

## THE LIPID RESERVES OF WHITE-CROWNED SPARROWS ON THE BREEDING GROUND IN CENTRAL ALASKA

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AMONG the conspicuous physiologic events in the annual cycle of most species of migratory birds are distinct, periodic fluctuations in lipid reserves (for reviews, see Farner, 1955, 1960). Because of the correlation between greatly increased reserves and the migratory periods, such reserves have been interpreted as a manifestation of basic metabolic adaptations that provide fuel for migratory flights and for other caloric demands associated with migration. Comparisons of migratory fat deposition among species have provided an indispensable basis for the identification of factors that influence the metabolic preparation for migration, and have contributed to a descriptive framework for the formulation of hypotheses concerning the regulation of migration *per se*. Among the most thoroughly investigated taxa in this respect are the crowned sparrows, *Zonotrichia* spp. (Linsdale and Sumner, 1934; Blanchard, 1941; Blanchard and Erickson, 1949; Odum and Perkinson, 1951; Weise, 1956; King and Farner, 1959, 1963; King, 1961, 1963; King *et al.*, 1963; Millar, 1960; Morton and Mewaldt, 1962; Wolfson, 1959, 1960); however, attention has been confined almost entirely to populations on the wintering grounds and in migration. There have been no systematic investigations of autumn premigratory fat deposition in *Zonotrichia* spp., and very few in other species (e.g., Nakamura and Tamura, 1962; Blyumental, 1961; Dolnik *et al.*, 1963). For description of the timing and magnitude of variation of lipid reserves in summer and early autumn we have previously relied on observation of captive populations maintained at the latitude of the wintering ground and on samples of the feral population captured in autumn migration (King *et al.*, 1963; King, 1963). The hazards of this analytical approach are obvious. Because of this hiatus in our knowledge we undertook a general investigation of the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*, on its breeding ground in central Alaska. This paper presents data on the variations of body weight and lipid reserves from May to September.

### ACKNOWLEDGMENTS

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## MATERIALS AND METHODS

Observations and collections were made in the Tanana Valley within a radius of 25 miles from Fairbanks, Alaska (64.8° N, 147.8° W). Field work continued from 30 June through 4 September 1962, and from 13 May through 14 June 1963. Our description of seasonal changes thus depends on combined data from two years. In many instances, data obtained at Fairbanks are compared with data obtained at Pullman, Washington (46.5° N, 117.1° W), at the northern edge of the wintering area of *Z. l. gambelii*.

In 1962 birds were collected chiefly in mist nets, although a few were shot; in 1963 all collections were made by shotgun. Immediately after collection, the birds were weighed with an accuracy of  $\pm 0.05$  g; various tissues were then excised and the carcasses were wrapped for storage at  $-20$  C. Frozen carcasses were subsequently shipped to our laboratory in Pullman and analyzed for total lipid content by the Soxhlet extraction method of McGreal and Farner (1956). The resulting data are expressed as the *lipid index*, denoting the percentage of the live weight of the bird consisting of ether-extractable fat. Because of the extensive dissection required in some cases, not all carcasses were suitable for lipid analysis; also, some birds were only examined, weighed, banded, and released. The number of individuals for which data on body weight were obtained therefore usually exceeds the number of lipid analyses. Detailed notes were made on the extent of molt, if any, and each bird was classified as being in "light," "medium," or "heavy" molt. For economy of presentation these categories have been assigned index numbers of 1, 2, and 3, respectively, and averages have been computed for each sample. Because postjuvenile molt in *Z. l. gambelii* involves only the contour feathers, whereas postnuptial molt involves all of the feathers, equivalent molt-index numbers do not indicate the same intensity of molt in adult and juvenile birds. The molt index can serve only to indicate the relative intensity of molt within each age class.

Observations were also made on a group of captives. Nine adult males, eight adult females, and one juvenile male were captured on 6, 7, and 8 July and placed in pairs in small (41 × 28 × 25 cm) cages in an unheated room. The north end of the room consisted of a window. The birds were therefore exposed to essentially normal temperatures and photoperiod. Water, chick-starter mash, and millet seed were freely available. Weights and observations of molt were recorded at 3- to 4-day intervals and the birds were killed for lipid analysis on 6 September.

## RESULTS AND DISCUSSION

White-crowned Sparrows were first reported at Fairbanks on 7 May in 1963. Our observations and collections began on 13 May. There were no females present until about 18 May. During this interval the population of males increased, indicating continued arrival. Pairs were formed immediately upon arrival of the females, and by 22 May most males had obtained mates. The first complete clutches of eggs were found on 26 May, and the first newly hatched chicks on 10 June. In 1962, the nesting period had almost terminated by the time field work was begun on 30 June. Most pairs were feeding fledglings by this time. The abandonment of territories and coalescence of family groups began after mid-July, and was substantially complete by the end of July. Adults, initially aloof, joined the large

TABLE 1  
BODY WEIGHT AND LIPID INDEX IN ADULT WHITE-CROWNED SPARROWS  
IN CENTRAL ALASKA

Period	Body weight (g)				Lipid index <sup>1</sup>			
	Male		Female		Male		Female	
	N	Mean <sup>2</sup>	N	Mean <sup>2</sup>	N	Mean <sup>2</sup>	N	Mean <sup>2</sup>
11-20 May	23	25.6 ± 0.31	—	—	15	4.1 ± 0.58	—	—
21-31 May	13	25.6 ± 0.40	15	28.0 ± 0.50	13	3.6 ± 0.71	4	5.0 ± 0.40
1-10 June	9	27.2 ± 0.83	6	27.7 ± 1.10	9	4.7 ± 0.31	6	6.0 ± 0.22
11-20 June	3	25.9 ± 0.40	2	25.3	—	—	—	—
1-10 July	13	25.0 ± 0.44	13	24.6 ± 0.50	4	4.5 ± 0.41	5	5.4 ± 0.36
11-20 July	11	27.8 ± 0.70	11	23.8 ± 0.41	8	4.4 ± 0.29	8	4.7 ± 0.34
21-31 July	6	27.2 ± 0.54	8	24.3 ± 0.79	4	4.2 ± 0.26	3	5.2 ± 0.50
1-10 Aug	12	28.4 ± 0.53	6	25.2 ± 0.26	11	3.6 ± 0.16	4	3.9 ± 0.38
11-20 Aug	12	27.8 ± 0.63	12	25.6 ± 0.78	10	3.8 ± 0.38	7	5.3 ± 0.77
21-31 Aug	14	27.5 ± 0.45	6	25.8 ± 0.18	7	7.1 ± 1.60	6	7.8 ± 0.73

<sup>1</sup> g ether-extractable lipid/100 g live weight.

<sup>2</sup> ± Standard error of the mean.

flocks of immature birds in early August. Molt began in both adults and juvenals in the second week of July and was completed by mid-August. By 17-20 August in 1962 the flocks began to disappear from areas formerly occupied. We assume that this indicated the onset of migration. Only a few White-crowned Sparrows remained in the area after 1 September.

*Lipid index and body weight in feral birds.*—In the terminal samples of migrating White-crowned Sparrows obtained in southeastern Washington in early May, the mean lipid index was 20.2 for males and 17.8 for females (King, 1963). Data in Table 1 and Figure 1 show that the lipid reserves are much lower when the birds reach the breeding grounds or soon thereafter. From mid-May to mid-August, lipid reserves were relatively stable and at a minimum level for the year (cf. King and Farner, 1959; King, 1963). This confirms the impression gained from the data on body weight given by Oakeson (1954) and Irving (1960), and implies that the birds do not restore the lipid reserves depleted during the terminal migratory flight, or that the tendency to maintain increased reserves diminishes as migration progresses. In either case it is clear that the lipid reserves are regulated at a new, lower level on the breeding grounds. In general, although there are no statistically significant differences between selected pairs of mean values, the lipid index of females was greater than that of males during the breeding season. We attribute this at least in part to the lipid content of the ova, which were included in the extraction. The greatest mean lipid index in females coincided with the peak of ovoposition (1-10 June). During the last 10 days of August there was an approximate two-fold increase in mean lipid index above midsummer values in both males and females.

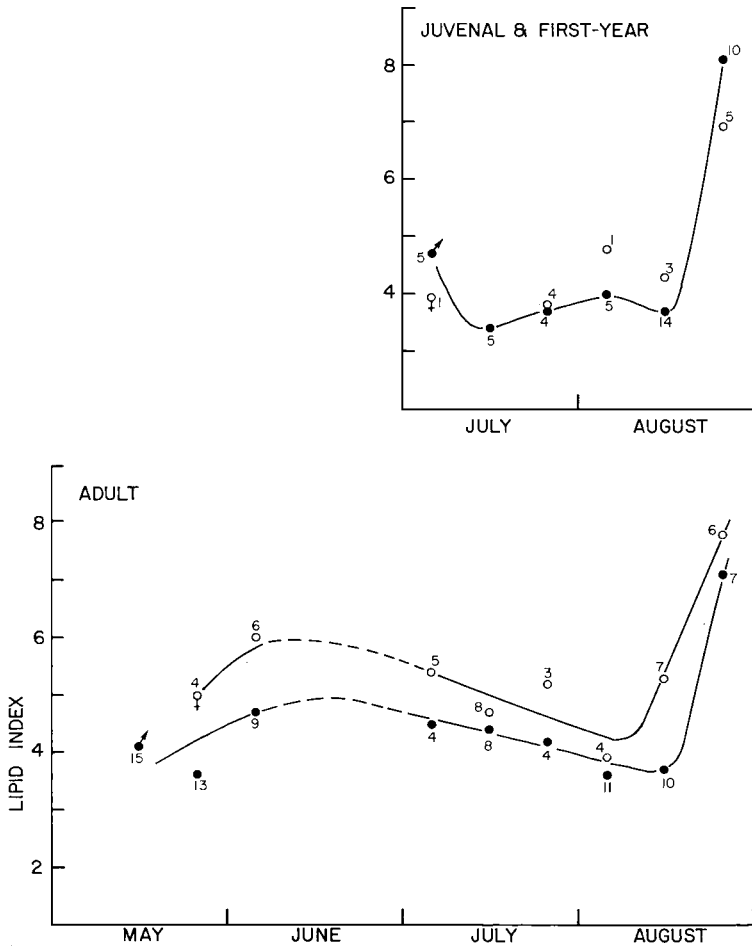


Figure 1. Variation of mean lipid index (g lipid/100 g total body wt) of feral White-crowned Sparrows at Fairbanks, Alaska. Each point indicates mean lipid index for a 10-day interval. Numerals at each point denote sample size; open circles indicate females; filled circles indicate males.

The increase was statistically significant in both sexes (11–20 August compared with 21–31 August,  $0.02 < P < 0.01$ ), the means approaching those found in migrant White-crowned Sparrows (16 males, 8.7; 21 females, 10.2) in southeastern Washington during the interval 11–20 September (King *et al.*, 1963, and unpublished data). A similar trend is evident in immature birds (Table 2, Figure 1). The increase (11–20 August compared with 21–31 August) is statistically significant in both males ( $P <$

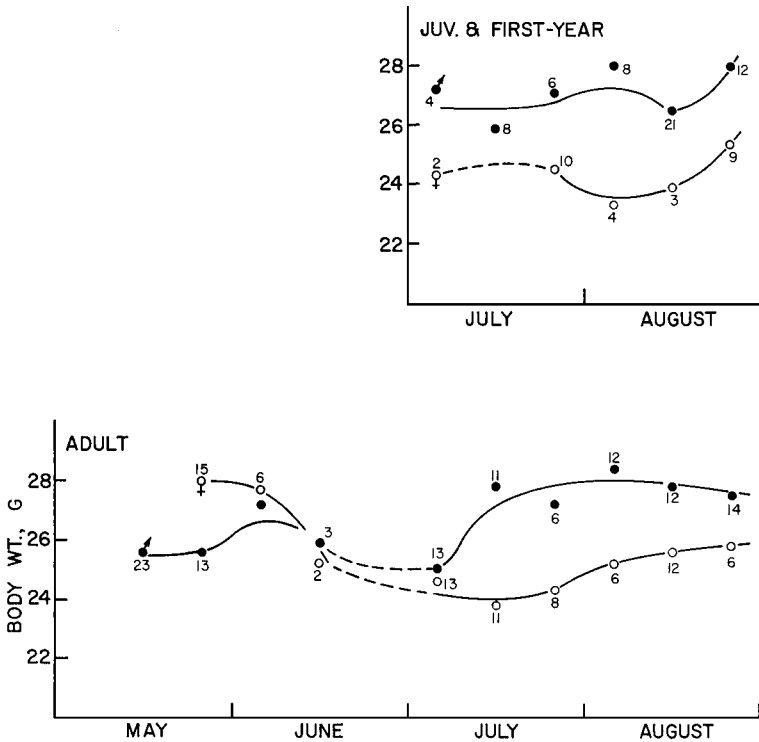


Figure 2. Variation of mean total body weight of feral White-crowned Sparrows at Fairbanks, Alaska. Symbols as in Figure 1.

0.01) and females ( $0.02 < P < 0.01$ ). These data therefore indicate a tendency toward premigratory fattening in late summer in both immature and adult birds. This appears to be somewhat less intensive than that observed in the spring, as King *et al.* 1963), and Millar (1960) had tentatively decided on the basis of samples of migrating *Zonotrichia leucophrys gambelii* and *Z. albicollis*, respectively.

Variations in total body weight were relatively small in adult males (Table 1, Figure 2) in spring and summer, but tended to increase during the postnuptial molt (see beyond). In females, maximum body weight accompanied the period (21 May–10 June) of maximum oogenesis, reflecting the development of the sex organs and ova. It should be noted, in adults of both sexes, that premigratory fattening, because of concurrent decrease in lean body weight (see below; Figure 3), was not reflected in an increase of total body weight. In immature birds, on the other hand, lean body weight was relatively stable or increasing in late August (see

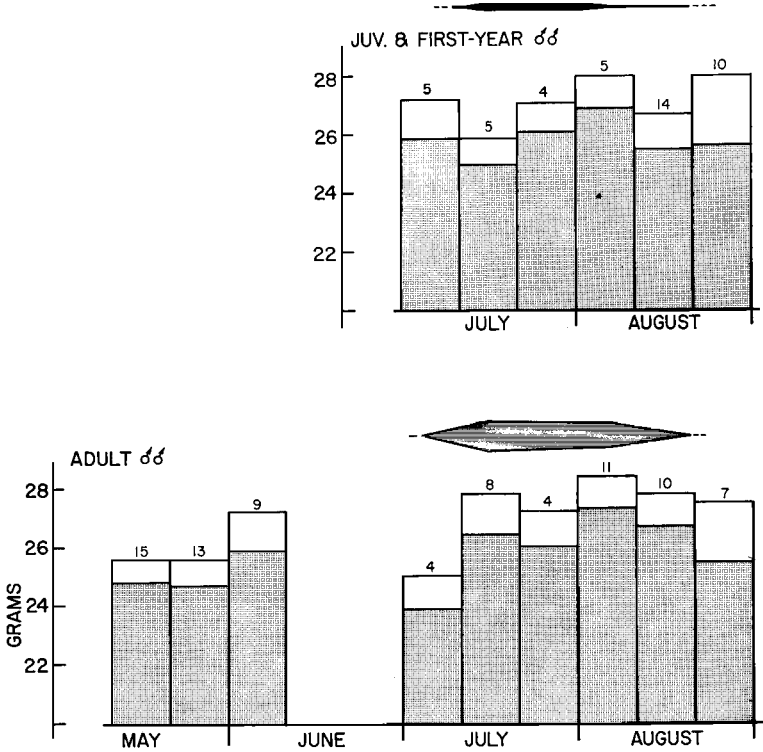


Figure 3. Variation of mean total body weight (total height of each bar), body fat (clear subdivision), and fat-free body weight (stippled subdivision) in feral male White-crowned Sparrows at Fairbanks, Alaska. Polygons depict duration and relative intensity of molt.

Table 4, below; Figure 3), and total body weight therefore reflects the increase in lipid reserves in both males and females. This was not true, however, in the combined data for both sexes of immatures (Table 2). These observations indicate that data on body weight are not necessarily reliable indexes of migratory fat deposition, and that the detection of functionally significant changes in lipid reserves may be masked by concurrent variations in the lean weight or by differences in the age- or sex-composition of the samples. A similar situation, involving a decrease in the mass of the digestive system, seems to have been observed by Dolnik (1963) in several species of migratory fringillids. This is unlike the relationship in White-crowned Sparrows in spring (King and Farner, 1959) and in the Great Reed Warbler (*Acrocephalus arundinaceus orientalis*) in autumn (Nakamura and Tamura, 1962), in which increase in body weight reflects with

TABLE 2  
BODY WEIGHT AND LIPID INDEX OF IMMATURE WHITE-CROWNED SPARROWS  
IN CENTRAL ALASKA

Period	Body weight (g)						Lipid index <sup>1</sup>			
	Males		Females		All <sup>2</sup>		Males		Females	
	N	Mean <sup>3</sup>	N	Mean <sup>3</sup>	N	Mean <sup>3</sup>	N	Mean <sup>3</sup>	N	Mean <sup>3</sup>
1-10 July	4	27.2±1.1	2	24.3	19	25.9±0.36	5	4.7±0.14	1	3.9
11-20 July	8	25.9±0.70	—	—	21	25.9±0.36	5	3.4±0.58	—	—
21-31 July	6	27.1±0.77	10	24.5±0.43	106	25.8±0.18	4	3.7±0.29	4	3.8±0.39
1-10 Aug	8	28.0±0.47	4	23.3±0.74	47	25.9±0.29	5	4.0±0.61	1	4.8
11-20 Aug	21	26.5±0.36	3	23.9±1.0	79	26.0±0.20	14	3.7±0.70	3	4.3±0.95
21-31 Aug	12	28.0±0.21	9	25.7±0.36	79	26.3±0.19	10	8.1±0.89	5	6.9±0.84

<sup>1</sup> g ether-extractable lipid/100 g live weight.

<sup>2</sup> Sex unknown in some individuals.

<sup>3</sup> ± Standard error of the mean.

reasonable fidelity at least the timing and rate of increase of lipid index. Putzig (1939) has also noted that body weight and fat content are not necessarily simply related in migrants. Taken together, however, our data indicate that statistical interpretations of body-weight data may be unable to reveal the presence or absence of migratory fat deposition in fall.

*Body weight and lipid index in captive adults.*—The data on body weights of captive White-crowned Sparrows at Fairbanks are shown in Figure 4. Like captives in the spring in southeastern Washington (King and Farner, 1959), these birds regulated body weight at a slightly lower level than the feral population. Of major interest is the sudden increase in body weight after 25 August, approximately coincident with the beginning of migration in the feral population. The mean terminal lipid index ( $\pm$  standard error) was  $21.3 \pm 1.03$  in males and  $22.3 \pm 1.66$  in females. In suddenness of inception and rate of change, this increase resembles closely that observed in captives in the spring in southeastern Washington (King and Farner, 1959; King, 1961). From this we infer that the basic tendency toward hyperphagia and fat deposition is as strongly developed in late summer as it is in spring. In feral birds, analysis of the data as daily samples rather than as means for 10-day intervals, shows that the increase in lipid index from midsummer levels began soon after 15 August and reached a maximum plateau by 22 August. The maximum lipid indexes in the daily samples, which are perhaps the best guide to the status of the fraction of the population which is prepared metabolically for departure, changed from 5.9 on 8 August, through 4.8 on 10 August, 6.8 on 15 August, 8.8 on 18 August, 9.6 on 21 August, to 15.8 on 22 August. Thus, as in spring, the increase in the mean and maximum levels of lipid reserves was accomplished within about one week. However, the mean

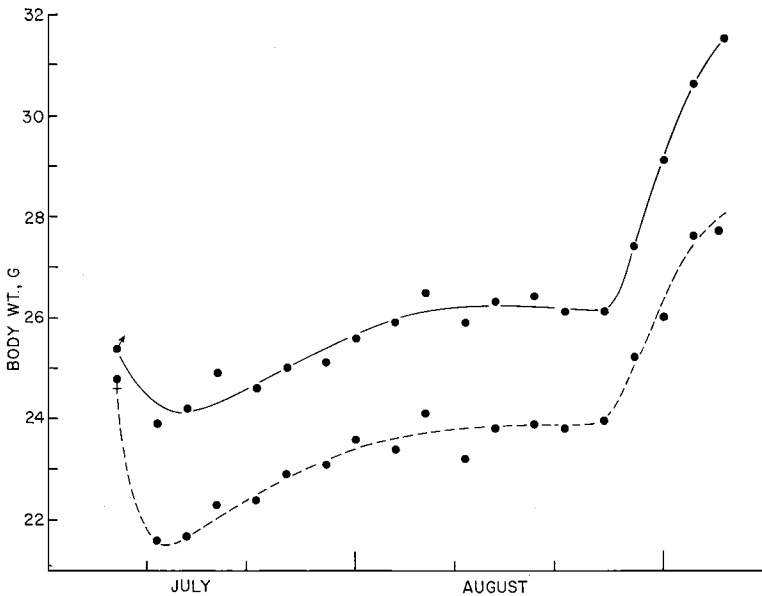


Figure 4. Variation in mean total body weight in captive male ( $n = 9$ ) and female ( $n = 8$ ) White-crowned Sparrows at Fairbanks, Alaska.

maximum lipid index in the feral population was less than the potential maximum suggested by the concurrent data for captives and was less than the mean vernal samples (20.2 in interval 1–10 May; King and Farner, 1959). We have suggested previously, on the basis of data obtained from migrants in transit, that the less intense fat deposition found in late summer may be an expression of adaptation to less demanding conditions (King *et al.*, 1963). However, we are also aware that in comparing feral and captive populations we are dealing with samples that may be very different statistically. First, the composition of the sample of captives is stable, while that of the feral population is variable with respect to individuals included. Second, the uniformity of social and physical environment leads to a temporal coincidence of response in the captives, producing a sharper image of the increase in lipid reserves and a greater mean value. All of the captives began to increase body weight within a span of about four days. In contrast, the samples of feral birds included individuals in various stages of postnuptial-premigratory adjustment, revealing an apparently less abrupt increase in lipid reserves and lower mean values. If we were able to trace premigratory fattening in individual feral birds or in a functionally homogeneous population, it is possible that we might discover a pattern resembling more closely that seen in captives.



TABLE 3  
LEAN BODY WEIGHT AND MOLT IN ADULT WHITE-CROWNED SPARROWS  
IN CENTRAL ALASKA

Period	Males			Females		
	N	Mean <sup>1</sup>	Molt	N	Mean <sup>1</sup>	Molt
11-20 May	15	24.6 ± 0.39	0	—	—	—
21-31 May	13	24.8 ± 0.36	0	14	26.7 ± 0.50	0
1-10 June	9	25.6 ± 0.51	0	6	25.3 ± 0.86	0
1-10 July	4	23.1 ± 0.54	0.5	5	23.8 ± 0.65	0.4
11-20 July	8	26.8 ± 0.75	2.9	8	23.0 ± 0.39	1.3
21-31 July	4	25.9 ± 0.62	2.8	3	24.3 ± 0.77	2.8
1-10 Aug	11	27.4 ± 0.57	2.3	4	24.2 ± 0.21	2.8
11-20 Aug	10	26.1 ± 0.36	0.9	7	24.1 ± 0.45	1.2
21-31 Aug	7	25.2 ± 0.30	0	6	23.8 ± 0.43	0

<sup>1</sup> ± Standard error of the mean (g).

*Variation in lean body weight.*—Data presented in Tables 3 and 4 and in Figure 3 suggest the existence of some functionally significant variations in lean body weight. In adults, there was a large apparent decline in lean body weight between early June and early July. This was statistically significant in adult males (1-10 June vs. 1-10 July,  $0.01 > P > 0.02$ ) and, over a longer period, also in females (21-31 May vs. 1-10 July,  $P > 0.01$ ). This coincides with the period of most intensive activity in feeding the young birds and with the involution of the reproductive organs. There appears to be also a cycle in lean body weight correlated with the postnuptial and postjuvinal molts. This is suggested most clearly by the data for adult males (Table 3, Figure 3), and is equivocal in the data for juvenal birds. Because the molt is a complete one in adults but involves only the contour feathers in juvenals, this difference might be expected. We have previously noted in adult males a variation of about 1 g in lean body weight correlated with the prenuptial molt (King and Farner, 1959). In the more demanding postnuptial molt, the change appears to approximate 2 g. Al-

TABLE 4  
LEAN BODY WEIGHT AND MOLT IN IMMATURE WHITE-CROWNED SPARROWS  
IN CENTRAL ALASKA

Period	Males			Females		
	N	Mean <sup>1</sup>	Molt	N	Mean <sup>1</sup>	Molt
1-10 July	5	25.9 ± 0.76	0.2	1	22.2	0
11-20 July	5	25.9 ± 0.32	2.5	—	—	—
21-31 July	4	26.9 ± 0.30	2.7	4	24.4 ± 0.85	2.0
1-10 Aug	5	27.2 ± 0.67	1.7	1	22.0	1
11-20 Aug	14	25.5 ± 0.37	1.2	3	22.4 ± 0.09	1.2
21-31 Aug	10	26.0 ± 0.50	0.1	5	23.8 ± 0.52	0.2

<sup>1</sup> ± Standard error of the mean (g).

though the components of this variation have not been investigated, it seems probable that follicular enlargement, growth of papillae, and variation in blood volume must contribute the major fractions. It is also noteworthy, however, that molt terminates as premigratory hyperphagia develops (King and Farner, 1956; King, 1961; Odum, 1960). It is known that changes in the rate of food ingestion may produce conspicuous effects on lipogenesis and body composition. Rats that are force-fed or trained to eat their daily ration in a short period show a significant increase in lipid content and a decrease in water content of the carcass (Cohn and Joseph, 1959, 1960). Also, lipogenesis is accelerated in force-fed rats (Hollifield and Parson, 1962). In chickens (*Gallus domesticus*), the evidence is equivocal (Lepkovsky *et al.*, 1960) or shows that the effects of force-feeding are the reverse of those observed in the rat (Feigenbaum *et al.*, 1962). The effects have not been investigated in other species of birds. If the premigratory increase in the rate of food ingestion (pre migratory hyperphagia) observed in wild birds induces changes in body composition like those found in the force-fed rat, then this mechanism might contribute a significant part of the reduction in fat-free body weight and concurrent increase in body fat occurring in the premigratory period. Because hyperphagia typically develops as the molt diminishes, however, it is not possible to distinguish the relative roles of these factors on the basis of the data now available. Irrespective of the mechanism involved, and as Dolnik (1963) has noted, the relative reduction in lean body mass in the premigratory periods can be regarded as an adaptive reduction in ballast that reduces the energy cost of migratory flight.

*Comparison of the events of the summer intermigratory period in captive and feral White-crowned Sparrows.*—The rapid postmigratory decrease of body weight (lipid reserves) in spring and the rapid premigratory restoration in late summer are particularly challenging with regard to the identification of causal factors. Some insight can be obtained through comparison of the variations in body weight of free White-crowned Sparrows with those of captives held at Pullman and Fairbanks (Figure 5). It should be noted first that the cycles are qualitatively similar in spring and early summer; both include a decrease in body weight from the vernal peak to a midsummer minimum. The increase in body weight during the postnuptial molt is not evident in captives, although the molt in these birds is at least superficially normal in timing and intensity. We know that the increase in total body weight in free birds results from an increase in fat-free body weight during the molt (Figure 3). If a similar change occurs in captives it is masked by a simultaneous decrease in lipid reserves. We have noted a similar difference in changes in body weight between free and captive White-crowned Sparrows during the prenuptial molt; body

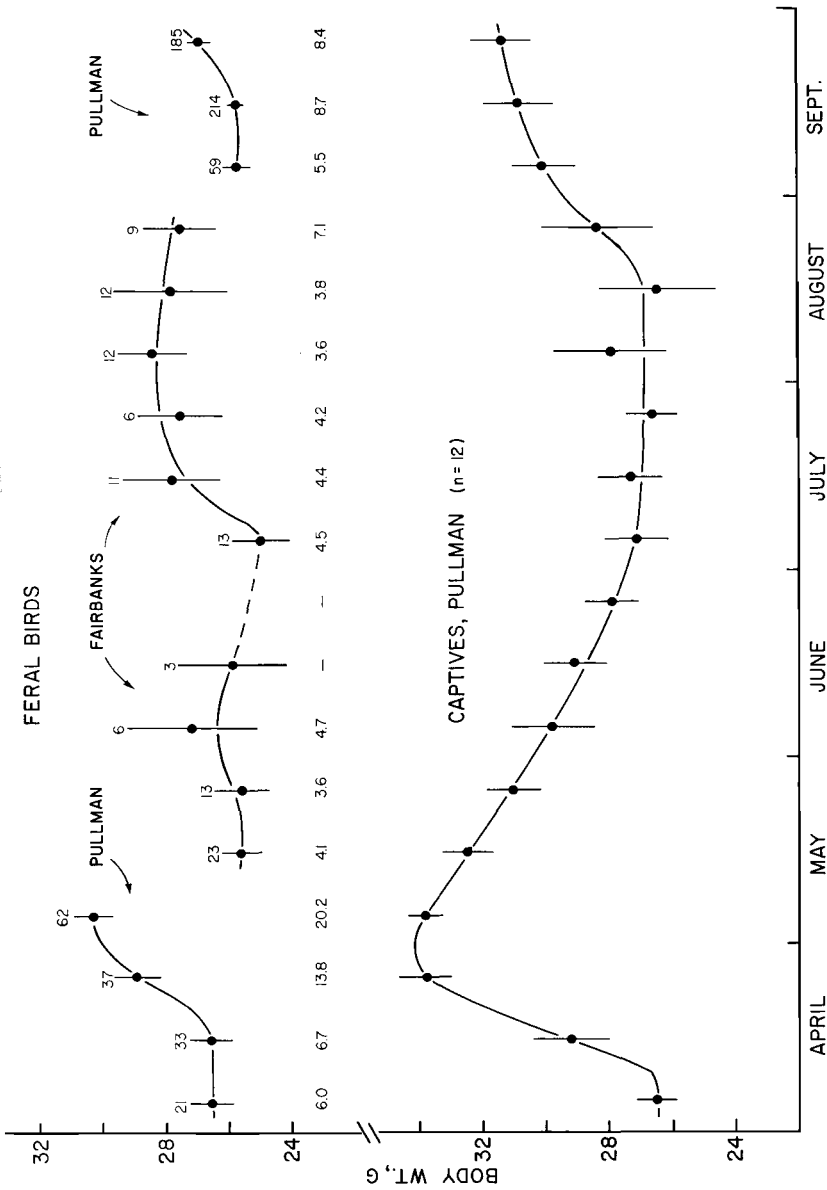


FIGURE 5. Comparison of variation in total body weight in free and captive male White-crowned Sparrows. Each point indicates mean value for a 10-day interval. Vertical bars through each point represent 95 per cent confidence interval; numerals above the bars on the upper curves denote sample size. The line of numerals beneath the upper curves indicate the mean lipid index for sample of males for corresponding 10-day intervals (data from Table 1 and from King and Farner, 1959; King *et al.*, 1963).

weight in captives is stable during this period, but feral birds show a molt-correlated increase resulting from increase in fat-free weight (King and Farner, 1959). Lacking sufficient data on the lipid index in captives, we cannot demonstrate the basis for this discrepancy, but it is noteworthy that fat-free body weight decreases by about one gram in captivity (King, 1961), and may be less variable than that of feral birds.

In late August there is a distinct increase in lipid reserves in both free and captive birds in Alaska (Figures 1 and 4) and in captives at Pullman (Figure 5). In the captive birds, this is reflected in an increase in total body weight and in visible subcutaneous and intra-abdominal fat. In the feral population, as we have already noted, total body weight does not significantly change despite rapid fat deposition; the latter is completely obscured in adult birds, and partially obscured in immatures, by the reciprocal decrease in fat-free body weight.

With regard to mechanisms regulating the lipid reserves, two observations merit special emphasis.

(1) Unlike the rapid postmigratory (or late migratory) decrease in lipid reserves detected in feral birds, the reserves decrease slowly through May and June in captives at Pullman. This is correlated with the maintenance of *Zugunruhe* beyond the end of the normal migratory period (Farner *et al.*, 1954; see also Putzig, 1939; Dolnik, 1962). *Zugunruhe*, regarded as the locomotor expression of the urge to migrate (see Palmgren, 1944; Farner, 1955) continues sporadically until the beginning of the post-nuptial molt. We have noted a similar relationship between *Zugunruhe* and large lipid reserves in autumn; both are maintained beyond the normal termination of migration (King and Farner, 1963).

(2) Premigratory fattening in autumn occurs very rapidly in captives held at Pullman, and is characterized by greater individual variation. This is associated with diminished temporal precision in the onset of *Zugunruhe*, as compared with the spring.

The implications of the similarities and differences in captive and free birds, although complex, are important in identifying significant problems and in guiding the formulation of meaningful hypotheses concerning the mechanisms that regulate the events of the annual cycle. We proceed from the premises that (1) appetite and the level of lipid reserves are regulated phenomena, (2) that change from one level to another is not casual, but reflects an adaptive regulatory mechanism, and (3), that the increasing vernal photoperiod, acting at least in part through the hypothalamo-hypophysial neurosecretory system (Farner, 1964), functions as a primary annual timer in the instigation of prenuptial molt, gonadal growth, fat deposition, and vernal migration (King, 1961; King and Farner, 1963). Within the limits of sampling error, these events are overtly identical in

free and captive birds in southeastern Washington in the spring. However, the mechanism that terminates migration at the latitude of the breeding grounds in the free population and concurrently terminates the period of higher lipid reserves either does not operate or operates less effectively in captives retained at the latitude of the wintering grounds. It seems reasonable to suppose that this mechanism must involve an interplay of psychic and neuroendocrine processes. We may guess that recognition of the ancestral breeding grounds, or the individual breeding locality, functions as a "migration terminator" (Farner, 1958, 1964), and that stimuli associated with the breeding area evoke mechanisms that inhibit the hyperphagia and hyperlipogenesis of the migratory season. In effect, these processes quickly become refractory to photostimulation. Captives, partially or completely deprived of the same secondary timing mechanism, remain in a migratory state of diminishing intensity until the onset of the prenuptial molt.

In late summer, fat deposition is rapid and relatively precisely timed among captives at Fairbanks, but typically is slower and straggling in those at Pullman. The histories of these groups differ obviously in three ways. First, the birds at Fairbanks had been in captivity a shorter time (*ca.* 2 months) than those at Pullman (8 to 10 months), making it possible to suggest that the lack of strong response in the latter group was a result of prolonged captivity. However, the fact that such birds display normal responses during the second spring season of captivity persuades us that captivity *per se* does not cause a decrease in responsiveness; the annual cycle can be "reset" if the birds are exposed to natural photoperiod.

Secondly, the captives at Pullman had not participated in vernal migration and nesting, and thus had a physiological history that deviated from that of captives at Fairbanks. It has been suggested previously (King, 1963) that autumn fat deposition could be a sequel to a chain of events, including reproduction, initiated in spring by the increasing daily photoperiod. Interruption of the sequence, as in the case of the captives held at Pullman, could delay or reduce late summer fat deposition. However, it is now known that rapid premigratory fat deposition occurs also in immature birds in late summer, making it necessary to abandon this hypothesis or to propose that autumn fat deposition is induced by different mechanisms in adult and immature birds.

Finally, it is obvious that captives at Pullman and at Fairbanks are exposed to physical environments that differ principally in the duration and rate of change of the daily photoperiod in summer. Extensive speculation concerning the possible roles of photoperiod or of other phasing mechanisms is premature. It is clear only that factors associated geographically with the breeding grounds or the psychophysiological complex of reproduction or both, accelerate depletion of vernal lipid reserves and

stimulate or at least intensify the restoration of these reserves in autumn. The fact that immature birds develop lipid reserves like those of the adults suggests that a distinct stimulatory process could be involved rather than simply a release from temporary inhibition of appetite and lipogenesis imposed at the time of arrival on the breeding grounds. The data may be interpreted as consistent with a hypothesis that postulates that the post-migratory decrease in lipid reserves reflects the development in adults of a vernal metabolic photorefractory phase that subsequently dissipates in midsummer, permitting late-summer or autumnal induction of fat deposition by the long daily photoperiod. This suggestion departs from the orthodox concept of a single annual photorefractory period that begins with gonadal regression and which is broken only by exposure of the birds to short winter days (Wolfson, 1952, 1959; Farner, 1964). However, we know of no information which makes it necessary to equate the characteristics of metabolic and gonadal photorefractoriness. On the contrary, there is circumstantial evidence that the mechanisms of metabolic and gonadal photorefractoriness are at least partly divergent (Shank, 1959; King *et al.*, 1960).

#### SUMMARY

The variation in lipid reserves in migratory birds during the vernal postmigratory-prenuptial phase and the autumnal premigratory phase of the annual cycle has not been systematically investigated previously in any species. Because descriptive data on changes of lipid metabolism on the breeding grounds are an essential basis for the formulation of meaningful hypotheses concerning the regulation of metabolic adaptations for migration, we initiated an investigation of the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) on its breeding grounds near Fairbanks, Alaska. Samples of the free population were obtained periodically from mid-May to early September, and observations were made on variation in body weight in a group of captives exposed to normal temperature and photoperiod.

Lipid reserves were minimal (3 to 4 per cent of total body weight) in the earliest samples, and were held at a low level until immediately before autumn migration. At this time there was a rapid increase in reserves in both adult and immature birds to a mean level of *ca.* 8 per cent of total body weight. Maximum lipid levels in individual birds, perhaps best representing the fraction of the population that was prepared metabolically for migration, reached *ca.* 16 per cent of body weight.

Total body weight in captive White-crowned Sparrows began to increase concurrently with fat deposition and the onset of migration in the feral population. The increase in body weight in captives was rapid and rela-

tively precisely timed among individuals, closely resembling the pattern observed in captives in spring at the latitude of the wintering grounds.

In the feral population, total body weight did not increase (adults) or increased only slightly (immatures) during premigratory fat deposition. This was the result of a concurrent decrease in fat-free body weight. The variation in fat-free body weight was closely correlated with the postnuptial molt. It is evident that variation in total body weight is not a reliable index of variation of lipid reserves in the White-crowned Sparrow in summer and autumn.

The data are discussed in relation to possible regulatory mechanisms which induce the postmigratory depletion of lipid reserves in spring and the premigratory restoration of these reserves in autumn. As a working hypothesis, it is proposed that the decrease of reserves from the vernal maximum reflects the development of a vernal metabolic photorefractory phase. If this phase dissipates during the summer, then premigratory fat deposition may be photoperiodically induced again in the autumn.

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