PREMIGRATORY CHANGES IN BODY WEIGHT AND FAT IN WILD AND CAPTIVE MALE WHITE-CROWNED SPARROWS

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It is now well established that migratory birds of many species develop large reserves of fat just prior to migration and maintain or periodically replenish these reserves during the migratory period. Indeed, in these species one of the most obvious criteria of the preparedness for migration in spring and fall is the sudden increase in the level of fat reserves. It is perhaps of special significance that sedentary species do not exhibit any analogous autumnal or vernal adiposity, thus emphasizing that intensive fat deposition is an event definitely associated with the migratory habit and presumably a major sign of the metabolic preparation for migration. This contrast has been especially well described for migratory and sedentary forms of *Junco* (Wolfson, 1942), *Fringilla* (de Bont, 1947; Koch and de Bont, 1952), and *Zonotrichia* (Linsdale and Sumner, 1934; Blanchard, 1941; Wolfson, 1945; Odum and Perkinson, 1951). The literature on the phenomenon of premigratory fattening in general has been reviewed by Wachs (1926), Wolfson (1945, 1952), Steinbacher (1951), Schüz (1952), Farner (1955), and Dorst (1956). It would appear that investigation of the external factors and internal mechanisms which initiate and maintain migratory fattening may be a profitable approach to an understanding of the basic physiologic processes in the regulation of migration itself. This paper summarizes some data obtained during the preliminary phases of investigations utilizing this approach. As a primary step in these investigations it was desirable to obtain a quantitative description of the seasonal changes in body weight and body fat in the wild population of White-crowned Sparrows from which the experimental birds were to be obtained. A logical secondary step then consisted of a comparison of the pattern of premigratory fattening in the wild birds and in the captive experimental birds exposed out of doors to natural conditions of temperature and photoperiod. Obviously, if captivity seriously distorts or suppresses the normal response, then the results of experimental studies of premigratory fattening are meaningless in the interpretation of the events which occur under natural conditions. It was our initial objective to determine whether such limitations exist.

MATERIALS AND METHODS

White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) were captured in Japanese mist nets from overwintering populations in the Snake River canyon a few miles south of Pullman, Washington. This population was sampled in the spring until the first week of May, when all birds had vacated the wintering grounds. Captive birds were weighed immediately in the field and those intended for body fat determinations were killed and frozen. Permanent records were made concerning the status of molt and the behavior of the birds in the field. All field data were collected between 11 a.m. and 5 p.m. Experimental birds were returned to the aviaries at Pullman and confined individually in small cages (22 × 41 × 26 cm.) in an isolated outdoor enclosure. Unless otherwise indicated, the phrase "captive birds" refers to males confined out of doors in these cages. The birds were fed *ad libitum* on a nutritionally adequate chick-starter mash and were weighed at regular, predetermined intervals. Fresh water was always available. Rigorous efforts were made to assure that the birds were disturbed to a minimum extent. Laboratory personnel were in the aviary for only a few minutes daily and the birds were not handled or moved except at 7-day intervals (4 days in 1956) when the cages were cleaned, the body weight determined, and the status of molt, if any, examined. The total ether-soluble lipid in the body was determined by the procedure described by McGreal and Farner (1956). The results are expressed in terms of a *lipid index,* which denotes the percentage of the body weight composed of ether-extractable fat, and in terms of the *lean body weight* (= fat-free body weight).

RESULTS AND DISCUSSION

Wild birds.—Data obtained from 114 wild males are shown in table 1 and in figures 1 and 2 (lower panel). It is evident that fat deposits decline from a midwinter high and are progressively reduced during the prenuptial molt, attaining a vernal minimum in the period between March 20 and April 10. In mid-April, as the intensity of molt declines, there is apparently a sudden alteration of physiologic status which results in a very intensive storage of fat. Within about 10 days at the end of April the *average* lipid index is more than doubled. For certain individuals this change is even more spectacular, as is suggested by observation of change in weight of captive birds.

Table 1

Variation in Total Weight, Lean Body Weight, and Lipid Index in Male *Zonotrichia leucophrys gambelii* in Late Winter and Spring

Period	Number of birds	Lipid index Mean	Lipid index SD	Body wt. (gms.) Mean	Body wt. (gms.) SD	Lean weight (gms.) Mean	Lean weight (gms.) SD
1. Winter							
1–10 January	2	10.8	......	27.3	......	24.4	......
11–20 January	8	9.8	2.7	27.6	0.8	24.9	0.4
11–20 February	8	7.9	1.4	27.2	0.8	25.0	0.8
2. Prenuptial molt							
1–10 March	8	6.7	0.9	27.6	0.8	25.8	0.8
11–20 March	18	6.0	1.0	28.0	2.1	26.3	1.9
21–31 March	3	6.3	0.5	28.7	1.1	26.9	1.1
1–10 April	23	6.0	0.9	28.4	2.4	26.6	2.2
11–20 April	6	6.7	1.7	27.8	1.2	25.9	0.9
3. Premigration and migration							
21–30 April	32	13.8	5.2	29.2	3.1	25.2	1.5
1–10 May	6	20.2	4.0	32.1	1.8	25.6	0.8

Our data are similar to those obtained by Odum and Perkinson (1951) for the White-throated Sparrow (*Zonotrichia albicollis*) in Georgia. The mean lipid indices for male White-throated Sparrows in several phases of the annual cycle were: midwinter, 12.4; prenuptial molt, 5.6; premigration, 17.2. The premigratory fat deposition was likewise accomplished in 7 to 10 days, beginning in mid-April.

Our data on total weight also agree within about one gram (5 per cent) with those reported by Blanchard and Erickson (1949) and Oakeson (1953) for *Z. l. gambelii* in California and Alaska. These authors also report that the premigratory fattening occurred within about 12 days before departure from the wintering grounds, which began during the second week of April.

A question of considerable interest to us concerns the validity of utilizing variation in total weight as an index of variation in the fat content of the body. Examination of figure 1 will reveal that body weight and lipid index do not vary seasonally in strict proportion to one another. This is the result of concomitant seasonal change in the lean body weight, which begins to increase slowly at the onset of prenuptial molt, attains a maximum during the period of most intense molt, and then declines to approximately its previous value as the molt ceases. Although the mean values of lean body weight for the

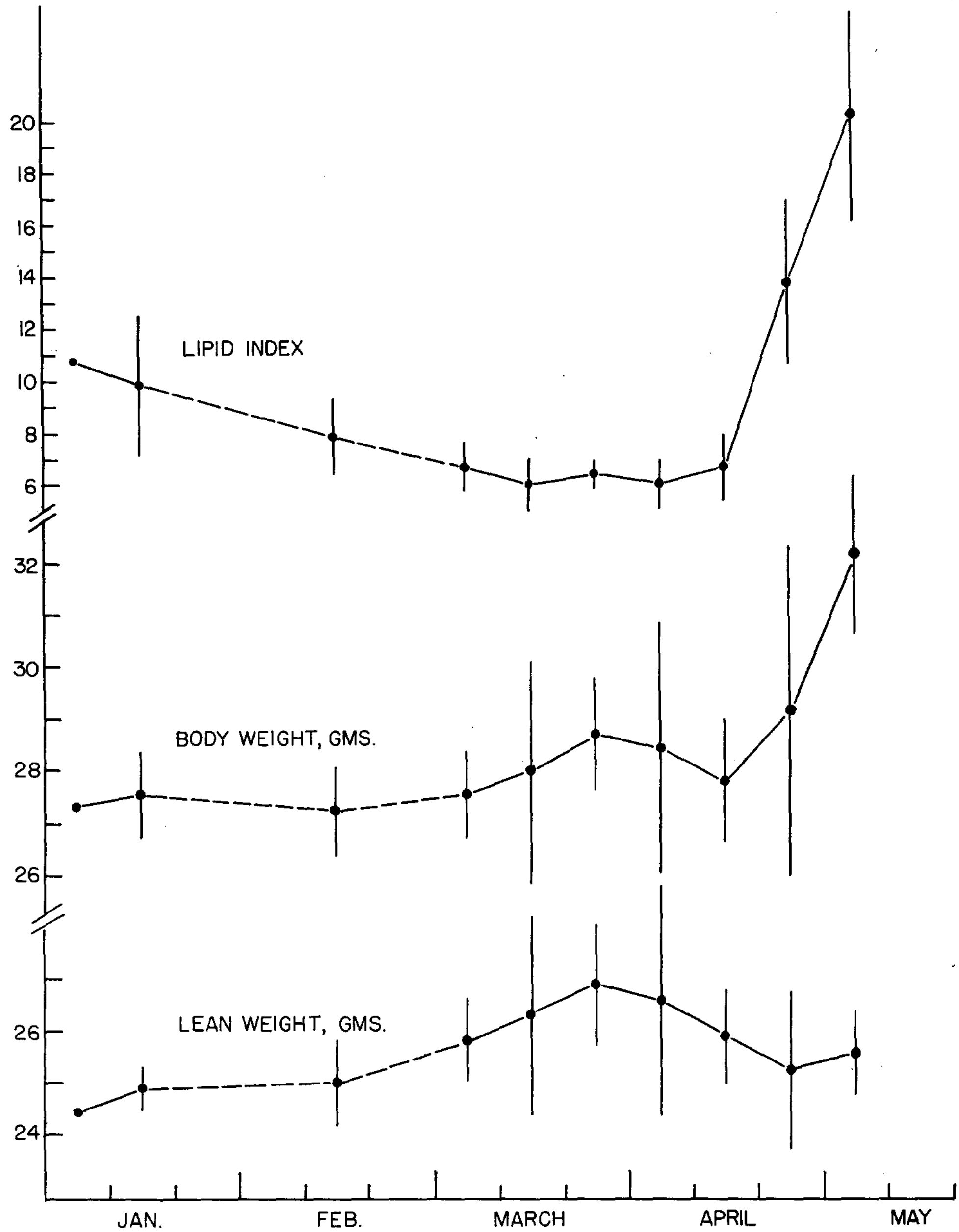

Fig. 1. Variation in mean values for total body weight, lean body weight, and lipid index in wild male *Zonotrichia leucophrys gambelii* in 1952-1953, summarized by 10-day intervals. Vertical bars show the standard deviation of the mean.

intervals shown are not statistically different at the 5 per cent level, the existence of a consistent trend is superficially clear and seems too regular to result from random variation. Furthermore, the close correlation of prenuptial molt and the increase in non-lipid components of the body suggests that the two events share a functional basis. It is feasible that the increase in lean weight results from change in fluid balance and increased storage and turnover of materials required in the keratin synthesis of feather production. We should point out, however, that the data of Odum and Perkinson (1951) on *Zonotrichia albicollis,* although presented somewhat differently than ours, do not reveal any maximum of lean weight during the prenuptial molt. Obviously, additional data are needed before it will be possible to assert definitely whether or not an increase in lean body mass is a normal concomitant of prenuptial molt.

Although the variation in lean body weight described above makes it improper to employ change in total weight as a strict quantitative index of change in fat content, it is evident that this index is entirely adequate for detecting the inception and describing the temporal pattern of premigratory fattening. We have used this procedure in the study of vernal fattening in captive birds.

Captive birds.—Because of the necessity for economy in the use of captive birds, it was not feasible to obtain lipid indices throughout the season. Accordingly, our data relating to premigratory fattening in captive birds consist principally of values for total weight. We also present, however, a few data on the lipid index and lean weight of captive birds sacrificed at the peak of fat deposition.

Table 2

Comparison of Weights of Wild and Captive Male *Zonotrichia leucophrys gambelii*

	Weight of captives		Comparison with wild birds	
Period	Mean	SD	Capt.-wild[1]	Capt./wild[2]
March 1–10	25.9 gm.	1.2	−1.7 gm.	93.9
March 11–20	25.5	1.0	−2.5	91.1
March 21–31	26.2	1.0	−2.5	91.2
April 1–10	26.4	0.8	−2.0	93.0
April 11–20	27.5	2.2	−0.3	99.0
April 21–30	30.2	3.2	+1.0	103.5
May 1–10	32.7	2.2	+0.6	101.9

[1] Difference between means.
[2] Mean weight of captives as a percentage of mean weight of wild birds.

Table 2 compares data from wild and captive birds in 1952–1953. It is evident that during the winter the wild birds are heavier than the captives by an average of about 2 grams. It should be emphasized that we refer here to captives confined to small cages. The difference is smaller (usually less than one gram) if the comparison is made between wild birds and captives kept in large aviaries ($4 \times 2.7 \times 2$ meters) with much flight space (Farner and Wilson, 1957:263). This suggests that the smaller body weight seen in captives may be a function of exercise, with the restriction of exercise by small cages resulting in a decrease in muscular mass. This suggestion is supported by our data on lean body weight of birds confined under different conditions. For 24 males confined out of doors in small individual cages, these data averaged 24.5 grams in late April and early May of 1953–1954. Still greater reduction in lean body weight has been found in experimental male birds confined in small cages indoors. For instance, the mean lean body weight for 24 males subjected to several different daily photoperiods was 23.5 grams at the termination of the experiments. By comparison, the mean lean weight for 38 *wild* males in the period from April 20 to May 10 was 25.5 grams, or one gram more than for birds confined outside and two grams more than the heterogeneous group of experimentals. All the captive birds mentioned had been in captivity for 4 to 9 months. The duration of captivity was more or less randomly distributed among the various groups of birds mentioned and is not a factor in these comparisons.

It appears from the foregoing that the low body weight observed in late winter in birds confined to small cages out of doors is the result in part of a decrease in the lean weight of the body. However, the average lean weight of captives is approximately only one gram less than that of wild birds, whereas the total body weight of the captives is about *two grams* less than that of wild birds. To account for this difference we must infer that wild birds are slightly fatter than captives during the late winter and early spring. Immediately before migration (April 15–May 10), however, this condition is gradually reversed so that the mean body weight of captives is slightly greater than that of wild birds (table 2). The mean lipid index of 24 captive males sacrificed during this period in 1953–1954 was 26.0. This may be compared with a mean of 20.2 for the wild population during a similar period of 1952–1953.

With regard to the temporal characteristics of vernal fattening in captive birds as compared with wild birds we may note the following. In the wild population in 1952 and 1953, premigratory fat deposition was a very rapid event beginning in the interval from April 11 to 20. The timing and magnitude of the change are most clearly shown in the lower panel of figure 2, where individual data for the lipid index are plotted. A curve drawn through these data would show a strong upward inflection between April 15 and 20. Accordingly, we might select April 18 as a representative, arbitrary date for the onset of vernal fattening. Comparison with the captive birds can be made only on the basis of variation in total weight, individual plots of which are shown in the upper part of figure 2. Although some relatively minor quantitative differences are apparent between the two years, we submit that a curve drawn through these data would exhibit an inflection nearly coincident with that for the wild population. Within the limits of our data it appears that confinement out of doors in small cages does not appreciably affect the timing of fat deposition.

A very interesting temporal feature of vernal fattening is its relatively high precision, both in successive years and among individuals within a given year. We employ the term "precision" here in the statistical sense denoting variance from a central datum, without implication as to the magnitude of variance. Although most of our data on seasonal variation in weight in captive birds were not obtained at sufficiently short intervals to permit a rigorous analysis of temporal precision, they do enable us to make a preliminary appraisal of this. The annual variation in the timing and pattern of vernal fattening is shown in the lower panel of figure 3, where the data on body weight are plotted as deviations from the minimum observed weight in order that all data might be readily shown on a short scale. It is apparent from inspection of this figure that the mean date of inception and the mean rate of development of the fat reserves were very similar during the five years indicated. We have obtained an estimation of the initial date of heavy fat deposition in individual birds by accepting as the most probable date of inception the median date of the four- to seven-day period during which definite fattening was first observed.

By averaging such dates for all the individuals a representative date for the year is obtained. For the period considered in this paper, these dates are: April 19, 1952, April 21, 1953, April 20, 1954, April 17, 1955, and April 13, 1956. For the five years combined, fat deposition began, on the average, on April 19 (57 birds), with a total variation (which was also equal to the standard deviation) of ± 8 days. Ninety-one per cent of the dates fell within the span of April 10 to 20.

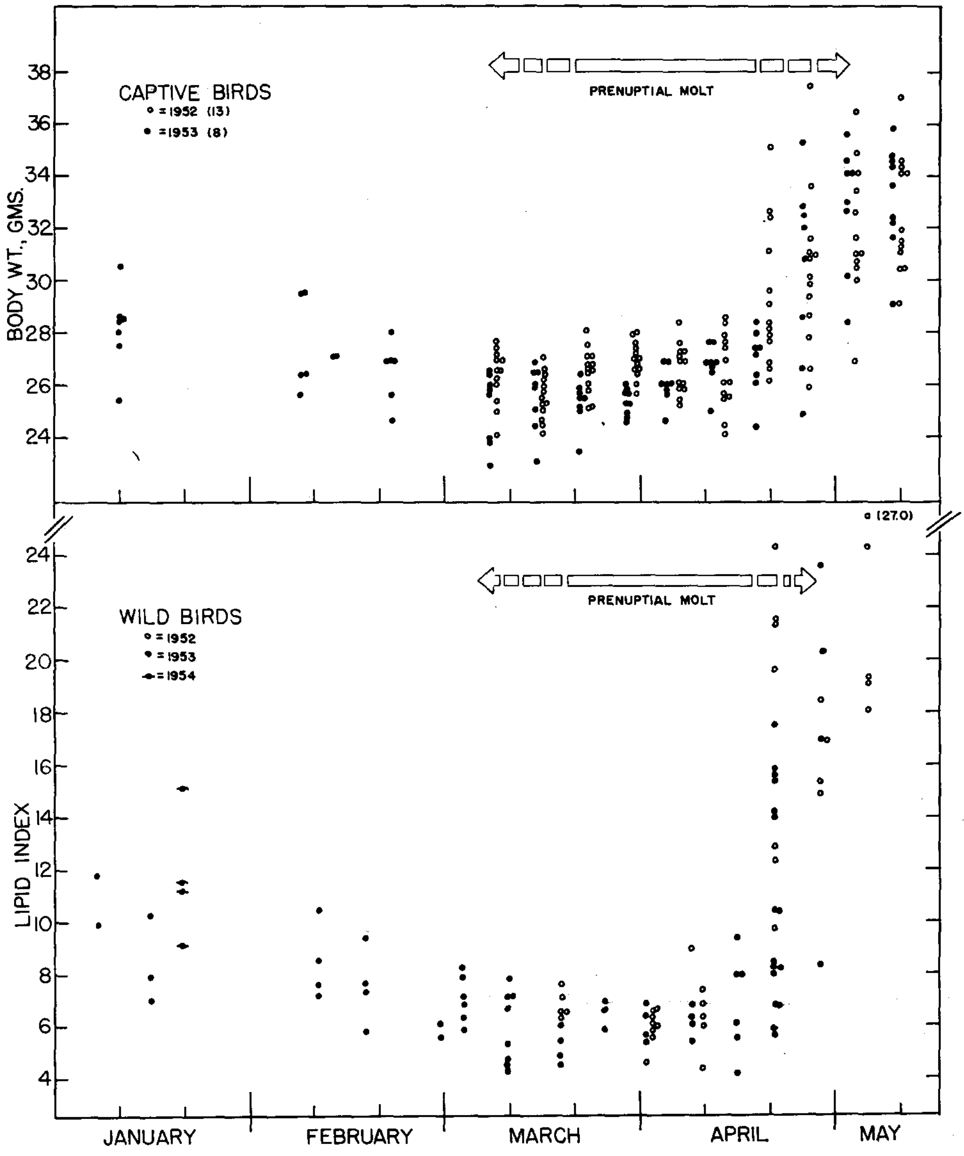

Fig. 2. Individual data on variation in lipid index (wild birds) and body weight (captives, confined out of doors) in male *Zonotrichia leucophrys gambelii*.

We cannot detect any consistent or definite pattern of relationship between the schedule of vernal fattening and the prevailing weather condition. These conditions were highly variable at Pullman during the five years of the study. Mean environmental temperature in March varied from 45 per cent to 118 per cent of normal (based on a 40-year mean); April averages varied from 57 per cent to 121 per cent of the normal. Precipitation in March varied from 38 per cent to 116 per cent, and 11 per cent to 146 per cent in April. It could be argued that the early date (April 13) in 1956 was influ-

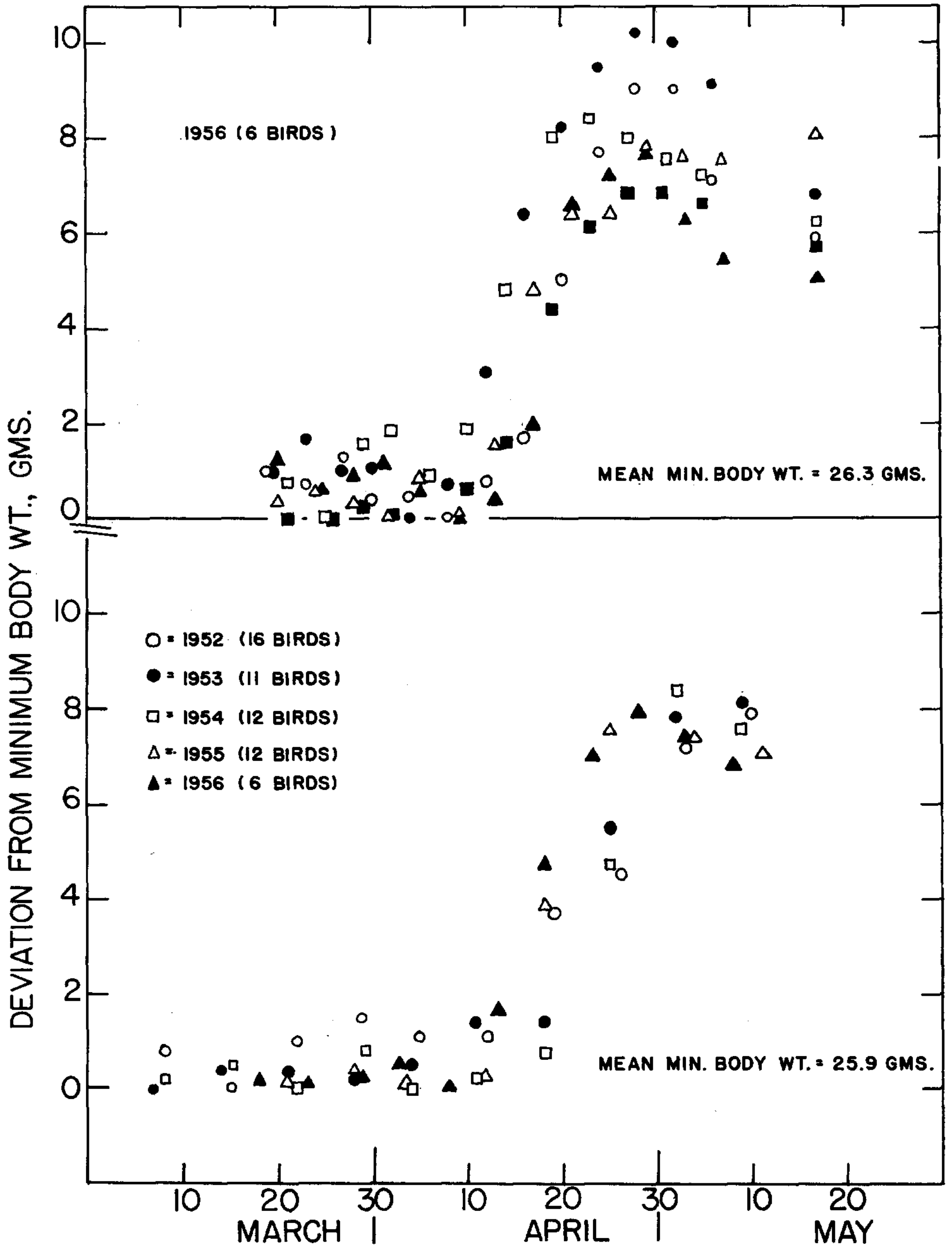

Fig. 3. Upper panel: variation in body weight among individual captive male *Zonotrichia leucophrys gambelii* in 1956; individual data are plotted by four-day intervals. Lower panel: variation in mean body weight in captive male *Z. l. gambelii* confined out of doors. Mean values for the annual groups are plotted by seven-day intervals (four-day intervals in 1956).

enced by warm (114 per cent of normal) and dry (11 per cent of normal precipitation) weather in April. The next earliest index date for the onset of vernal fattening, April 17, 1955, however, occurred in a year characterized in April as cold (mean temperature 57 per cent of normal) and wet (precipitation 146 per cent of normal). In the three other years, in which the index dates for vernal fattening are nearly the same, falling on April 19, 20, and 21, mean temperature in April varied from 76 to 121 per cent of normal and precipitation was between 36 and 93 per cent of normal. On the basis of present evidence we are led to agree with Odum and Perkinson (1951) that climatic conditions appear to affect the schedule of vernal fattening to only a minor degree.

With respect to variation of timing among individuals within a given year, our data for 1956 show that this may be relatively small (upper panel, fig. 3). The mean date for the earliest detectable fattening was April 13, with extremes at ± 3 days. We restrict our discussion of individual variation to this single year because the birds were weighed at four-day intervals, in contrast with seven-day intervals in earlier years, and are accordingly more meaningful in the evaluation of individual variation. Individual variation within the years 1952 to 1955 was not greater than ± 5 days from the median date, and possibly it was less.

In view of the many nutritional, behavioral, and ecological variables which might affect fat and energy metabolism, it appears that temporal variation in vernal fattening in captive birds is remarkably small. Our data from wild birds in 1952–1953 (lower panel, fig. 2), as well as field observations of the Snake River populations in subsequent years strongly suggest that this relative precision prevails also in the wild population.

In conclusion, certain characteristics of vernal fattening place important and useful limitations on hypotheses concerning the etiology of this metabolic adaptation in the White-crowned Sparrow. These include: (1) the apparent year to year precision, (2) the abruptness of the metabolic change, which raises the possibility of a threshold mechanism, and (3) the annual similarity in the rate of fat deposition, even when environmental temperature varied widely from year to year. It has previously been shown in several laboratories that heavy fat deposition can be induced in certain passerines, including the White-crowned Sparrow, by manipulation of the daily photoperiod (Wolfson, 1952, 1954; Koch and de Bont, 1952; Schildmacher and Steubing, 1952; Odum and Major, 1956; King and Farner, 1956). It appears to us that our data are consistent with the hypothesis that vernal increase in the daily photoperiod is the primary timer in the induction of premigratory fattening in the wild population also. Climatic conditions apparently exert only a minor influence over the timing of this important step in the metabolic preparation for migration by *Z. l. gambelii.*

SUMMARY AND CONCLUSIONS

Males of *Zonotrichia leucophrys gambelii* exhibit an abrupt and extensive deposition of body fat in the spring. This adjustment in the level of fat reserves occurs during a span of about 10 days immediately preceding northward migratory movement. On the average, it results in an approximate doubling of the quantity of reserve fat.

Confinement in small cages does not appear to alter appreciably the temporal characteristics of vernal fattening in males of this form. The major effect of captivity consists of an exaggeration of the magnitude of the reserves accumulated during the period of active vernal fattening. In view of the abundant food supply available to captives and the curtailment of their muscular activity this is a predictable difference.

During the prenuptial molt, which occurs undistorted in captive birds, the captives weigh *less* than the wild birds. In part, this results from a loss of lean body weight by captives, presumably as a consequence of the relative disuse and atrophy of the flight

muscles. In addition, we infer that captive birds had smaller fat reserves than wild birds during this period.

Especially interesting characteristics of vernal fat deposition include its typically abrupt inception, precipitant rate of development, and the rather high degree of precision in the timing of annual recurrence. These characteristics appear to be affected to only a minor degree by year to year differences in weather conditions.

Vernal fattening by captive birds exposed to natural environmental temperature and photoperiod is a reasonably good reflection of the event as it occurs in the free-living population. It is evident that the psychological stress of captivity does not interfere with the major regulatory factor or factors which initiate premigratory fattening. We submit that the effects observed in captive birds as a result of experimental manipulation of these factors are therefore meaningful in the interpretation of the regulatory basis of premigratory fattening in wild birds.

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