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Title AN INVESTIGATION OF THE FEEDING PATTERN OF CAGED WHITE-CROWNED SPARROWS, *ZONOTRICHIA LEUCOPHRYS GAMBELII* (NUTTALL), IN RELATIONSHIP TO VERNAL FAT DEPOSITION

Abstract approved [redacted]

Zonotrichia leucophrys gambelii is a strongly migratory race of white-crowned sparrow that exhibits a marked deposition of fat during the vernal migratory period. The physiological basis for fat deposition is a positive energy balance which results from a photoperiodically induced hyperphagia. Simultaneously with the increased caloric intake there is an adjustment of the intermediary metabolism so that the excess calories are deposited as fat rather than glycogen. The possible mechanism by which the intermediary metabolism is altered was the subject of this investigation. It was surmised that a photoperiodically stimulated change in the feeding pattern, along with hyperphagia, might induce the metabolic alterations necessary for lipogenesis and fat deposition. This idea was prompted by investigations with force-fed rats and rats limited to a two-hour feeding period per day.

Ten immature *Z. l. gambelii* were confined individually to small breeding cages modified to measure perch and feeding

activity. The feeding activity was recorded by means of a mechanically operated feeder which electrically activated a pen on an Esterline-Angus recorder whenever the bird placed its head in the feeder to obtain food. The motor activity was registered similarly with each movement of a perch-activated microswitch. Recordings of the feeding and perch activity were made continuously throughout the premigratory and migratory periods of March, April and May. During the experimental period the birds were weighed at least twice a week with observations of molt being recorded.

Prenuptial molt, fat deposition and Zugunruhe occurred essentially at the same time and magnitude as previously reported for caged and wild white-crowned sparrows. The median date for the onset of fat deposition was determined as April 11 $\pm$ 1 day. With fat deposition the mean body weight of six birds increased from 26.5 grams to 34.3 grams in 13 days. Prenuptial molt occurred at maximum intensity during the first ten days of April. The median date for the onset of Zugunruhe was determined as April 17.

The mean daily feeding and perch activity of six birds were determined for five one-week periods chosen in relationship to fat deposition. The feeding activity was analyzed by the frequency, the number of feeding periods in each half-hour per bird per day, and by the duration, the total number of minutes spent at the feeder in each half-hour per bird per day. The perch activity was presented as the number of activity units per half-hour per bird per day. The results indicated a general feeding pattern with two phases: a morning phase characterized by numerous trips to the feeder of short duration interrupted by the high motor activity of the bird, and an afternoon phase distinguished from the morning phase by low perch activity and relatively less frequent feeding periods of longer duration.

The feeding day was initiated almost invariably at the beginning of the morning civil twilight. The termination of the feeding day, before and after hyperphagia, was relatively constant and somewhat independent of the increasing evening photoperiod. During hyperphagia, the last feeding period occurred gradually later for each succeeding day.

Hyperphagia was evident in the feeding patterns of the weeks before and during fat deposition. For the week prior to fat deposition, the duration increased to 3.8 minutes/half-hour/bird/day and 112 minutes/bird/day from 3.6 minutes/half-hour/bird/day and 97 minutes/bird/day of the preceding week. The duration during the week of fat deposition increased to 4.7 minutes/half-hour/bird/day and 142 minutes/bird/day. The frequency showed similar results. The mean environmental temperature increased for each week.

During hyperphagia no change in the over-all feeding pattern was indicated from those of other weeks. Under the conditions of this investigation, it was concluded that there appears to be no change in the food intake pattern of *Z. l. gambelii* which can be construed as a mechanism for inducing metabolic alterations necessary for vernal fat deposition.

AN INVESTIGATION OF THE FEEDING PATTERN OF CAGED WHITE-CROWNED SPARROWS, *ZONOTRICHIA LEUCOPHRYS GAMBELII* (NUTTALL), IN RELATIONSHIP TO VERNAL FAT DEPOSITION

by

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INTRODUCTION

Most, if not all, migratory birds deposit large quantities of fat prior to and during the migratory periods. This close relationship has been well illustrated with many small migratory species and emphasized by the fact that sedentary species fail to exhibit an analagous adiposity. Presumably, the storage of fat is a metabolic adaptation that provides the maximum storage of energy with a minimum increment of weight, which is advantageous for long migratory flights (for reviews see Farner, 1955; Helms & Drury, 1960).

Obviously, the accumulation of such fat reserves results from a state of positive energy balance, where the energy input must exceed the energy output. However, the source of energy necessary for such a positive balance has been the subject of much investigation and has resulted in several hypotheses. According to Farner (1960), the hypotheses advanced fall into three categories and assert that a positive energy balance may be attained by 1) a reduction in energy expenditure, or 2) an increase in energy intake, or 3) by a combination of both.

The first of these hypotheses has been called the "energy-sparing" hypothesis and contains premises of several authors (Farner, 1960; King, 1961a). Such mechanisms as the reduction of the basal metabolic rate of Groebbels (1928, 1930) and the increased efficiency of energy utilization of Wachs (1926) have been suggested. These, however, lack sufficient supporting evidence. Kendeigh (1934, 1949) and others (Seibert, 1949; Davis, 1955; West, 1960) have suggested a combination of energy-sparing effects in the spring as the source of surplus energy for fat deposition. These effects include the declining demands for thermoregulation with the increasing temperature, the cessation of the prenuptial molt, and the increasing time for feeding with the lengthening of the photoperiod.

The second hypothesis contends that the surplus energy necessary for a positive energy balance is derived from an increase in energy intake or hyperphagia. This idea was first suggested by Zedlitz (1926) and has been confirmed subsequently for the vernal fat deposition in the chaffinch, Fringilla coelebs (Koch & deBont, 1952), white-crowned sparrow, Zonotrichia leucophrys gambelii (King, 1961a; King & Farner, 1956), white-throated sparrow, Zonotrichia albicollis (Odum & Major, 1956), and the tree sparrow, Spizella arborea (Weise, 1956). In the case of F. coelebs, Z. l. gambelii, and Z. albicollis, the hyperphagia has been shown to be photoperiodically controlled and induced by the lengthening of the days in the spring. Other species, such as the golden-crowned sparrow, Zonotrichia atricapilla, Harris's sparrow, Zonotrichia querula (Farner, King & Wilson, 1957), brambling, Fringilla montifringilla (Lofts & Marshall, 1960; Schildmacher & Steubing, 1952), slate-colored Junco, Junco hymelis (Wolfson, 1942), and the Oregon Junco, Junco oreganus (Wolfson, 1954) exhibit a similar photoperiodically induced vernal fat deposition but the actual bioenergetics for fattening in these species apparently has not yet been established.

The third view, proposed by Merkel (1938, 1940), suggests that the combination of energy-sparing effects along with a moderate increase in food uptake furnishes the surplus energy necessary for a positive balance and fat deposition.

The physiological mechanisms concerning the vernal migratory phase in the annual cycle of Zonotrichia leucophrys gambelii have been the subject of intense research in the laboratories of Farner and King. This race of white-crowned sparrow is strongly migratory and breeds in the boreal zone of western North America, ranging from Alaska through western Canada to northern Washington. It migrates through the western United States and overwinters in a range from California north to southern Washington, east to Utah, and south to northern Mexico.

Since it can be captured easily from large flocks on the wintering grounds and during migration, Z. l. gambelii is an exceptionally good experimental bird. They can be maintained individually in small cages with only a slight initial mortality, and, most important, the confinement to small cages does not alter appreciably the temporal characteristics of vernal fat deposition or migration. King and Farner (1956, 1959), have shown that the inception of fat deposition and migratory behavior (Zugunruhe) of caged individuals coincides almost precisely with the inception of fat deposition and normal migration of the feral population. Fat deposition begins abruptly about mid-April at the cessation of the prenuptial molt and is subsequently followed by the northward migration or, as in caged birds, by Zugunruhe. The deposition of fat develops in visceral and subcutaneous depots of which, in the latter, there are fifteen distinct morphological bodies (McGreal & Farner, 1956). The prenuptial molt occurs undistorted in the captive birds.

A study comparing the vernal fat reserves in wild and captive white-crowns by King and Farner (1959) revealed the magnitude of the reserves to be somewhat exaggerated in the confined birds. They believe that this was due to the abundant food supply and the curtailment of muscular activity in the caged individuals. They conclude by stating, "...vernal fattening in caged birds exposed to natural environmental temperatures and photoperiod is a reasonably good reflection of the events as it occurs in the free living population," and "...that the psychological stress of captivity does not interfere with the major regulatory factor or factors which initiate premigratory fattening in wild birds."

As previously stated, Z. l. gambelii obtains its surplus energy for fat deposition by an increase in food uptake or hyperphagia. This relationship was demonstrated by King (1961a). He measured the energy intake and energy expenditure of captive white-crowns under natural photoperiods and weather conditions during the vernal premigratory and migratory period. During this time, while the total energy expenditure remained unchanged, there was a sharp increase in the gross energy intake which was simultaneous with the deposition of premigratory fat. These results indicated that the source of surplus energy is derived from an increase in appetite rather than energy-sparing measures.

In two more recent experiments, King (1961b) demonstrated that the hyperphagia of the white-crown sparrow was directly stimulated by the increasing photoperiod and was not just a result of increased time for feeding.

In the first experiment, by increasing the photoperiod from a non-stimulatory 9 hours per day to a stimulatory 20 hours per day, he showed that white-crowns were artificially induced into a migratory state evident by their increased food intake, fat deposition and Zugunruhe. To show that the hyperphagia was due to the direct stimulatory effect of the increased photoperiod and not to a prolonged time for feeding, a second experiment was conducted in which two groups of birds were subjected essentially to a constant feeding time but different lengths of photostimulation. The control group was exposed to a continuous photoperiod of 9 hours and 27 minutes, while the experiment group was subjected to 9 hours of continuous photoperiod and an additional 9 hours of one minute intermittent flashes every 20 minutes. In the latter group the combination continuous and intermittent flash photoperiod was equivalent to 18 hours of photostimulation but only 9 hours and 27 minutes of feeding time (cf. see Farner, 1959). The results show that the group with the increased photostimulation exhibited a marked increase in appetite and fat deposition, while the control group exhibited no increase in food uptake or in body weight. Since the birds were also under constant temperature, these experiments further discount any possibility of temperature dependent energy-sparing mechanisms being responsible for the increase in fat reserves in this species.

Although the close interrelationship of photoperiod, hyperphagia, and fat deposition appears established for this species, there still remain many questions as to the mode and site of regulation of the events. How does the photoperiod change the feeding regulatory mechanisms so that the bird becomes hyperphagic? Once the bird becomes hyperphagic, how is the intermediary metabolism altered so that the increased caloric intake is deposited primarily as fat?

King (1961b) has proposed two working hypotheses based on information gathered primarily from work on mammals. He suggests that the photoperiod could act directly on the hypothalmic feeding centers, via the retina and optic tract, causing either a stimulatory effect on the "appetite" center or an antagonistic inhibitory effect on the "satiety" center. The result would be, in either case, an excessive energy intake and subsequent alteration in the intermediary metabolism so that the caloric intake would be deposited primarily as fat.

King's alternative, or concurrent, hypotheses suggests that the photoperiod could act, again via the retina and optic tract on the hypothalmic neurosecretory nuclei, by stimulating the release of trophic and metabolic hormones from the anterior pituitary. In turn, the hormones would induce shifts in the intermediary metabolism towards lipogenesis and fat deposition. The resultant drain of the circulating metabolites would, thus, indirectly stimulate the animal to greater appetite.

In conjunction with the first working hypotheses, King refers to the interesting work of Cohn and Joseph (1959a) on force-fed rats. These researchers have shown that when laboratory rats, which are normally "nibblers" (eat small meals all day), are forced to eat "meals" two times a day, from a stomach tube, there was a marked increase in lipogenesis and fat deposition. Control animals fed the same caloric intake ad libitum showed no significant increase in body fat. Concomitant with this increased lipogenesis in force-fed rats, Cohn and Joseph (1959b) also showed that there was an increase in hexose monophosphate shunt activity. The hexose monophosphate shunt pathway, it was pointed out, is known to be an important source of reduced triphosphopyridine nucleotide, which is essential in reducing crotonyl coenzyme A to butyryl coenzyme A in fatty acid synthesis. This indicated to them that the increased rate of ingested food results in increased traffic over alternate metabolic pathways and a tendency to conserve energy as fat.

Hollifield and Parsons (1962b) showed similar results using rats trained to eat a 24 hour portion of food in two hours. After ten weeks, rats trained to feed in this manner were 30 percent heavier than animals allowed food ad libitum. It appeared to them that the increase in weight was due to fat deposition associated with increased food intake. Measurements of glucose-6-phosphate dehydrogenase and 6-phosphogluconate dehydrogenase activity of adipose tissue showed over a 200 percent increase by the fifth day of the feeding program (1962a). These enzymes are associated with the hexose monophosphate shunt.

Farner et. al. (1961) comparing the effects of long daily photoperiods on the energy storage in tissues of Zonotrichia leucophrys gambelii, Junco oreganus, and Passer domesticus, found that migratory forms, which were photoperiodically stimulated into a migratory state, showed a marked increase in the lipid levels of the pectoral muscle and liver tissues and a corresponding decrease in the glycogen content. The non-migratory form, Passer domesticus, showed no such change. The authors suggest that the decrease in glycogen levels in stimulated migratory forms could be an indication of greater hexose monophosphate shunt activity analagous to that of force-fed rats. In the light of this possibility it was further suggested that there may exist a photoperiodically induced alteration in the feeding pattern along with the increased caloric intake of Z. l. gambelii.

Therefore, it is the purpose of this paper to investigate the feeding pattern of Z. l. gambelii in relationship to vernal fat deposition based on the following hypothetical scheme: with the increaseing photoperiod in the spring, Z. l. gambelii is stimulated not only to a greater appetite but also to an alteration in its feeding pattern. The change could possibly be from a nibbling type pattern to one of meal eating. The meal eating pattern could be analagous to force-feeding in rats with the higher rate of ingested food resulting in utilization of an alternate metabolic pathway, such as the hexose monophosphate shunt, and subsequent lipogenesis and fat deposition. It is hoped that the results will elucidate this possibility and aid in determining the regulatory mechanisms of vernal fat deposition.

METHODS AND MATERIALS

The white-crowned sparrows used in this investigation were captured in early February, 1962, with Japanese mist nets, from an overwintering population in the Snake River Canyon near Pullman, Washington. The birds were transferred to the Washington State University campus and placed in large outdoor aviaries where they were maintained on chick-starter mash and water, ad libitum, prior to the experiment.

Approximately two weeks later, ten immature birds were removed from the aviary and confined individually in Hendryx breeding cages (23x36x28 cm.) which were modified to measure the feeding and motor activity of the bird in the cage. The cages were situated out-of-doors, on large tables in a walled enclosure on the roof of the science building, where they were relatively free from extraneous noises, human disturbances, and artificial light. The tables were roofed and positioned against the walls of the enclosure so that all the cages were adequately protected from the wind and rain. Since the environmental temperature, humidity and photoperiod of the captive birds were essentially similar to those of the feral population, the conditions for the experiment were regarded as "natural."

The apparatus for recording the feeding activity of each bird consisted of a mechanical feeder, two electrical circuits connected by a relay, and an Esterline-Angus recorder. The feeder, illustrated in Figure 1, was constructed of one-eighth inch plastic and Duco cement and was mounted on a wooden stand outside of the cage.

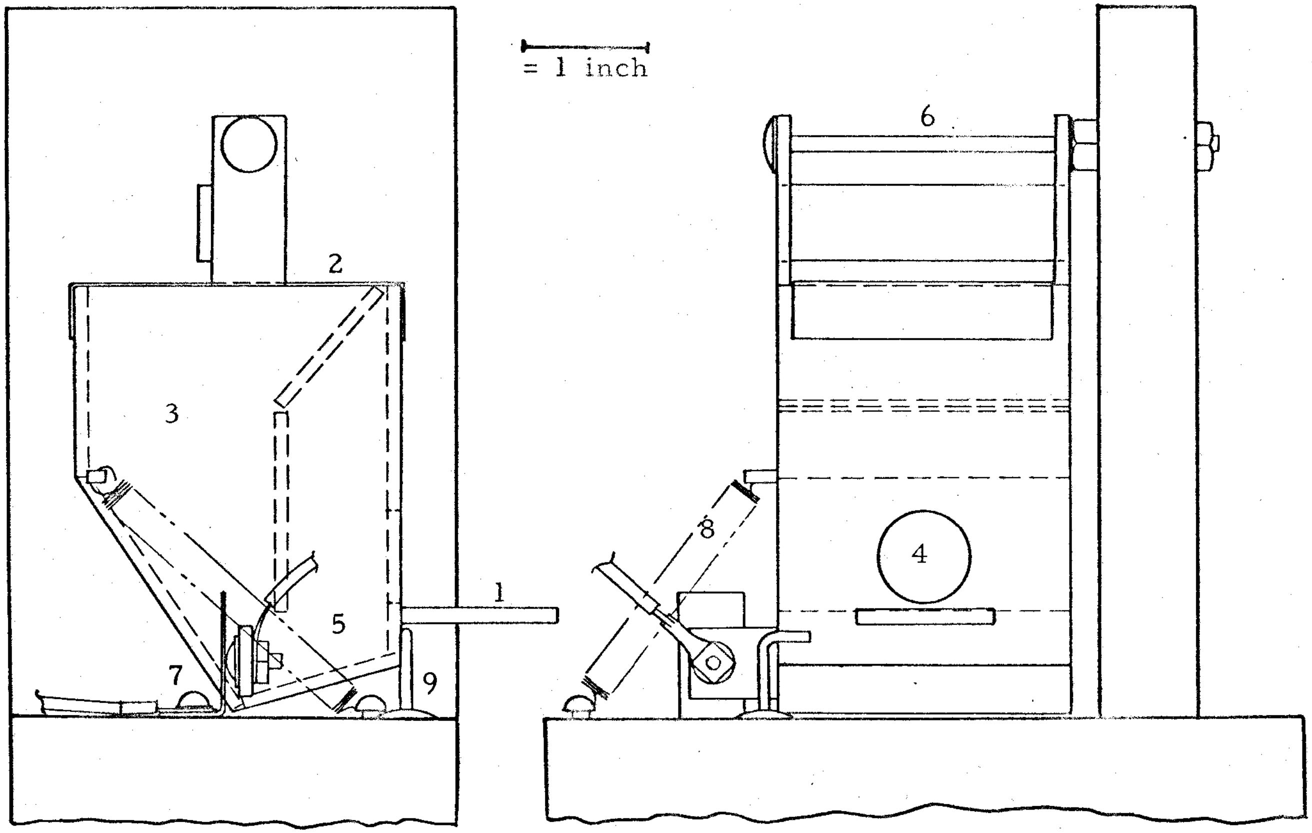

Figure 1. Mechanical electrical-recording feeder. See text for explantion.

The breast plate (1) protruded into the cage between the wires. The sheet metal cover (2) prevented vagrant animals from obtaining food from the food reservoir (3). The feeder was activated when the bird placed its head through the aperture (4) into the food chamber (5) and pushed against the breast plate. This caused the feeder to swing backwards on the pivot (6) and the points (7) to touch. The spring (8) maintained the feeder in a forward position against the bumper (9) so that contact was made only when pressure was put on the breast plate.

The points of the feeder were connected to an electrical circuit which contained a rectified 24 volt current supply and a relay switch. When the points were in contact the circuit was closed and the relay switch was activated. The relay controlled the individual circuits which supplied the power to the pens of the Esterline-Angus recorder. When the current in the recorder circuit was momentarily interrupted by the activated relay, the pen would disengage and cause a mark or "blip" on the recording paper.

To insure that the birds would obtain all food from the activity feeder and not from the floor, the floor of the cage was replaced with one-half inch hardware cloth and raised approximately one-half inch above the top of the table. The cleaning tray was then placed on top of the table beneath the hardware cloth floor. This permitted any food that was spilled from the feeder to drop through the floor and out of reach of the bird.

The method of recording the perch activity was, with few modifications, similar to that of Farner and Mewaldt (1953). The apparatus for each cage consisted of a double electrical circuit, a two-way microswitch, a capacitor, and a relay switch. The capacitor-discharging circuit, containing the capacitor and the relay, was closed when the microswitch was mechanically depressed by the weight of the bird on the perch. The capacitor then discharged through the relay which, in the same manner as in the feeder circuit, broke the circuit to the recorder pen and resulted in a mark on the recording paper. When the bird chose to leave the perch, the microswitch would immediately reverse and open the capacitor-discharging circuit and close the capacitor-charging circuit. The capacitor was then immediately recharged by a 45 volt power supply and remained charged until the bird again chose to alight on the perch.

Since the Esterline-Angus recorder was equipped with twenty pens, the feeding and perch activity of the ten birds were simultaneously recorded on the one machine. The recording paper was graduated into tenths of an inch and passed through the recorder at a rate of six inches per hour.

Continuous recordings, with the exception of about one week in June, were made from the end of February to mid-June of 1962. During this time every effort was made to keep the birds relatively free of human disturbances. Feeding, weighing, and cleaning activities were coordinated and minimized as much as possible.

Except during the period from April 3 to May 5, at which time weighing was every other day, each bird was weighed twice a week to the nearest tenth of a gram with a Welch triple beam balance. At the time of weighing the condition of the prenuptial molt was checked and recorded according to arbitrary units designated for the intensity of molt (1=light, 2=medium, 3=heavy). During the time of weighing each cage was cleaned once a week.

Since the food reservoir held a relatively large supply, feeding was restricted to every second or third day depending upon the amount of food consumed. The food consisted of a two to one mixture of chick-starter mash and millet seed. The millet seed, in addition to supplementing the diet, aided in preventing the mash from caking and, thus, allowed it to flow freely from the reservoir. Each cage was provided with two containers of water. Feeding and watering was done only during the time of weighing.

Records of the daily high and low environmental temperatures were obtained from a recording thermometer located approximately four miles from the city of Pullman, on the Washington State University experimental farm.

At the termination of the experiment the birds were sacrificed in order to determine the sex.

From the recorded data, five one-week periods, chosen in relationship to the fat deposition of each of six birds, were selected for analysis of the feeding and perch activity patterns. The weeks chosen were designated A, B, C, D, and E. Weeks A and B were, respectively, during the winter and early spring, well in advance of fat deposition. Week C was just prior to fat deposition and during the prenuptial molt. Week D was during fat deposition and just before the onset of *Zugunruhe* while week E was after fat deposition and during *Zugunruhe*. Only six of the ten experimental birds were used in determining the feeding and perch activity patterns because the combined methods of analysis proved to be so time consuming and laborious.

The method of analyzing the feeding data for each bird was based on the number and length of the feeding periods in a half-hour interval. A feeding period was designated as a number of grouped marks or "blips" on the recording paper that were not interrupted by a period of one or more minutes. The total number of feeding periods recorded in a half-hour was considered as the frequency, or the number of times the bird went to the feeder per half-hour. The length of each feeding period was then measured with a scale to the nearest two-tenths of a minute with the total length of time in the half-hour designated as the duration, or the total number of minutes the bird spent at the feeder per half-hour. The total number of feeding periods and the total number of minutes of each half-hour interval were averaged for the seven days in order to obtain the mean daily activity pattern for both the duration and frequency during the five selected weeks.

The perch activity was used primarily to determine the onset of Zugunruhe and was analyzed as units of activity per half-hour, similar to the method of Weise (1956). The method involved simply counting the number of "units" in the prescribed half-hour interval that showed one or more activity marks. The one-tenth inch graduations on the recording paper were conveniently taken as the standard units.

RESULTS

The mean body weight of the six experimental birds is plotted in Figure 2 (lower panel) and shows the typical abrupt nature of the vernal fat deposition. The median date for the onset of fattening was determined as April 11 ± 1 day. This date is relatively consistent with those of King (1961a) who reported median dates for 1955 and 1956 as April 17 ± 4 days and April 13 ± 3 days, respectively. He attributed the later date in 1955 to the lower environmental temperatures in the spring of that year. The ambient temperatures for this experiment closely resemble those obtained by King in 1956.

The average body weight for the experimental period prior to the onset of fat deposition was 26.5 grams with a range of 1.8 grams. At the height of maximum fattening the mean weight for a twenty-four day period was 34.3 grams with a range of 1.3. The percent increase of body weight calculated from these mean values was 29 and required an average span of 13 days for development. King (1961a) reported percent increases of 27 and 30.

The duration and intensity of the prenuptial molt is illustrated in relationship to the body weight by a black polygon in Figure 2. The median dates for the start and cessation of the molt were, respectively, March 17 and April 18 ± 1 day. Maximum intensity occurred prior to fattening during the first ten days of April and lasted for approximately one week. The last traces of the molt were observed when the body weight was near the plateau of maximum fattening.

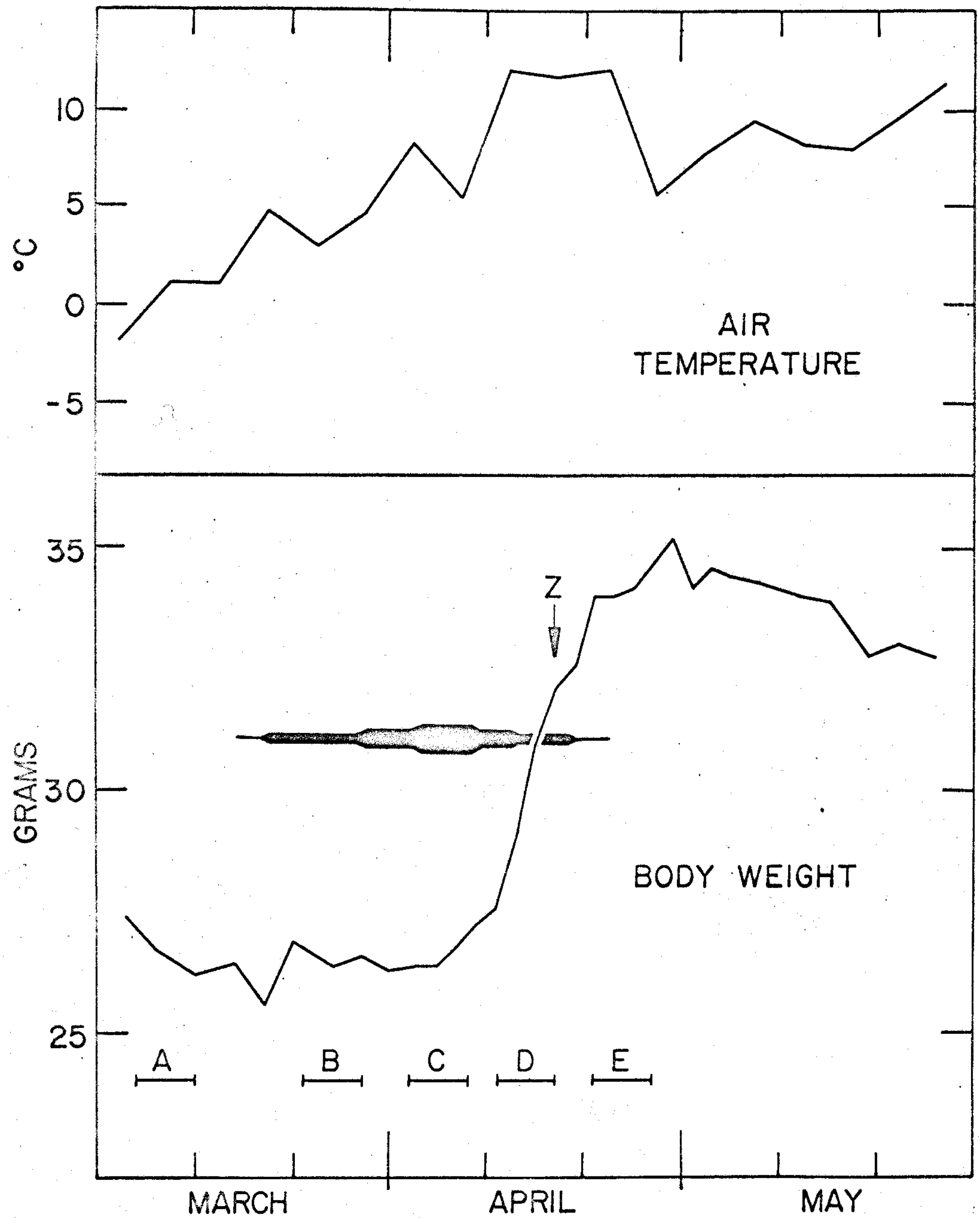

Figure 2. Upper panel: mean environmental temperatures for five-day periods. Lower panel: mean body weight of six male *Zonotrichia leucophrys gambelii*. Black polygon represents intensity and duration of molt. Z-arrow indicates onset of *Zugunruhe*. Lettered bars represent weeks analyzed.

The lettered bars in Figure 2 show the five weeks, in relationship to the mean body weight, that were analyzed to determine the composite feeding and perch activity patterns for six birds. Week A represents March 4-10; week B, March 21-27; week C, April 2-8; week D, April 11-17; week E, April 21-27. Each week comprises 42 bird days (six birds for seven days) of recorded data except for week B which comprises 35 bird days (five birds for seven days).

The frequency feeding pattern (lowest line) and the durational feeding pattern (middle line) are illustrated for each week in Figures 3 through 7. The frequency feeding pattern is expressed as the number of feeding periods for each half-hour per bird per day and, presumably, represents the average number of times that the birds moved to the feeder to obtain food. The durational feeding pattern represents the average time for each half-hour that the birds spent at the feeder in the process of obtaining food and is expressed as minutes per bird per day.

The averaged data for the two feeding patterns of each week is summarized in Table I along with the length of the natural photoperiod and the feeding day. Figure 8 compares the total duration and the total frequency of each week with the length of the photoperiod and the feeding day. The length of time from the first recorded feeding period to the last constitutes the feeding day and was averaged per bird per day. The photoperiod is presented as the length of time from sunrise to sunset, including civil twilight, of the median day of each week. The percentage of the photoperiod that was utilized for

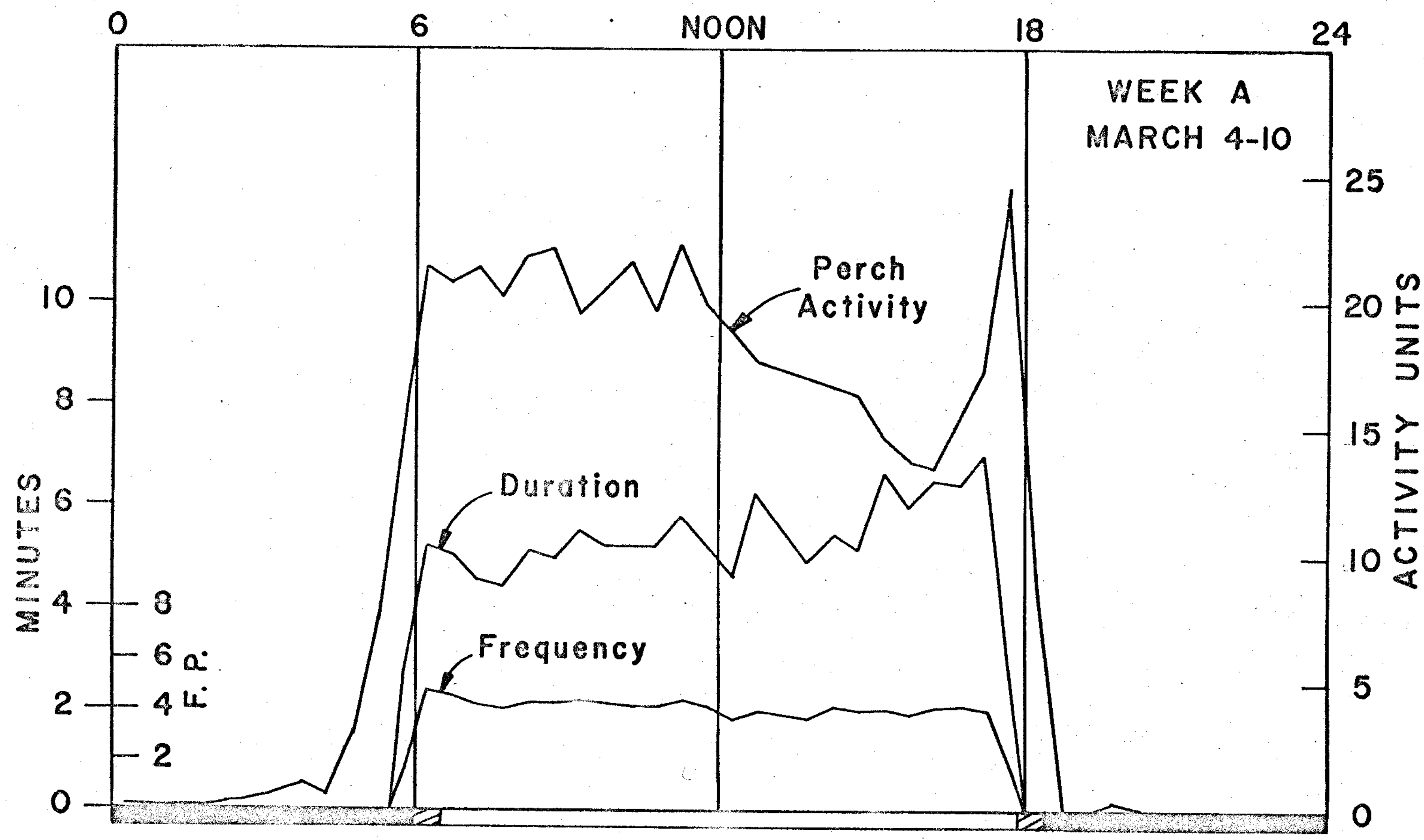

Figure 3. Mean perch and feeding activity of six male Zonotrichia leucophrys gambelii. Black horizontal bars represent night hours; cross-hatched bars, civil twilight. Open bar represents period between sunrise and sunset. Perch activity represents the activity units/bird/day for each half-hour; duration, minutes/bird/day; frequency, feeding periods (F. P.)/bird/day.

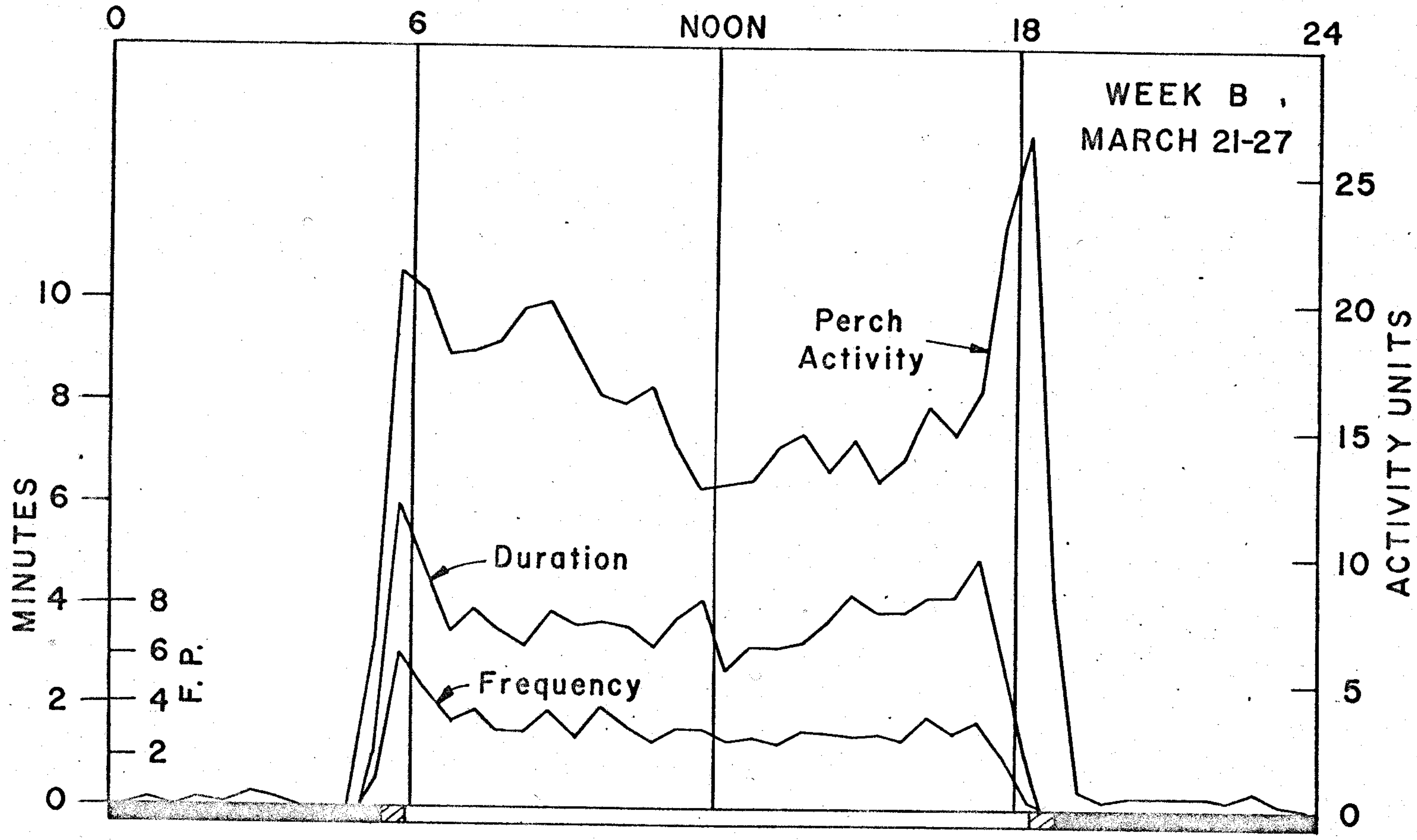

Figure 4. Mean perch and feeding activity of five male <u>Zonotrichia</u> <u>leucophrys</u> <u>gambelii</u>. See Figure 3.

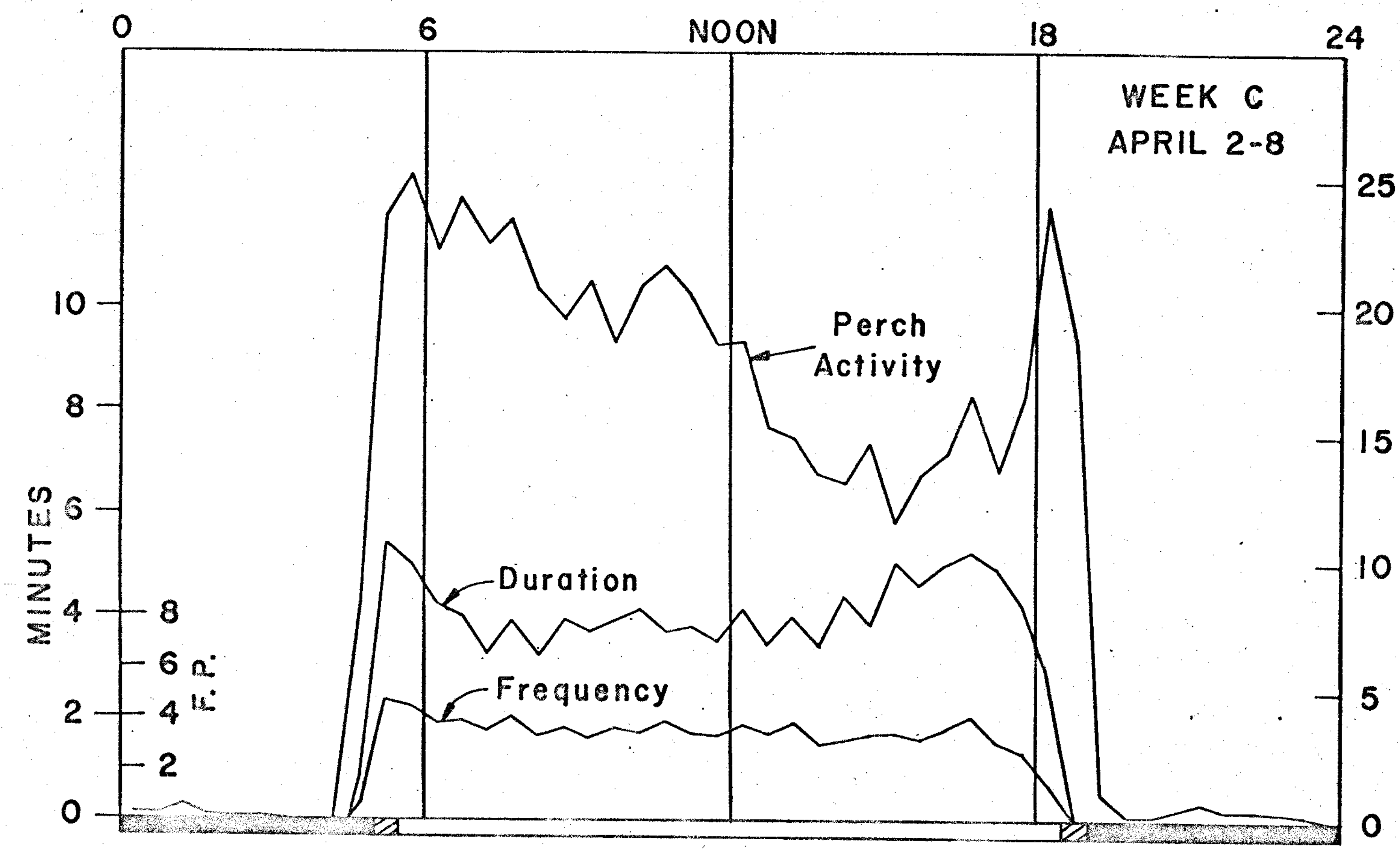

Figure 5. Mean perch and feeding activity of six male Zonotrichia leucophrys gambelii. See Figure 3.

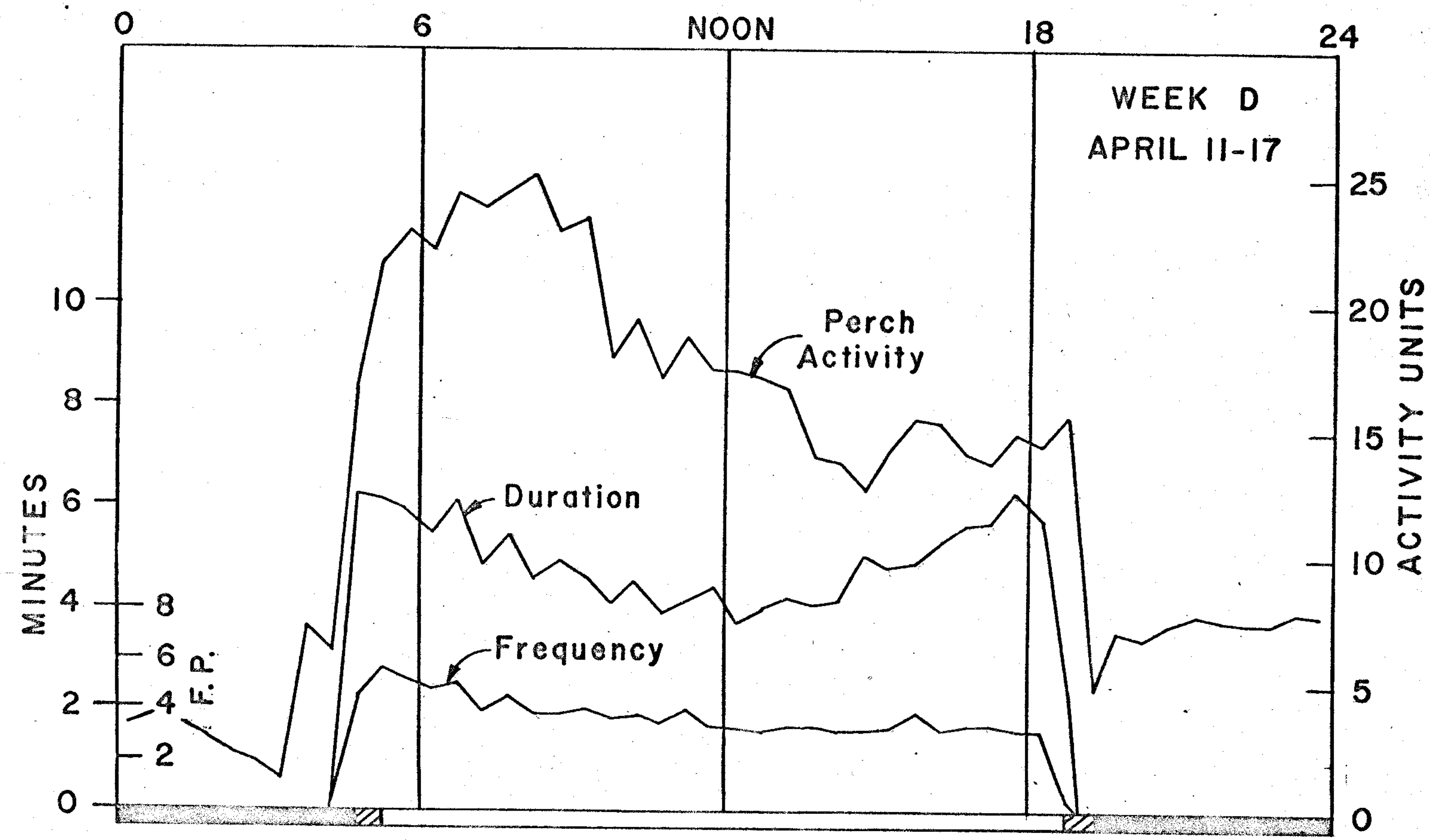

Figure 6. Mean perch and feeding activity of six male Zonotrichia leucophrys gambelii. See Figure 3.

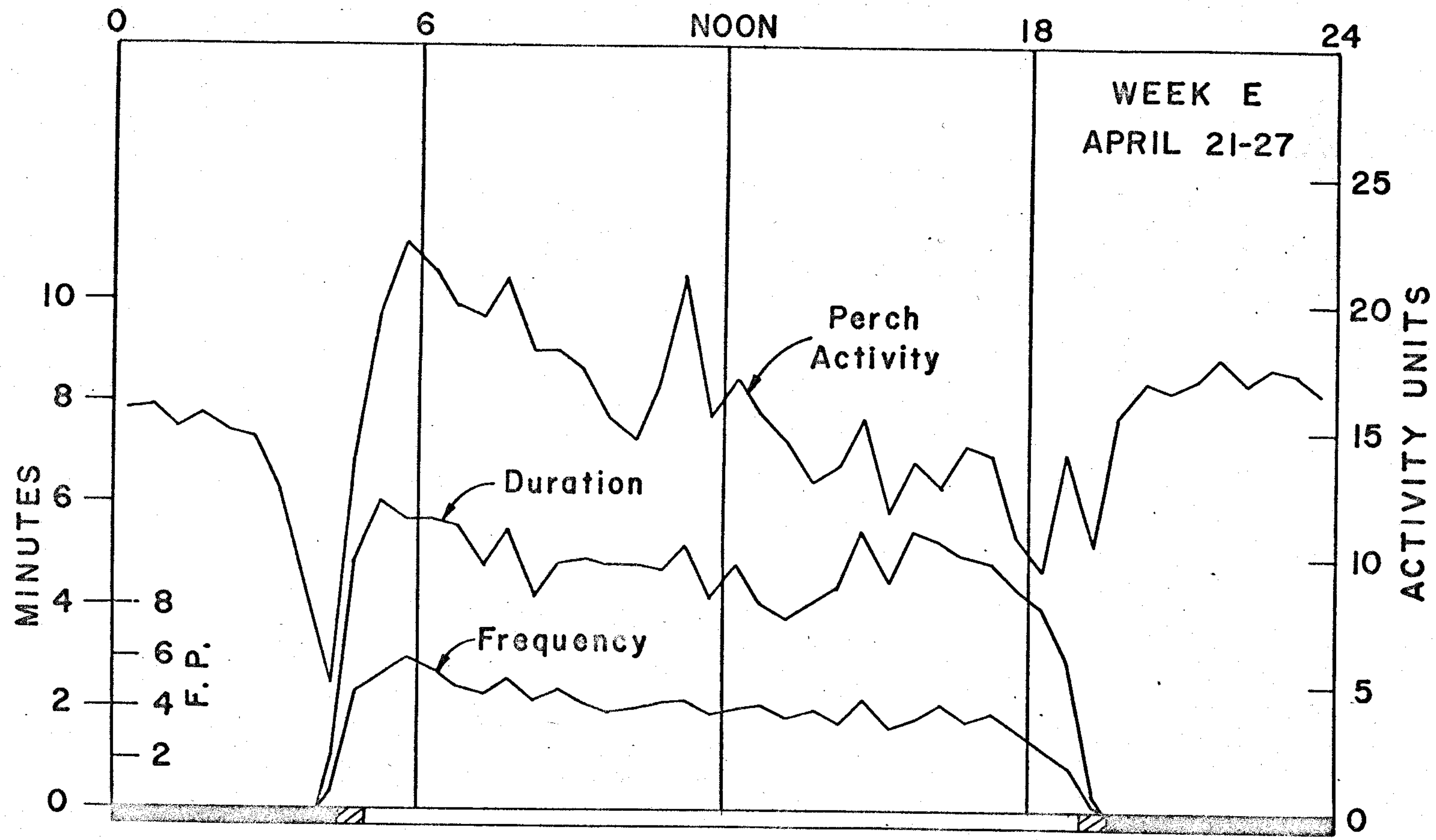

Figure 7. Mean perch and feeding activity of six male <u>Zonotrichia leucophrys gambelii</u>. See Figure 3.

Table I.

Summary of average data for each week of analysis.

Week	Temperature (C.)	Photoperiod (hr.)	Feeding Day (hr.)	Duration * (1)	Duration * (2)	Frequency ** (1)	Frequency ** (2)
A	1.4	12.43	11.68	5.1	128	3.8	96
B	3.5	13.38	12.33	3.6	97	3.1	83
C	7.5	14.01	13.17	3.8	112	3.3	94
D	11.8	14.57	13.95	4.7	142	3.6	107
E	10.4	15.11	13.99	4.5	140	3.9	120

*Duration: (1) = min./half-hour/bird day

(2) = min./bird/day

**Frequency: (1) = feeding periods/half-hour/bird/day

(2) = feeding periods/bird/day

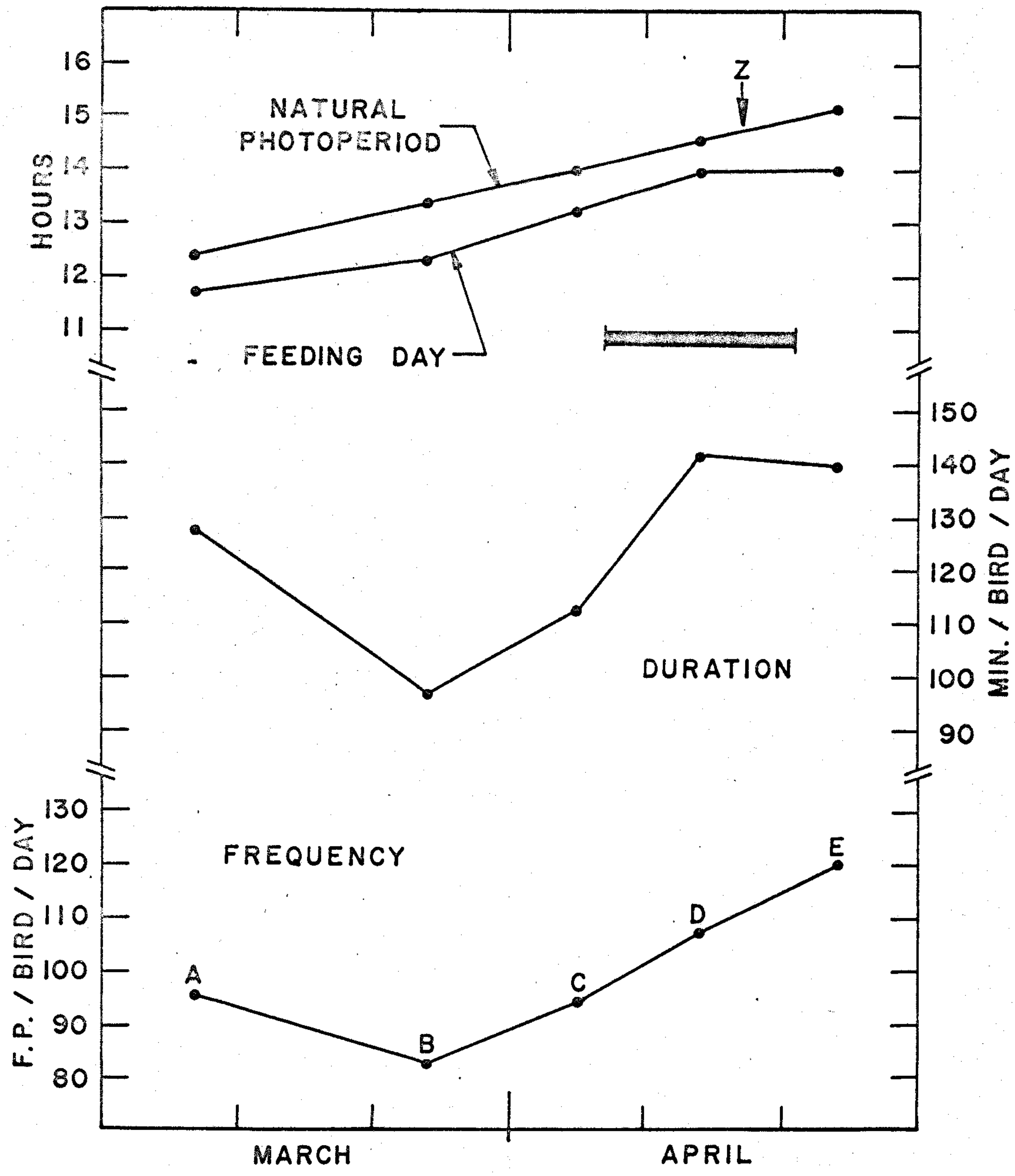

Figure 8. Comparison of the photoperiod, length of feeding day, total duration, and total frequency for each week of analysis. Z-arrow indicates onset of Zugunruhe; black bar, period of maximum fattening.

the feeding day is, respectively, for each week: 94, 92, 94, 96 and 93. The percentage of time that the birds spent at the feeder during the feeding day was 18, 13, 14, 17, and 17, respectively.

The relationship between the initiation and termination of the feeding day with sunrise and sunset is illustrated in Figure 9. The data of ten birds was averaged over five-day intervals. It is readily apparent that the inception of the feeding day was synchronized with the sunrise. Only a slight deviation from this pattern is observed at the onset of *Zugunruhe*. The termination of the feeding day, however, was somewhat independent of the sunset. During most of March the feeding day ended at approximately the same time, 1740 hours. There was then a gradual extension of the feeding day towards the end of civil twilight until the onset of *Zugunruhe*. At this point the termination of the feeding day became constant at about 1840 hours regardless of the increasing photoperiod in the evening.

The mean daily perch activity is illustrated for each week by the upper-most line in Figures 3 through 7. The pattern represents the total number of activity units in each half-hour per bird per day.

Although analyzed in a different manner, the diurnal and nocturnal patterns resemble closely those obtained by Farner, Mewaldt and King (1954). The diurnal pattern, before *Zugunruhe* (Figures 3, 4 and 5), was characterized by a high incidence of activity in the morning hours which declines to lower levels in the afternoon. At twilight there was an abrupt spurt of perch activity which lasts generally for a period of about one-half hour until almost dark. During this activity period there was essentially no feeding recorded, and

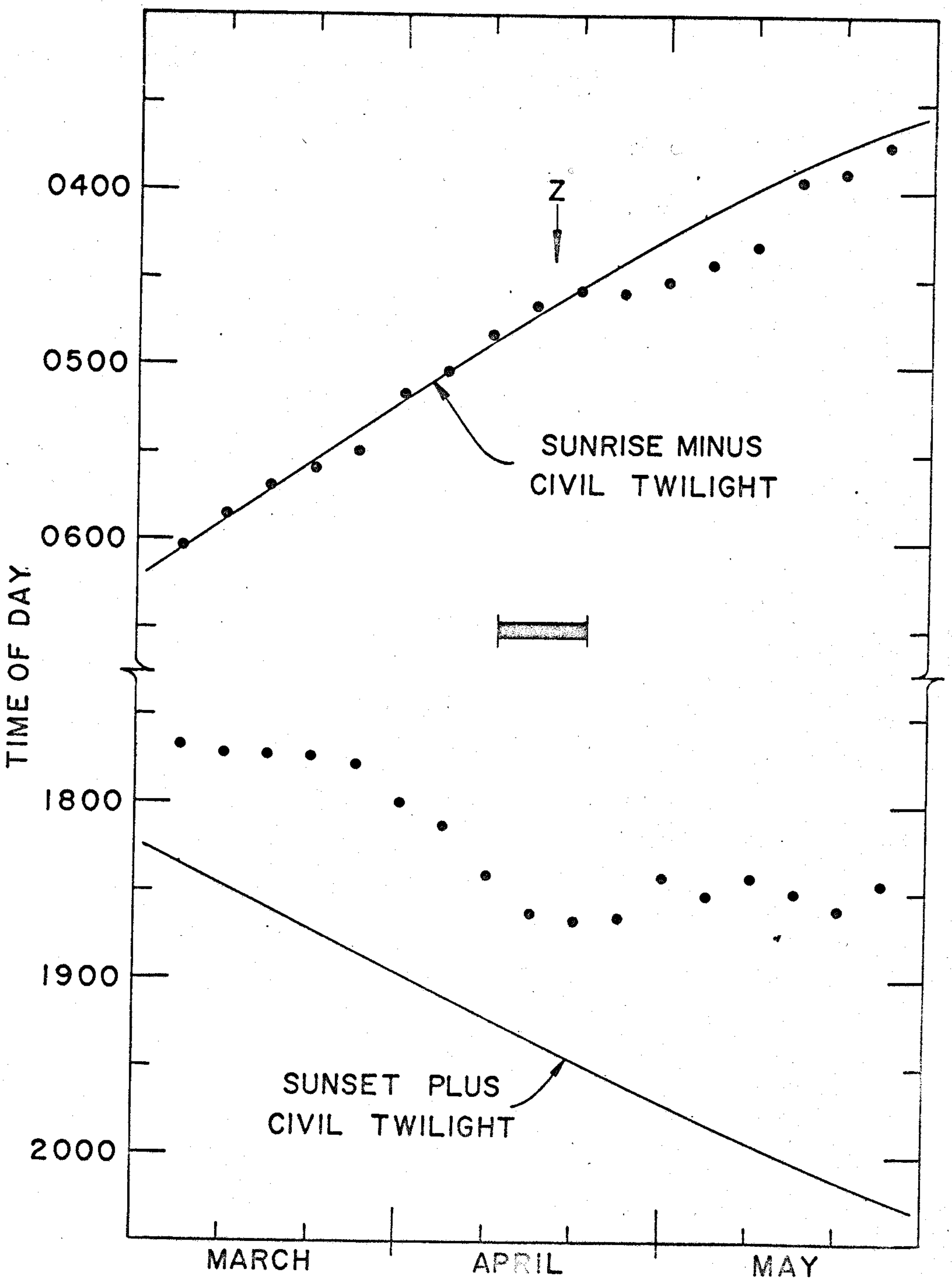

Figure 9. The initiation and termination of the feeding day. Each dot represents the mean of ten birds over a five-day period. Symbols as in Figure 8.

with the inception of a period of nocturnal unrest or Zugunruhe, the peak disappeared (Figures 6 and 7).

April 17 was the median date for the onset of Zugunruhe. It was first observed on April 11 and by April 23 was well established among all the birds except for one. The exceptional bird was unique in that it failed to show any appreciable nocturnal unrest until May 1 after a strong initial onset on April 23. The other five birds began Zugunruhe abruptly and maintained it intensely for at least five of the seven following nights. In relationship to fat deposition nightly unrest began, for each bird, at a point somewhere between mid-maximal and maximal body weight. Zugunruhe, at near maximal intensity, is illustrated along with the diurnal activity pattern in Figure 7.

The daily high and low environmental temperatures were averaged over five-day periods and are shown in Figure 2 (upper panel). During March and the first ten days in April the mean daily temperatures exhibited a fluctuating but steady increase. The highest temperatures were recorded during a span from April 11 to April 25 when the mean ambient temperature was 12°C. During this time the vernal fat deposition was at its highest rate of incidence and reached a plateau. The mean five-day temperatures dropped somewhat after this period but then gradually climbed through May until the termination of the experiment when the five day average was 11.4°C. The mean daily temperatures for each of the five weeks chosen for analysis are shown in Table I.

DISCUSSION

The purpose of this investigation was solely to determine if there was any change in the feeding pattern of Zonotrichia leucophrys gambelii in relationship to vernal fat deposition. It has been shown that the white-crown is stimulated into a greater appetite with the increasing spring photoperiod (King, 1961 a, b). Simultaneously with this increased energy intake, there is an alteration in the intermediary metabolism whereby the increased caloric intake is stored primarily as fat rather than glycogen (Farner, et al. 1961). It was surmised that a possible alteration in the feeding pattern, conceivably from a nibbling type to one of meal-eating, could be the mechanism responsible for the altered intermediary metabolism. This idea was prompted by investigations on force-fed rats and rats trained to eat their daily food requirements in two hours (Cohn and Joseph, 1959a, b; Hollifield and Parsons, 1962a, b).

Information concerning the feeding pattern of caged birds, as well as birds of feral populations, is surprisingly scarce. Measurements of the total food intake of birds in relationship to fat deposition are more numerous, but the actual pattern of the intake throughout the feeding day, as far as this author can determine, has not been studied. Studies concerning total food intake and food intake patterns are somewhat more evident among the mammals, particularly rats. These studies, carried out under a variety of experimental conditions, are concerned primarily with the general over-all regulation of food intake in relation to internal and external cues. Although the original idea for the present investigation was prompted by studies on rats, it is difficult to relate any of these works to the results of this investigation because of the rather wide separation of the two taxa. This is especially true when considering the feeding habits of the two animals. Rats feed both during the day and night hours while the white-crown is purely a diurnal feeder.

Baldwin and Kendeigh (1938) have reported the results of an unpublished study which summarized observations on the feeding activities of several species of birds, mostly passerines. The results indicate that, during July, small birds have a major feeding period in the morning and a minor feeding period in the evening. This pattern was correlated with the change in body weight which increased from a morning low to a late afternoon high by about three percent. Beer (1961) studied the winter feeding patterns of the non-migratory house sparrows by observing them at a feeding station. He found that the highest number of birds visiting the feeder typically occurred at two peaks: in the morning just after sunrise and in the evening just before sunset. The afternoon period was the time of greatest feeding activity. Except at extremely cold temperatures (below -20°C.), this pattern was evident with little variation at temperature ranges below 0°C. During the coldest days the morning peak was exaggerated and the evening peak suppressed. Although analyzed in a different manner, caged white-crowns exhibit essentially the same type of feeding pattern. There are two major feeding periods: one in the morning and one in the evening. In the case of the white-crown, however, the two major feeding periods differ in the manner by which the food is ingested. This is evident when the combined feeding patterns and perch activity pattern are examined.

The durational feeding pattern is represented by two peaks. The first peak occurs in the morning just after sunrise while the second occurs in the late afternoon. The frequency feeding pattern, represented by the number of visits to the feeder for each half-hour, shows a relatively higher frequency during the morning than during the afternoon. The higher morning frequency is concurrent with the morning durational peak while the lower frequency occurs with the increased durational feeding peak in the late afternoon. The perch activity is greatest during the morning hours and subsides to an afternoon low. An evening burst of perch activity occurs just before sunset. Therefore, the morning hours are characterized by high activity: a durational feeding peak, a high frequency of trips to the feeder (relative to the afternoon), and high perch activity. The afternoon shows a shift to a somewhat reversed situation. The durational peak is accompanied by a reduction in frequency and a reduction in motor activity.

This relationship between the number and duration of the feeding periods throughout the day, along with the perch activity pattern, suggest the biphasic type of feeding pattern for Z. l. gambelii. The first phase of the pattern begins at sunrise and lasts until about noon. During this time the birds are hyperactive and feeding is characterized by numerous feeding periods of relatively short duration which are interrupted by the motor activity of the bird. The second phase begins in the mid-afternoon when the perch activity has subsided. The feeding periods then become slightly less frequent than in the morning but of a longer duration. The perch activity appears to be restricted mainly to the acquisition of food. The afternoon feeding reaches its peak and comes to an abrupt end just prior to the evening burst of perch activity. During this activity period no feeding, in any case, was observed.

This general feeding pattern was evident more or less for each week, except that in weeks A and E there was some variation. Week A was unique in that the duration of feeding, once initiated, increased erratically throughout the day so that only one peak was reached just prior to the evening burst of perch activity. There was no midday low. Gibb (1956), studying the food and feeding habits of the rock pipit, found similar results. He states of the species: "...the urge to feed was least in the mid-morning while they had to feed especially hard in the afternoon to survive the winter nights". Beer (1961) also found that the house sparrow, in winter, showed the greatest feeding activity during the late afternoon peak. This may be the case for the wintering white-crown, since the day length during week A is relatively short and the temperature averaged near freezing (1.4°C.). This pattern evidently reflects the need for added energy intake to survive the long winter nights. The average duration per half-hour for week A was the highest recorded for the five weeks (5.1 min./half-hour/bird-day).

The duration of feeding pattern for week E differs from the other weeks in that the afternoon peak is reached much earlier in the day and then gradually declines. The frequency declines concurrently with the duration. During week E, when nightly unrest is near maximal, the evening spurt of perch activity disappears as already shown by Farner, Mewaldt, and King (1954). Wallgren (1954) has suggested that the elimination of this activity peak during actual migration has an energy-sparing effect. This decreased feeding and motor activity in the late afternoon, along with a probable earlier termination of the feeding day (see Figure 9), suggests a period of preparation for the pending migratory flight. It can be speculated that, during this time, the earlier ingested food is metabolized into fat with less additional food being ingested so that very little remains in the stomach at the time the bird actually takes flight. The elimination of the evening activity period provides time for rest in order to conserve energy as suggested by Wallgren.

The feeding day for caged white-crowns is initiated, with clock-like regularity, at the beginning of morning civil twilight. The slight deviation from this pattern, observed once Zugunruhe began, was probably due to the suppression of the normal migration. Since the birds are physiologically ready for migration and the urge to move is great, the morning onset of feeding was probably thrown off due to the persistent all-night hopping in the cage.

The termination of the feeding day exhibits some rather different and more interesting results. Throughout March the feeding day ended at a more or less definite time regardless of the increasing evening photoperiod. Near the first of April the feeding day showed a gradual lengthening which continued until the inception of Zugunruhe. At that time, the feeding day once again ended at a constant time irrespective of the termination of daylight. Evidently this lengthening of the feeding day denotes hyperphagia, since there is a utilization of the additional daylight for feeding. According to King (1961a) hyperphagia was first apparent for caged white-crowns, confined out of doors, from 4 to 8 days prior to the onset of fat deposition. His results also show that the gross energy intake declines with the initiation Zugunruhe. Since the onset of fat deposition for this investigation was determined as April 11 ± 1 day, hyperphagia should have begun approximately between April 3 and 7 and lasted until about April 17. The pattern exhibited by the termination of the feeding days is in good agreement with these dates and, thus, appears to reflect the onset and duration of the hyperphagia. It has already been pointed out (King, 1961a) that the increasing spring photoperiod directly stimulates Z. l. gambelii into over-eating and fat deposition rather than the mere existence of increased time for feeding. However, it is apparent that the increasing amount of evening daylight is utilized for acquiring additional food once hyperphagia has begun.

If the dates for the onset and end of hyperphagia, as calculated from King's data, are reasonably correct, any change in the diurnal feeding pattern concurrent with an increased gross energy intake should be most evident during weeks C (April 2-8) and D (April 11-17). Evidence for the observation of an increased energy intake in the feeding pattern for these two weeks is contained in Table I and Figure 8. The total duration of feeding per bird per day and the mean duration per half-hour per bird per day of each week increased above those recorded for week B. The frequency of feeding shows similar results. King (1964) reports that the O_2 consumption and the voluntary energy intake in Z. l. gambelii are inverse linear functions of the air temperature between 0 and 23°C. During this investigation the ambient temperature fluctuated continuously and always below 15° C. However, temperature does not appear to be the reason for the increase in duration or frequency of feeding, since each week shows an average increase in temperature above the preceding week. Week C shows an average increase of four degrees over week B, while week D shows an average increase of 4.3 degrees over week C. In these cases, the duration and frequency is increasing directly with temperature. Prior to hyperphagia the reverse is true. With an increase in temperature from week A to week B, there was a decrease in the frequency of feeding periods and amount of time spent at the feeder. Also, once Zugunruhe began, there was a leveling off of the duration of time spent at the feeder per week and per half-hour as shown for week E (Table I and Figure 8). Thus, it is apparent that the increase in the number of visits to the feeder and time spent at the feeder during weeks C and D is not due to any increased intake for thermoregulation but is actually due to a hyperphagia as reported by King.

Although an increase in energy intake was evident during weeks C and D, the pattern of the intake exhibited no significant change which might suggest a photoperiodic mechanism for altering the metabolism associated with fat deposition. The increased energy intake appears to be equally distributed over the general feeding pattern and the increased daylength. Cohn and Joseph (1959a, b) showed that rats force-fed twice a day will gain weight due to fat deposition. Hollifield and Parsons (1962 a, b) subjected rats to a single two hour per day feeding program in order to induce similar results. Normally, rats feed all day and all night with the minimum intake between 0700 and 1200 hours and the maximum intake between 0200 and 0500 hours (Siegel, 1961). If this extreme alteration of the food intake is necessary to alter the metabolism of Z. l. gambelii, it is definitely not visible in the results of this experiment. However, the white-crown is already well adapted for rapid lipogenesis and fat deposition once the photoperiod induces hyperphagia and, therefore, the change in feeding pattern need not be so spectacular. A simple shift in rate of intake only may be necessary. In reference to this, it might be pointed out that, although the durational feeding pattern obtained in this investigation is a good indication of the amount of food eaten at a feeding period, it is not conclusive. The actual amount of food eaten might be entirely different. A mechanical feeder which could automatically measure the food consumed by changes in weight for each half-hour would be a decided advantage in analyzing the food intake pattern. This method might reveal a change in the feeding pattern not evident by the method used in this study. Also, maintaining birds in constant temperature rooms under a simulated natural photoperiod may produce less variable and more interpretable results.

On the other hand, Feigenbaum, Fisher and Weiss (1962) have shown recently that "meal-eating" as opposed to "nibbling" has a reverse effect on the body composition of chickens. Evidently, the effects of imposed force-feeding or meal-eating is not of general occurrence in all animals and, thus, tends to support the results of this work.

In conclusion, Z. l. gambelii exhibits a feeding pattern in the cage similar to that of other wild birds. There are two major feeding periods, one in the morning and one in the late afternoon, which are separated by a midday trough. The results suggest that the morning feeding is characterized by numerous trips to the feeder of short duration while the afternoon is characterized by less frequent trips of longer duration. Hyperphagia was observed during the weeks prior to and during fat deposition but no significant change in the overall intake pattern was indicated. An altered feeding pattern does not appear to be the mechanism for the altered metabolism associated with fat deposition.

SUMMARY

Zonotrichia leucophrys gambelii is a strongly migratory race of white-crowned sparrow that exhibits a marked deposition of fat during the vernal migratory period. The physiological basis for fat deposition is a positive energy balance which results from a photoperiodically induced hyperphagia. Simultaneously with the increased caloric intake there is an adjustment of the intermediary metabolism so that the excess calories are deposited as fat rather than glycogen. The possible mechanism by which the intermediary metabolism is altered was the subject of this investigation. It was surmised that a photoperiodically stimulated change in the feeding pattern, along with hyperphagia, might induce the metabolic alterations necessary for lipogenesis and fat deposition. This idea was prompted by investigations with force-fed rats and rats limited to a two-hour feeding period per day.

Ten immature *Z. l. gambelii* were confined individually to small breeding cages modified to measure perch and feeding activity. The feeding activity was recorded by means of a mechanically operated feeder which electrically activated a pen on an Esterline-Angus recorder whenever the bird placed its head in the feeder to obtain food. The motor activity was registered similarly with each movement of a perch-activated microswitch. Recordings of the feeding and perch activity were made continuously throughout the premigratory and migratory periods of March, April and May. During the experimental period the birds were weighed at least twice a

week with observations of molt being recorded.

Prenuptial molt, fat deposition and Zugunruhe occurred essentially at the same time and magnitude as previously reported for caged and wild white-crowned sparrows. The median date for the onset of fat deposition was determined as April 11 $\pm$ 1 day. With fat deposition the mean body weight of six birds increased from 26.5 grams to 34.3 grams in 13 days. Prenuptial molt occurred at maximum intensity during the first ten days of April. The median date for the onset of Zugunruhe was determined as April 17.

The mean daily feeding and perch activity of six birds were determined for five one-week periods chosen in relationship to fat deposition. The feeding activity was analyzed by the frequency, the number of feeding periods in each half-hour per bird per day, and by the duration, the total number of minutes spent at the feeder in each half-hour per bird per day. The perch activity was presented as the number of activity units per half-hour per bird per day. The results indicated a general feeding pattern with two phases: a morning phase characterized by numerous trips to the feeder of short duration interrupted by the high motor activity of the bird, and an afternoon phase distinguished from the morning phase by low perch activity and relatively less frequent feeding periods of longer duration.

The feeding day was initiated almost invariably at the beginning of the morning civil twilight. The termination of the feeding day, before and after hyperphagia, was relatively constant and somewhat independent of the increasing evening photoperiod. During hyperphagia, the last feeding period occurred gradually later for each succeeding day.

Hyperphagia was evident in the feeding patterns of the weeks before and during fat deposition. For the week prior to fat deposition, the duration increased to 3.8 minutes/half-hour/bird/day and 112 minutes/bird/day from 3.6 minutes/half-hour/bird/day and 97 minutes/bird/day of the preceding week. The duration during the week of fat deposition increased to 4.7 minutes/half-hour/bird/day and 142 minutes/bird/day. The frequency showed similar results. The mean environmental temperature increased for each week.

During hyperphagia no change in the over-all feeding pattern was indicated from those of other weeks. Under the conditions of this investigation, it was concluded that there appears to be no change in the food intake pattern of *Z. l. gambelii* which can be construed as a mechanism for inducing metabolic alterations necessary for vernal fat deposition.

BIBLIOGRAPHY

1. Baldwin, S. Prentiss and S. Charles Kendeigh. Variations in weights of birds. Auk 55:416-467. 1938.

2. Beer, James R. Winter feeding patterns in the house sparrow. Auk 78:63-71. 1961.

3. Cohn, Clarence and Dorothy Joseph. Changes in body composition attendant upon force feeding. American Journal of Physiology 196:965-968. 1959a.

4. ________________. Effect of rate of ingestion of the diet on hexosemonophosphate shunt activity. American Journal of Physiology 197:1347-1349. 1959b.

5. Davis, Earle A. Seasonal changes in the energy balance of the English sparrow. Auk 72:385-411. 1955.

6. Farner, Donald S. The annual stimulation of migration: its physiologic basis. In: A. Wolfson's Recent studies in avian biology. Urbana, University of Illinois, 1955. p. 198-237.

7. ________________. Photoperiodic control of annual gonadal cycles. In: R. B. Withrow's Photoperiodism and related phenomena in plants and animals. Washington D. C., 1959. p. 717-750. (American Association for the Advancement of Science. Publication, no. 55)

8. ________________. Metabolic adaptations in migration. In: Proceedings of the XII International Ornithological Congress, Helsinki, 1958. Helsinki, Tilgmannin Kirjapaino, 1960. p. 197-208.

9. Farner, Donald S., James R. King and A. C. Wilson. The development of vernal migratory behavior in caged individuals of several taxa of Zonotrichia. Anatomical Record 128:546. 1957.

10. Farner, Donald S. and L. R. Mewaldt. The recording of diurnal activity patterns in caged birds. Bird-Banding 24:55-65. 1953.

11. Farner, Donald S., L. R. Mewaldt and James R. King. The diurnal activity patterns of caged migratory white-crowned sparrows in late winter and spring. Journal of Comparative Physiological Psychology 47:148-153. 1954.

12. Farner, Donald S., et al. A comparison of the effect of long daily photoperiods on the pattern of energy storage in migratory and non-migratory finches. Comparative Biochemistry and Physiology 2:125-142. 1961.

13. Feigenbaum, A. S., Hans Fisher, and H. S. Weiss. Effect of "meal eating" versus "nibbling" on body composition and digestive organ weight of normal and cropectomized chickens. Journal of Clinical Nutrition 11:312-316. 1962.

14. Gibb, John. Food, feeding habits and territory of the Rock Pipit, Anthers spinoletta. Ibis 98:506-530. 1956.

15. Groebbels, F. Zur Physiologie des Vogelzuges. Verhandlungen der Ornithologischen Gesellschaft in Bayern 18:44-74. 1928.

16. ________________.Bausteine zur einer Physiologie und Histophysiologie des Zugvogels. I. Mitteilung:Physiologische Untersuchungen an Helgoländer Zugvögeln. Zeitschrift für vergleichende Physiologie 12:682-702. 1930.

17. Helms, Carl W. and William H. Drury, Jr. Winter and migratory weight and fat field studies on some North American buntings. Bird-Banding 31:1-40. 1960.

18. Hollifield, Guy and William Parsons. Metabolic adaptations to a "stuff and starve" feeding program. I. Studies of adipose tissue and liver glycogen in rats limited to a short daily feeding period. Journal of Clinical Investigation 41:245-249. 1962a.

19. ________________.Metabolic adaptations to a "stuff and starve" feeding program. II. Obesity and the persistence of adaptive changes in adipose tissue and liver occuring in rats limited to a short daily feeding period. Journal of Clinical Investigation 41:250-253. 1962b.

20. Kendeigh, S. Charles. The role of environment in the life of birds. Ecological Monographs 4:299-417. 1934.

21. ________________. Effect of temperature and season on the energy resources of the English sparrow. Auk 66:113-127. 1949.

22. King. James R. The bioenergetics of vernal premigratory fat deposition in the white-crowned sparrow. Condor 63:128-142. 1961a.

23. ______________. On the regulation of vernal premigratory fattening in the white-crowned sparrow. Physiological Zoology 34:145-157. 1961b.

24. ______________. Oxygen consumption and body temperature in relation to ambient temperature in the white-crowned sparrow. Comparative Biochemistry and Physiology 12:13-24. 1964.

25. King, James R. and Donald S. Farner. Bioenergetic basis of light-induced fat deposition in the white-crowned sparrow. Proceedings of the Society for Experimental Biology and Medicine 93:354-359. 1956.

26. King, James R. and Donald S. Farner. Premigratory changes in body weight and fat in wild and captive male white-crowned sparrows. Condor 61:315-324. 1959.

27. Koch, H. J. and A. F. deBont. Standard metabolic rate, weight changes and food consumption of Fringilla c. coelebs L. during sexual maturation. Annales de la Société Royale Zoologique de Belgique. 82:1-12. 1952.

28. Lofts, B. and A. J. Marshall. The experimental regulation of Zugunruhe and the sexual cycle in Bramblings, Fringilla montifringilla. Ibis 102:209-214. 1960.

29. McGreal, Robert D. and Donald S. Farner. Premigratory fat deposition in the Gamble white-crowned sparrow: some morphologic and chemical observations. Northwest Science 30:12-23. 1956.

30. Merkel, F. W. Zur Physiologie der Zugunruhe bei Vögeln. Berichte des Vereins schlesischer Ornithologen 25:1-72. 1938.

31. ______________. Neuerer Untersuchungen über die Ursachen des Vogelzug-Triebes. Natur und Volk 70:167-178. 1940.

32. Odum, Eugene P. and James C. Major. The effect of diet on photoperiod-induced lipid deposition in the white-throated sparrow. Condor 58:222-228. 1956.

33. Schildmacher, Hans and Lore Steubing. Untersuchungen zur hormonalen Regulierung des Fettwerdens der Zugvögel im Frühjahr. Biologisches Zentralblatt 71:272-282. 1952.

34. Seibert, Henri C. Differences between migrant and non-migrant birds in food and water intake at various temperatures and photoperiods. Auk 66:128-153. 1949.

35. Siegel, Paul S. Food intake in the rat in relation to the dark-light cycle. Journal of Physiological Psychology 54:294-301. 1961.

36. Wachs, H. Der Wanderungen der Vögel. Ergebnisse der Biologie 1:479-637. 1926.

37. Wallgren, H. Energy metabolism of two species of the genus Emberiza as correlated with distribution and migration. Acta Zoologica Fennica 84:1-110. 1954.

38. Weise, Charles M. Nightly unrest in caged migratory sparrows under outdoor conditions. Ecology 37:275-287. 1956.

39. West, George C. Seasonal variation in the energy balance of the tree sparrow in relation to migration. Auk 77:306-329. 1960.

40. Wolfson, Albert. Regulation of spring migration in juncos. Condor 44:237-263. 1942.

41. _______________. Production of repeated gonadal, fat, and molt cycles within one year in the junco and white-crowned sparrow by manipulation of day length. Journal of Experimental Zoology 125:353-376. 1954.

42. Zedlitz, O. Vogelgewichte als Hilfsmittel für die biologische Forschung. Journal für Ornithologie 74:296-308. 1926.