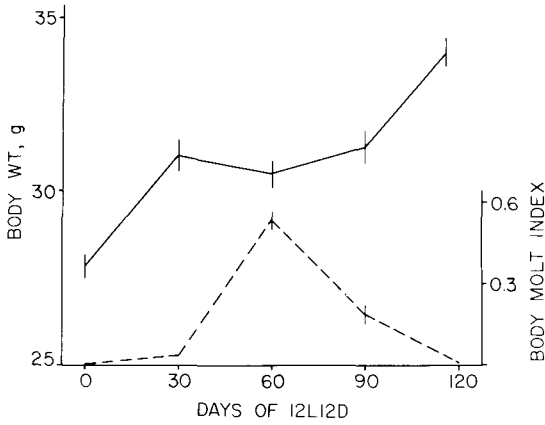


FIGURE 4. Body weight (solid line) and index of body molt (broken line) of *Z. l. gambelii* in Experiment III during the first 120 days after they were transferred from 8L 16D to 12L 12D ($n = 59$). Values are $\bar{x} \pm SE$.

Body weight. Data are combined for controls and Group T60 prior to day 60 and for groups T31 and R70 prior to day 70, both in Figure 3 and for statistical analysis, since treatments prior to those days were identical (Fig. 1).

Body weights of all birds were near-maximal on days 21 and 37, as a result of photoperiodically induced premigratory fattening (cf. King 1961, 1963, King et al. 1965). Control birds and those in Group T60 lost weight sharply between days 37 and 56 (Fig. 3a) as they presumably ended migratory hyperphagia. In contrast, subjects transferred to 12L 12D on day 31, while their weights were still high, did not show a subsequent sharp decrease in body weight (Fig. 3b). Despite several significant fluctuations in weight thereafter, they averaged 4–6 g heavier than controls for the remainder of the experiment ($P < 0.001$ on days 56–88; $P < 0.05$ on day 99). However, body weights of birds in Group R70 decreased to levels of controls after they were returned to 20L 4D on day 70 (Fig. 3b) and were significantly less than those of birds in Group T31 which remained on 12L 12D ($P < 0.01$ on days 88 and 99). Thus vernal premigratory fattening and hyperphagia persisted in birds on 12L 12D unless they were returned to long days.

The weights of control birds and those in Group T60 did not change significantly after day 56, but the progressive increase beginning late in molt likely represents the onset of autumnal premigratory fattening (cf. King 1963, King et al. 1965). Birds in Group T60 were significantly heavier than controls on days 81 and 88 ($P < 0.05$ on both days), indicating that autumnal fattening began sooner in birds transferred to 12L 12D, consistent with their more rapid molt.

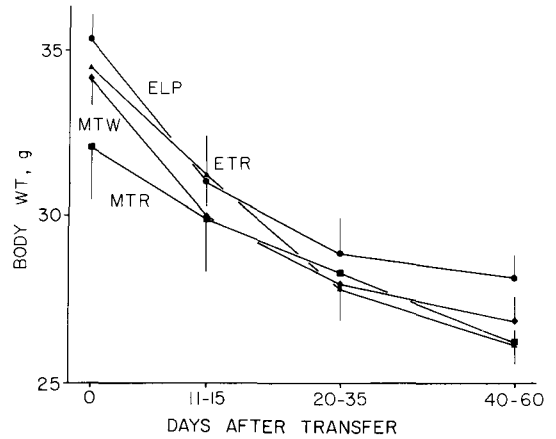


FIGURE 5. Changes in the body weight of *Z. l. gambelii* transferred from 12L 12D to 20L 4D at different stages of testicular development in Experiment III. ELP—birds transferred at the end of the logarithmic phase of testicular growth, $n = 8$ (circles); MTW—at maximum testicular weight, $n = 11$ (diamonds); MTR—midway through testicular regression, $n = 15$ (squares); ETR—at the end of testicular regression, $n = 8$ (triangles). Symbols are means; vertical lines are SE; the latter are not shown where they overlap.

EXPERIMENT III: TRANSFER FROM 12L 12D TO 20L 4D

Molt. All subjects underwent an apparently normal prenuptial molt after 30–120 days of exposure to 12L 12D (Fig. 4). None molted any primary remiges until transfer to 20L 4D (Table 2). Neither onset nor duration of molt of primary remiges differed significantly among the groups transferred to 20L 4D at different stages of gonadal development ($P > 0.90$ for both parameters). Combining and comparing these data with those from birds in Experiment I that were transferred from 8L 16D to 20L 4D (Table 2), reveals that those in Experiment

TABLE 2. The effect of transferring *Z. l. gambelii* from 12L 12D to 20L 4D at various phases of the testicular cycle on the onset and duration of postnuptial molt of the primary remiges (Experiment III). Values in the table are $\bar{x} \pm SE$.

Stage of testicular development at transfer	n	Molt of primary remiges	
		Onset (days after transfer)	Duration (days)
End of logarithmic growth (Group ELP)	9	48.7 \pm 1.3	34.1 \pm 2.3
Maximum weight (Group MTW)	6	48.7 \pm 0.6	31.0 \pm 1.8
Midway through regression (Group MTR)	11	47.6 \pm 1.7	31.6 \pm 2.3
End of regression (Group ETR)	5	49.0 \pm 1.6	30.4 \pm 1.4

III began to molt sooner ($P < 0.001$), although the duration of molt in the two experiments was not significantly different ($P > 0.50$).

Body weight. We combined the data on body weight of all groups for the first 120 days of the experiment since all were exposed to 12L 12D until then (Fig. 4). Body weight increased significantly by day 30 of exposure to 12L 12D, remained at this level until the birds finished molting, and then increased again. It did not decrease until the birds were placed on 20L 4D, whereupon it decreased sharply in all groups (Fig. 5).

Body weight did not differ significantly among the groups on any post-transfer day ($P > 0.20$). Therefore, we pooled the data and found that the decrease in body weight following transfer was highly significant ($P < 0.001$). This response paralleled that of birds in Group R70 of Experiment II, which also maintained heavier weights on 12L 12D until returned to long days (Fig. 3).

DISCUSSION

The foregoing data strongly support our first hypothesis, i.e., that the expression of autumnal functions is a remote consequence of vernal photostimulation. Birds in Experiment I became photorefractory and began postnuptial molt after being subjected to an apparently *fixed number of long days* of constant duration, although the number of days required varied inversely with daylength (cf. Harris and Turek 1982). As predicted by this hypothesis, the number of long days required to induce postnuptial molt was independent of the stage of testicular development at the time of transfer to long days (Experiment III). Two mechanisms have been proposed to explain this remote effect of photostimulation: (1) vernal photostimulation initiates an endogenous annual rhythm that is not self-sustaining and that must be "reset" each year by exposing the birds to short days (King 1968, Farner and Lewis 1971, 1973, Gwinner 1972) or (2) the birds count the number of long days, sum the daylength, or both (Evans 1970, Dolnik and Gavrilov 1972, Gavrilov and Dolnik 1974, King and Mewaldt 1981). This latter possibility is consistent with our observations (1) that longer days advanced the onset of autumnal functions in Experiment I, (2) that pre-treating birds with 12L 12D advanced the onset of autumnal functions by about 10 days in Experiment III as compared to their onset in those birds transferred directly from short to long days in Experiment I, regardless of the duration of the pretreatment, and (3) that birds did not express these autumnal functions on shorter days unless they were first exposed to

at least 31 long days. A further possible mechanism, that daylength entrains a self-sustaining endogenous rhythm of autumnal functions (Dolnik 1974, Gwinner 1975, Sansum and King 1976, Farner et al. 1980, Farner and Gwinner 1980) does not seem likely because these functions were not expressed repeatedly when *Z. l. gambelii* were kept on constant conditions for long periods (Sansum 1974, Farner et al. 1980).

Our data also support our second hypothesis, i.e., that autumnal functions are *internally coupled*. The hypothesis would have been disproven if the birds in Groups T31 or R70 in Experiment II had molted since they did not become photorefractory. The fact that these birds did not molt and the finding that birds in Group T60 molted on a nonstimulatory photoregime after they became photorefractory are both consistent with predictions of this hypothesis. However, it is also possible that the control systems for molt and refractoriness respond independently to long days. Nevertheless, the correlations between timing of gonadal regression and onset of molt noted in individual birds in Experiment II and across treatment groups in Experiment I suggest that these functions are tightly coupled. The finding that *Z. l. gambelii* maintained on 12L 12D for long periods did not undergo postnuptial molt and failed to become photorefractory also supports this hypothesis (Farner et al. 1980; R. S. Donham, M. C. Moore, and D. S. Farner, unpubl.). Thus, in studies to date, these sparrows have not been found to undergo postnuptial molt without first becoming photorefractory.

Although autumnal processes have a long-day requirement, they appear to occur at rates that are inverse functions of daylength. Thus in Experiment I, molt proceeded more rapidly on shorter days. Birds molted at the same rate when exposed to 20L 4D in both Experiments I and III, even though their previous photoperiodic treatments were very different. Molt occurred most rapidly on 12L 12D in Experiment II, primary remiges being shed so rapidly that flight was impaired. Subjects in this group also fattened more rapidly than birds on 20L 4D. In Chaffinches (*Fringilla coelebs*) treatment first with long days and then with shorter days also accelerated molt (Gavrilov and Dolnik 1974, Noskov 1977, 1978, Dolnik 1980). Similar results have also been obtained with other passerine species (Rymkevich 1976; for summaries, see Assenmacher 1958, Stresemann and Stresemann 1966, and Berthold et al. 1970).

Acceleration of both molt and fattening in response to shortening days of late summer

would be adaptive for those birds in which these functions are delayed by reneating, if it results in their being prepared to migrate at the normal time (Berthold et al. 1970, Payne 1972, Wingfield and Farner 1979, Dolnik and Gavrilov 1980). It would be especially important in forms, such as *Z. l. gambelii*, that nest in harsh northern environments with short summers. In the more southern races of White-crowned Sparrows (*Z. l. pugetensis* and *Z. l. nuttallii*), the duration of postnuptial molt appears to be controlled by genetically fixed programs that are unaffected by daylength (Mewaldt and King 1978a). Differences in the photoperiodic control of molt have also been noted among different populations of *F. coelebs* (Dolnik and Gavrilov 1972, Gavrilov and Dolnik 1974, Dolnik 1975, 1976, 1980, Noskov 1975, 1977).

The relatively few data that we collected on vernal functions are consistent with the hypothesis that they are at least relatively *independent* events that are synchronized by differential photoperiodic responses (King and Farner 1963, King 1968). Prenuptial molt precedes vernal fattening in nature (King 1968), but followed it in birds held on 12L 12D in Experiment III. Controls in Experiment II on 20L 4D apparently did not undergo prenuptial molt (since they retained the brown and tan head pattern of first-winter birds until postnuptial molt), although they fattened. These observations and those of Farner and Mewaldt (1955), King (1961), King and Farner (1963), King (1968), and Mattocks (1976) demonstrate that, unlike the autumnal functions, vernal functions can be induced separately, can be easily uncoupled via photoperiodic manipulations, and can be elicited in different sequences.

Furthermore, our data support the hypothesis that vernal and autumnal functions are induced independently (Farner et al. 1980, Farner and Gwinner 1980). Since a photoperiod of 12L 12D initiated gonadal growth, vernal fattening, and prenuptial molt, but failed to cause postnuptial molt or refractoriness (Experiment III), autumnal functions appear to require longer days for their induction than do vernal functions. Even when the latter were induced by long days in Experiment II, the birds did not undergo autumnal functions later, when transferred to 12L 12D near the end of the gonadal growth phase. Vernal hyperphagia persisted in both Experiments II and III as long as birds were maintained on 12L 12D, but disappeared when they were shifted to long days. Therefore, it is possible that termination of this process in the spring requires days in which the photoperiod exceeds 12 h.

In conclusion, we propose that daylength independently controls at least four phases of the annual cycle of *Z. l. gambelii*: (1) Increasing daylengths in late winter induce directly the vernal functions—gonadal development, prenuptial molt, migratory fattening and migration. (2) Subsequently, they also induce a separate autonomous process that eventually induces the internally coupled sequence of late-summer and autumnal events—development of photorefractoriness, postnuptial molt, and migratory fattening. (3) The decreasing daylengths of late summer accelerate the late-summer and autumnal events inversely with the daylength that exists when these events occur. (4) Short days terminate photorefractoriness (for review, see Wingfield and Farner 1980).

Since control mechanisms for annual cycles appear to be of multiple evolutionary origin, it is not surprising that no single model has been proposed that satisfactorily explains these mechanisms in all species of birds (e.g., Farner and Follett 1979). Although our results are generally consistent with those on Chaffinches (Dolnik 1976, Noskov 1977), other species appear to rely more heavily on non-coupled endogenous circannual periodicities than does the White-crowned Sparrow (Farner and Gwinner 1980). We have proposed that autumnal functions in this species are coupled because they always occur in a specific order after breeding ends and because the latter is not synchronous within a population and therefore is not uniformly coincident with any environmental stimuli. Vernal functions are not internally coupled, or are easily uncoupled, either because selection pressures for strong coupling similar to those in autumn do not exist, or for some as yet unidentified selective advantage of weak coupling or non-coupling. Nevertheless, if the degree of internal coupling and reliance on external information varies between seasons within a single species in response to different selection pressures, then analogous differences in selection pressures may account, at least in part, for the interspecific differences in the mechanisms that control annual cycles.

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RECENT PUBLICATIONS

The molt of Scrub Jays and Blue Jays in Florida.—G. Thomas Bancroft and Glen E. Woolfenden. 1982. *Ornithological Monographs* No. 29, American Ornithologists' Union, Washington, DC. Paper cover. 51 p. \$8.00 (\$6.50 to AOU members). Source: Assistant to the Treasurer of the AOU, Dr. Glen E. Woolfenden, Dept. of Biology, University of South Florida, Tampa, FL 33620. In the study of molt, one of the basic questions concerns its temporal relationship to other events in the annual cycle. To address that question, Bancroft and Woolfenden investigated the schedule of molts in two species of jays in a subtropical region. All of the Scrub Jays examined were already banded, and most were of known age, sex, and breeding status. This information permitted a much more detailed analysis than is customary in such studies. The monograph describes and compares the molts of the two species, and estimates the metabolic costs of feather growth. It discusses the evolutionary and ecological factors that appear to be responsible for the differences in molt schedule between the species. The separation of molt and breeding in these jays seems to be due to a combination of temperature and water regulation and perhaps flying efficiency, more than energy requirements. A valuable contribution to understanding the physiological adaptations for molt. Graphs, references.

The Effect of Weather on Avian Mortality.—James A. Gessaman and Gary L. Worthen. 1982. Utah State University. 173 p. Paper cover. \$12.00 from the senior author, UMC 53, Logan, UT 84322. This bibliography was garnered "from a systematic perusal of the indexes of ornithological journals, *Wildlife Reviews* and *Biological Abstracts*, and from the bibliographies of articles." Nowhere in the volume is there a list of the sources reviewed. Aside from the title, the criteria for selection of an article for inclusion are unexplained. As a result, some titles known to this reviewer from major journals that would seem to apply, could not be found. Color-coded pages identify the separate indexes for key words, author/co-author, year of publication, geographic location, and species. Best suited for the researcher seeking a quick answer to a specific question.—J. Tate.

Care and Rehabilitation of Injured Owls, Second edition.—Katherine McKeever. 1980. Published by W. F. Rannie for the Owl Rehabilitation Research Foundation, Vineland, Ontario, Canada. 112 p. Paper cover. \$12.00 prepaid. Source: W. F. Rannie, P.O. Box 700, Bearnsville, Ontario, Canada L0R 1B0. This practical manual is based on the experience of the author and her husband over 15 years in developing a facility for the treatment of injured raptors and the breeding of unreleasable owls in Ontario. The first part, which is more or less applicable to all raptors, deals with the manipulation of the injured bird itself, from capture and examination through treatment, convalescence, and release. The second part, which applies to owls, describes the facilities and procedures needed for pre-release training or captive breeding. Beyond basic instruction, the book discusses some of the problems faced in evaluating and managing injured birds, and explains why certain practices are recommended. The text is abundantly illustrated with useful photographs and building plans. Having treated more than 1,000 injured hawks and owls, the McKeever's know what they are talking about—and more than many academic ornithologists. Their manual should be on the reference shelf of every veterinarian, wildlife agency, nature center or other institution that cares for injured raptors.

A Natural Collection.—Steven C. Wilson and Karen C. Hayden. 1981. Entheos, Bainbridge Island, Washington. Paper cover. \$10.00. Source: National Audubon Society, 950 Third Ave., New York, NY 10022. Photographs, some of them stunning, all of them unusual, highlight the Aransas National Wildlife Refuge, the Padre Island National Seashore, and adjacent areas of the Texas coast. Indeed, this small-format volume is meant to be displayed and enjoyed. The book views the works of man as acceptable, even desirable. There is no mention in the text that publication was underwritten by Conoco, Inc., which has produced petroleum in the Aransas Refuge since 1947—a period during which the Whooping Crane population increased from 31 to 76. The acknowledgments, the notes on the photographs, and the phototitles, are creatively written, producing an empathy with the pleasures and hardships felt by the author-photographers.—J. Tate.