DIURNAL FEEDING PATTERNS IN WHITE-CROWNED SPARROWS, *ZONOTRICHIA LEUCOPHRYS GAMBELII*

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One of the many activities of wild birds that have a regular daily periodicity is the procurement of food. In small birds feeding often has morning and evening maxima (Baldwin and Kendeigh, 1938; Lees, 1948; Owen, 1954; Gibb, 1954, 1956; Eber, 1956; Quay, 1957, 1958; Beer, 1961; Schmid, 1965). Insectivorous species are exceptional in that they feed most intensively in the afternoon when food is more readily available (Kuusisto, 1941; Verner, 1965). Many factors may modify the rate of caloric intake at a given time of day. For example, availability of food and water, air temperature, incident radiation, wind velocity, light intensity, photoperiod, social interactions, and reproductive status logically could all affect the daily pattern of caloric intake.

It is reasonable that seasonal changes in the feeding pattern may occur also. This would seem especially true of migratory species since they often show large regulated changes in energy intake and storage at the time of migration. One of the most intensively studied migratory birds is the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). In the wild and in captivity under natural photoperiods, this finch deposits fat at the times of vernal migration (King and Farner, 1956) and autumnal migration (King *et al.*, 1965). The vernal fattening is photoperiodically induced (King and Farner, 1956); it involves an alteration in intermediary metabolism with a shift in stored reserves from glycogen to fat (Farner *et al.*, 1960; King and Farner, 1965); and has its basis in an abrupt, regulated increase in appetite (King and Farner, 1956; King, 1961a, b). It is likely that changes occur in the diurnal pattern of caloric intake during this period of hyperphagia. However, daily and seasonal adjustments in the feeding pattern must be compatible with a host of other functions that may have a daily or seasonal periodicity in avian migrants. Among these is migratory movement itself. It was desirable, therefore, to investigate photoperiodically induced hyperphagia and the relationship between the temporal pattern of feeding and migratory behavior in *Z. l. gambelii* through the critical examination of seasonal changes in the daily feeding pattern. It is conceivable that adjustments of food intake during the daily feeding period have adaptive value in themselves when viewed within the context of the daily and seasonal routines of migratory birds.

Feeding activity has been measured in small captive birds by monitoring activity at food cups (Vaugien and Vaugien, 1962, 1963; Marsh, 1965; Moldenhauer, 1965) or by the frequency of pecking on a key following conditioning (Adler, 1963a, b). But the feeding pattern has not been investigated in a strictly quantitative manner by the continuous measurement of caloric intake. Such measurements have been obtained in this study of captive *Z. l. gambelii* under a variety of experimental conditions. Observations of free-living flocks on the Snake River Canyon wintering grounds and during vernal migration have provided a basis for interpretation of the results of experiments in the laboratory.

MATERIALS AND METHODS

FIELD INVESTIGATIONS

During the winter and spring of 1964 and 1965 observations were made on flocks of White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) overwintering in the Snake River Canyon near Pullman, Washington. The flocks were distributed along a 14-km section of canyon on the northeast side of the Snake River between Wawawai and Clarkston, Washington. They inhabited the floodplains between the edge of the river and the lower slope of the canyon wall. This strip is a mosaic of fruit orchards, feedlots, gardens, pastures, and natural vegetation that varies in width from only a few meters to nearly 400 meters. The Agropyron–Poa Zone of Daubenmire (1942) extends nearly to the river bottom in this area, but the flocks of *Z. l. gambelii* generally did not penetrate this habitat. Rather they occupied the edges and discontinuities of the floodplains. The agriculture in the area tends to modify the vegetation from year to year, and suitable habitat areas may be destroyed and others created over short periods of time. The topography and vegetation of the Snake River Canyon near the study area has been described recently by Buss and Wing (1965).

Wintering flocks in the canyon and flocks of vernal migrants on the nearby upland prairies were observed for 240 and 50 hours, respectively. Twenty-three flocks were observed routinely in the canyon in 1964 and 20 in 1965. The flocks ranged in size from 6 to about 150 birds. Birds were not marked, but individual flocks could be recognized because they were consistently found at the same locations with about the same number of birds. In each of the two years seven flocks were depleted (or reduced) by as much as 75 per cent by mist-netting; however, there was no evidence of subsequent infiltration from neighboring flocks despite the fact that infiltration may occur when there is a much higher density of wintering birds (Mewaldt, 1964).

It was necessary to determine the daily pattern of food intake in wild flocks as an adjunct to laboratory studies of feeding activity. Preliminary observations indicated that these birds foraged almost continuously throughout the day, but that the intensity of foraging varied considerably. A foraging index (FI) was therefore devised as an indicator of the relative rates of ingestion. A specific value was assigned for each five consecutive minutes, the standard observation period. FI is the product of the fraction of a flock actually engaged in feeding during the observation period and the estimated intensity at which feeding members were procuring food. To the latter, subjective integral values from 0 to 10 were assigned. For example, if 0.8 of the flock was feeding at an intensity of seven the assigned FI was 5.6 (*i.e.*, 0.8 × 7).

Observations of environmental conditions were made throughout the study. Air temperature was measured in the shade with a standard dry-bulb thermometer. Light intensity was measured with a Weston Model 756 photometer. Incident solar radiation was measured with a General Electric Model DW 50 radiometer. Animals were collected by shooting or with mist nets. Gonads were fixed in AFA for five days; transferred to 70 per cent ethanol for five days; and then weighed to the nearest 0.1 mg. Stomachs (proventriculus plus gizzard) were placed immediately in formaldehyde. The stomach contents were separated, with the aid of a dissecting microscope, and estimated volumetrically.

EXPERIMENTAL INVESTIGATIONS

Experimental birds were captured with mist nets from the Snake River Canyon population or from migratory flocks on the prairie near Pullman. The birds were held in a large outdoor aviary for at least two weeks before they were placed individually in cages, 41 × 22 × 26 cm. They were fed *ad libitum* with a chick starter mash with a caloric value of 4.5 kcal per gram dry weight. Water was available at all times. The experimental cages contained a central perch which activated a microswitch to give an index of locomotor activity (Farner and Mewaldt, 1953). This activity was recorded by an Esterline–Angus operations recorder and by digital counters that gave hourly totals of recorded hops.

The feeding activity of each bird was determined with an apparatus already described in detail (Morton, 1965a). Briefly, it consisted of a Plexiglass food cup suspended from a cantilever beam of spring steel. Strain gages at the base of the beam transduced weight change (food withdrawal) into an electrical signal that was amplified and recorded graphically once every 15 minutes for up to 10 channels, or recorded continuously for a single channel. Spillage was negligible with this system except for occasional birds that tended to scatter their food, and these were not used in the experiments. It was possible with this equipment to determine simultaneously the daily pattern and total of caloric intake for up to 10 birds. It was possible also to determine the exact time and amount of food consumed by one bird at a time by immobilizing the unit at a particular channel. Feeding and locomotor activities under constant conditions were determined for birds in individual sound-proof isolation chambers with inside dimensions of 31 × 50 × 47 cm. Within a chamber each bird was confined to a standard experimental cage.

RESULTS

FLOCK TERRITORIES

In the Snake River Canyon the territories of the wintering flocks are firmly delineated by early December. The territories are linear in sequence because the suitable habitat is usually too narrow to accommodate more than one flock between the canyon wall and the river. The territories do not overlap; they are frequently separated by unsuitable habitats such as an open pasture or orchards so that opportunity for contact is greatly reduced. White-crowned Sparrows are known to occupy stable winter territories with little or no overlap of range or interchange of members (Price, 1931; Blanchard, 1941; Blanchard and Erickson, 1949).

ANNUAL EVENTS

The conspicuous events in the annual cycle of the Snake River Canyon population were followed during 1964 and 1965. The time and the magnitude of the changes in fat reserves, testicular development, prenuptial molt, and the time of migration agreed closely with the results of previous investigations of this population (King and Farner, 1956, 1959; Farner and Wilson, 1957; King *et al.*, 1963). A more detailed presentation of these data has been given by Morton (1966).

FEEDING MODES

A variety of motor patterns is exhibited during foraging activities. Most often the birds hop or run along the ground pecking several times after each stop, sometimes pausing to scratch vigorously and then peck. Open, rather bare ground is essential for this kind of foraging, and indeed it seems to be an essential component of their habitat.

The birds often feed exclusively on low green grass for hours at a time. Grass blades are nipped off directly from above or the bird tilts its head to the side, snips off the top one to two centimeters of a blade, then quickly turns the piece and swallows it end first. Birds often move slowly over the tops of boulders gleaning food from the surface. They also move through the tops of bushes and low trees when they are taking buds. They even climb along the large limbs and leaning trunks of trees searching the bark for food. They feed avidly on arthropods, and individuals often engage exclusively in foraging activities associated with taking arthropods. Storer (1919) and Mailliard (1919) have reported flycatching activities in a number of fringillid species; Mailliard observed *Z. l. nuttalli* catching air-borne arthropods by leaping short distances into the air for them. Brown (1954) and Morton (1965b) have reported the same behavior for *Z. leucophrys* and *Z. querula*. Usually in *Z. l. gambelii* the taking of air-borne arthropods is incidental to their other foraging activities. However, during warm days, particularly in the late afternoon when flying insects are highly visible in the low-angled sunlight, the birds take this food source exclusively for periods as long as 20 to 30 minutes. Often they take insects from a prominent perch in a manner similar to that of a tyrant flycatcher.

FEEDING HABITS

To supplement the field observations of feeding activities, the stomach contents of 88 birds collected from January to May in both years were analyzed. Several

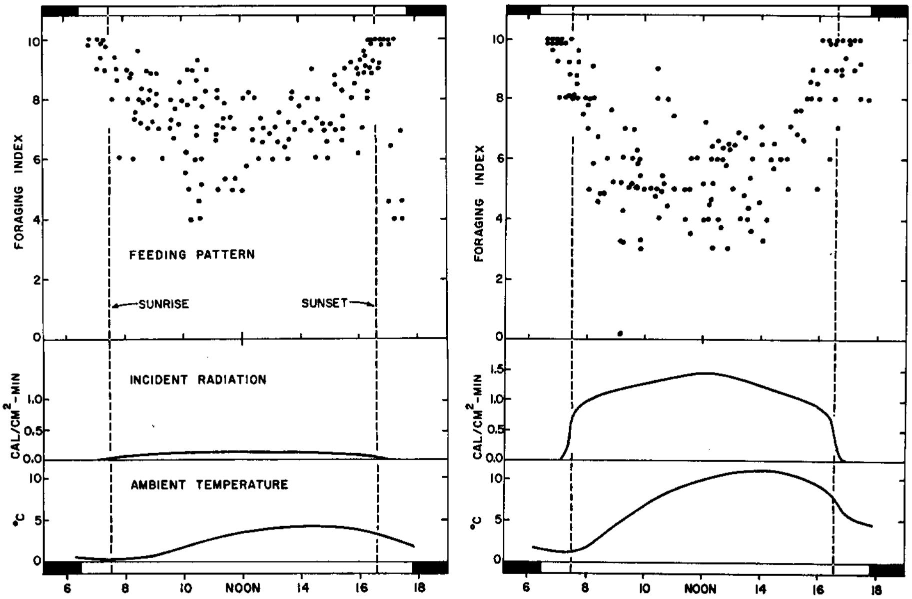

Figure 1. Diurnal feeding patterns of wild *Zonotrichia leucophrys gambelii* in midwinter. Left: data from five cold, cloudy days. Right: data from six warm, sunny days. Daily trends in air temperature and insolation are also shown. Horizontal bars represent the photoperiod.

changes in the relative importance of the various foodstuffs occurred with season. Seeds, particularly those of pigweed (*Amaranthus spp.*), were present in the greatest amount in January. Beal (1910) also found that pigweed was the most common kind of weed seed eaten by White-crowned Sparrows. In February there was an increase in consumption of green plant material. Direct observations revealed that a major shift in the type of plant material taken occurred in late March and early April when the birds reduced their intake of grass and began to feed extensively on buds, particularly those of hackberry (*Celtis douglasii*). With the onset of mild spring weather there was a noticeable increase in invertebrates, especially of flying insects. This was reflected by about a 125 per cent increase in animal material in the stomachs and by an increase in insect-chasing activities of birds under observation.

These data cannot be interpreted rigorously because of the differential rate of digestion that occurs in bird stomachs, even after death (Dillery, 1965). Coupled with direct observations, however, they are useful for depicting seasonal changes in food habits.

Feeding Patterns of Wild Flocks

The diurnal feeding patterns of wild flocks varied considerably with environmental conditions. On cold, cloudy days (fig. 1, left) the birds foraged at the maximum possible intensity in the early morning (FI = 10), and in the late afternoon just before they went to roost. On warm, sunny days (fig. 1, right) there was a greater decrease in feeding after the initial early-morning maximum and hence a more distinctly bimodal feeding pattern than on cold, cloudy days. The early-morning decrease in the intensity of feeding began at about the time the birds were first exposed to sun-

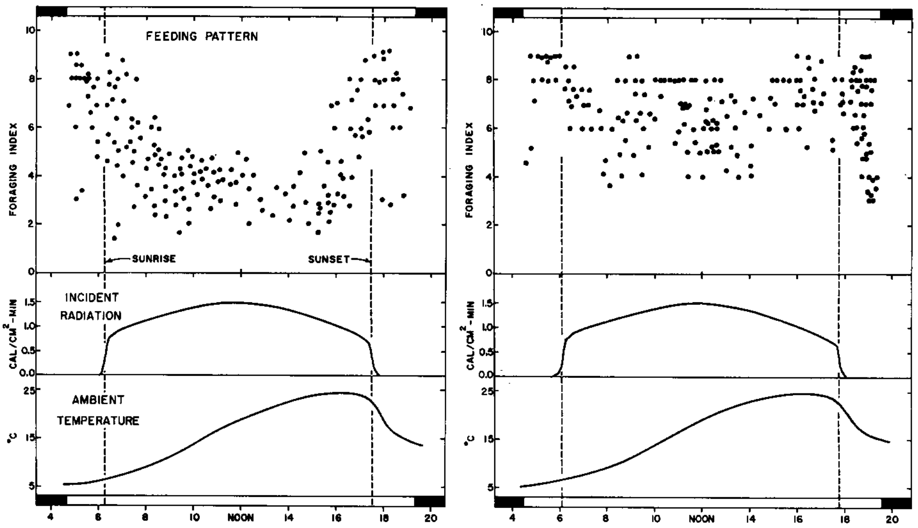

Figure 2. Diurnal feeding patterns of wild *Zonotrichia leucophrys gambelii* in April. Left: data from seven days in early April. Right: data from five days in late April, during hyperphagia and just prior to migration. Daily trends in air temperature and insolation are also shown. Horizontal bars represent the photoperiod.

shine. At this time the level of solar radiation increased from near zero to about 1 cal/cm^2–min within a few minutes after the sun cleared the canyon rim. The ambient temperature did not begin to rise until about 30 minutes later. Throughout the morning and early afternoon there was a continued decrease in feeding intensity as the ambient temperature increased. At sunset insolation levels and ambient temperature dropped quickly. A peak in feeding activity occurred at this time. These birds do not have a functional crop so they cannot accumulate food in this organ in the evening as is the case, for example, in the Savannah Sparrow, *Passerculus sandwichensis* (Quay, 1958). The transition from feeding to roosting occurs over about a 30-minute period during which the proportion of foraging birds decreases until near the end of civil twilight when all have settled in the roosting cover.

Later in the season the weather was consistently milder, with higher ambient temperatures and solar radiation levels. The birds did not forage at the maximum possible intensity in the early morning and late afternoon, and the midday decrease was more definite than it was earlier in the season (fig. 2, left). During the last two weeks in April the birds were hyperphagic, feeding intently and at a fairly constant rate throughout the day (fig. 2, right). Flocks migrating through the nearby prairies in early May displayed this same type of feeding pattern.

Feeding Patterns of Outdoor Captives

To study diurnal patterns of food intake more assiduously, especially during the period of hyperphagia, the food intake of *Z. l. gambelii* confined outdoors under natural photoperiod and temperature was measured continuously from February to June. Nearly all feeding was accomplished during the light period, and feeding ended in the evening at a higher light intensity than when it began in the morning (fig. 3). There is no obvious correlation between these winter feeding patterns and a repre-

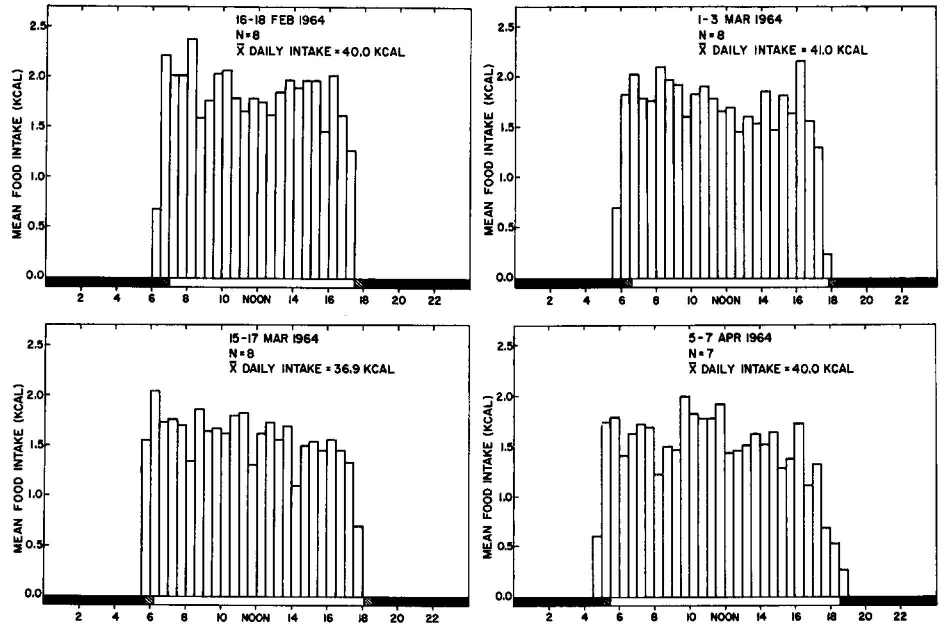

Figure 3. Diurnal feeding patterns of *Zonotrichia leucophrys gambelii* caged outdoors. Horizontal bars represent the photoperiod, the hatched areas showing the duration of civil twilight.

sentative winter locomotor activity pattern (fig. 4, upper). Energy intake during this wintering period was regulated at a maintenance level, and body weights were relatively stable. The prenuptial molt occurred in its usual intensity and temporal sequence in the annual cycle. During the period of hyperphagia, as reflected in increased body weight and food intake, the feeding pattern (fig. 5, upper) was, in its salient features, like that of maintenance feeding. As the birds attained maximum body weight and began to show *Zugunruhe* (fig. 4, lower), a dramatic change occurred in the feeding pattern. Abruptly they began to cease feeding about 75 minutes before the end of civil twilight and the onset of *Zugunruhe* (fig. 5, lower). Previously they had always stopped feeding 30 minutes or less before the end of civil twilight.

To gain information about this change in the termination of feeding and its relationship to *Zugunruhe*, some simple experiments were performed. One group of three birds (experimentals) was deprived of food for various periods, and another group of three (controls) was allowed to feed freely. The experiments were not performed on consecutive days nor necessarily on the same groups. In the first experiment (fig. 6a) the food was removed 60 minutes before the usual time that feeding voluntarily ceased and was not returned that night. The control birds stopped feeding at the usual time, and *Zugunruhe* commenced in both groups at the usual time. These birds were in sight and sound of one another, but their normal, slightly different, individual starting times for *Zugunruhe* were maintained. In the next experiment (fig. 6b) the food was removed 270 minutes prior to the usual cessation of feeding. It was still daylight when the food was returned, but the experimental birds did not eat! *Zugunruhe* began at the expected time. In another manipulation (fig. 6c) the experimental birds were deprived of food for 330 minutes and presented with food 30

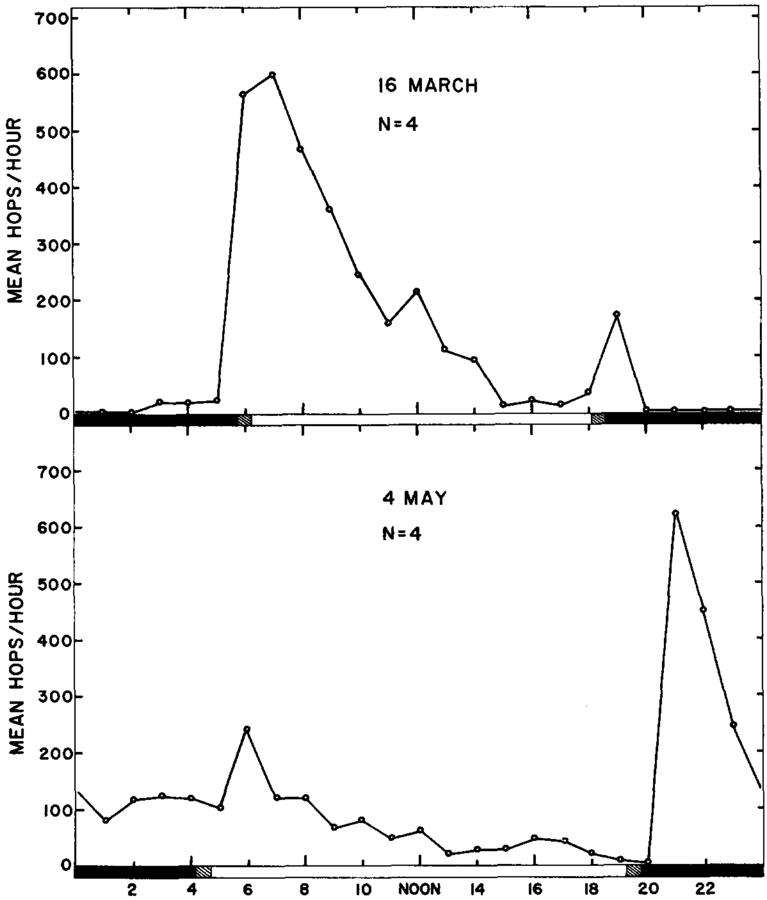

Figure 4. Diurnal patterns of locomotor activity in *Zonotrichia leucophrys gambelii* caged outdoors. Upper: pattern shown in winter. Lower: pattern during migratory readiness, showing *Zugunruhe*. Horizontal bars represent the photoperiod, the hatched areas showing the duration of civil twilight.

minutes before the usual cessation of feeding. They fed during the next 30 minutes but not with unusual intensity, and stopped feeding at the same time as the controls. Once more *Zugunruhe* began as usual. In a final, more drastic, starvation regime (fig. 6d), the period of deprivation was enforced for 570 minutes, and the food was returned 90 minutes before the normal termination of feeding. The experimental birds began feeding at once and continued until it was nearly dark, but the onset of *Zugunruhe* was not affected.

The period of deprivation had some effect on recorded locomotor activity (table 1). The experimental birds tended to become more active as deprivation time increased, and during the 570-minute period of deprivation they were significantly more active than the control birds.

Pertinent to the above are field observations made on flocks of spring migrants during stopovers on the prairie near Pullman. In 1964 it was apparent that migrants left the prairie in at

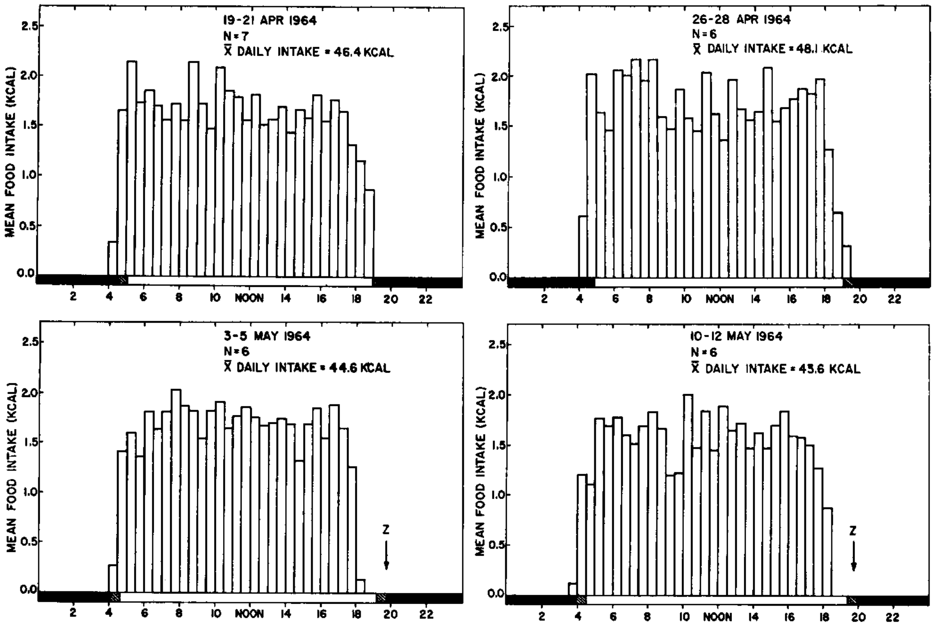

Figure 5. Diurnal feeding patterns of *Zonotrichia leucophrys gambelii* caged outdoors. Horizontal bars represent photoperiod; vertical arrows, onset of *Zugunruhe.*

least two major movements, one on the night of 7 May and the other on the night of 15 May. On 7 May continuous observations were made on a flock of 23. These birds stopped feeding about 60 minutes before the end of civil twilight and went to roost in nearby bushes. Since the flock could not be found the next morning, it was assumed to have joined in the general exodus that occurred during the night. Other flocks of migrants observed on the three consecutive previous evenings prior to the general movement fed until 30 minutes or less before the end of civil twilight. Additional observations were made on a flock of 28 that was identifiable because of its persistent appearance at a specific site and because it contained a Golden-crowned Sparrow (*Z. atricapilla*). On three consecutive evenings (12 to 14 May) the birds in this flock stopped feeding and went to roost about 30 minutes before the end of civil twilight. On the evening of 15 May, except for some sporadic foraging by a few individuals, they ceased feeding about 60 minutes before the end of civil twilight. The next morning only four birds could be found at the site, and again a general movement from the prairie occurred during the previous night. Two movements were also observed during the spring migration of 1965. One occurred on the night of 26 April and the other on the night of 7 May. A flock of 21 was observed at intervals during the day and then continuously in the evening until dark on the three nights previous to the first movement. These birds discontinued foraging 15 minutes earlier than usual on the evening just before migration evidently occurred. Especially good observations were obtained on a flock of 24 that appeared on the prairie on 2 May. This group was observed intermittently during the day and continuously every evening until dark from 2 May through 7 May. The birds fed far into civil twilight on 2 May through 5 May and stopped feeding at a light intensity of 2 to 10 lux. On 6 May they stopped feeding 20 minutes earlier than usual and at a time when the ambient temperature was 10 C and the sky was overcast. The flock was still present the next morning; it ceased foraging that evening (7 May) about 30 minutes earlier than it had on 2 to 5 May. These birds could not be found in the area on the next day. It should be emphasized that there was not perfect synchrony in the termination of feeding in any of these flocks, and several minutes elapsed between the time the first and last birds settled in cover. Also, individuals often returned to the ground several times

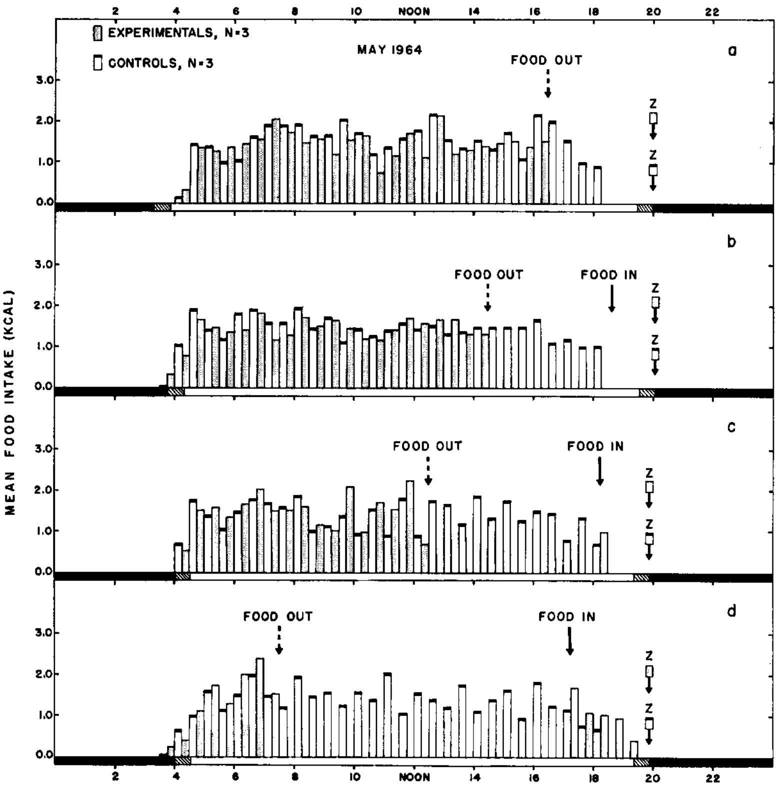

Figure 6. Diurnal feeding patterns of *Zonotrichia leucophrys gambelii* caged outdoors. Experimentals were deprived of food for periods indicated. Controls were not deprived. Bar-arrows indicate beginning of *Zugunruhe* for individual groups; horizontal bars, the photoperiod, with the duration of civil twilight shown as the hatched area.

for brief bursts of foraging before finally ceasing to feed altogether. Even in the flocks that as a whole stopped foraging 30 minutes or so earlier than usual, a few birds would sometimes continue to forage sporadically. Perhaps it is significant that a few birds were sometimes still present after the subsequent migratory movement.

A critical but unknown factor is the actual time at which migratory flight begins in these wild flocks. Gaymer (1962) has indicated that migratory flight begins before dark in *Z. albicollis*, but this was not true for the flocks of *Z. l. gambelii* that I have observed. On the evenings just prior to migration the birds were obviously "restless," *i.e.*, after foraging had ceased they would flutter and hop around in the bushes at least until it was too dark to see them any longer. Some particularly informative observations were made on the flock that migrated the night of 7 May 1965. At 1850 when the light intensity was 740 lux the flock as a whole had ceased foraging, and the birds were sitting in dense bushes five meters high. They preened, hopped, or fluttered from branch to branch or sat quietly for the next 45 minutes. At 1945 no light could be detected with the photometer. The birds could be seen, however, until 2000 silhouetted against the skyline. By then the moon and stars were plainly visible in the clear sky. At 2030 a search was made through the bushes with a flashlight, but the birds were no longer there. The evidence is circumstantial to be sure, but it suggests that this flock could have begun its migratory flight between 2000 and 2030.

TABLE 1

PERCENTAGE OF TOTAL DAILY (24-HR) RECORDED HOPS OF *Zonotrichia leucophrys gambelii* DURING PERIODS OF FOOD DEPRIVATION. $N = 3$ FOR EACH TREATMENT.

Minutes of deprivation	Experimentals (deprived)	Controls (not deprived)
60	3%	2%
270	12	8
330	43	24
570	60[a]	34

[a] Significantly different from controls ($P < 0.05$).

EFFECTS OF AIR TEMPERATURE ON FOOD INTAKE

The mean total daily intake in relation to mean daily air temperature in birds confined outdoors but always in the shade is shown in figure 7. The onset of hyperphagia on about 10 April, as evidenced by the increased food intake and by the sudden increase in body weight, made it necessary to compare food intake and temperature in two separate time periods, before and after 10 April. Also, the prenuptial molt was confined mostly to the former period. Correlation coefficients for these two periods were calculated through an analysis of covariance (Moroney, 1956). When food intake and temperature were compared on the same day from 12 February to 9 April, $r = -0.254$ ($0.10 > P > 0.05$). During the same period, $r = -0.313$ ($0.05 > P > 0.02$) when food intake was compared with the temperature of the previous day. For the period 10 April to 19 May, $r = -0.567$ ($P < 0.01$) when the two are compared on the same day, and $r = -0.464$ ($P < 0.01$) when food intake is compared with the temperature of the previous day. Obviously the ambient temperature did have an effect on food intake, but probably not on the diurnal pattern of feeding.

FEEDING PATTERNS UNDER ARTIFICIAL PHOTOSTIMULATION

"Premigratory" hyperphagia and fattening can be induced in *Z. l. gambelii* by exposing them to artifically lengthened daily photoperiods (King *et al.*, 1960). Gonadal hypertrophy, migratory restlessness (*Zugunruhe*), and an incomplete molt are induced concurrently by this treatment. It seemed advisable to examine the changes in feeding pattern during the development of hyperphagia induced by long artificial photoperiods.

The experimental birds were brought indoors in late January and held at 19° C for 92 days on an eight-hour photoperiod (8L 16D). One group of four (experimentals) was exposed to a photoperiod lengthened in one increment to 16 hours (16L 8D). The remaining group of four (controls) was retained on 8L 16D for the duration of the experiment. All light intensities were 200 lux. Recorded locomotor activity was light throughout the experiment, but *Zugunruhe* probably began in the experimental birds after 14 days of 16L 8D. By the 15th day of photostimulation the experimental birds had begun to show light molt in the capital, spinal, and ventral tracts. The control birds did not molt. Thirty-five days after the beginning of the experimental lighting regime, all birds were killed. The mean testicular weight was 1.9 mg (SD = 1.33) for the control birds and 317.8 mg (SD = 30.0) for the experimental birds.

The feeding patterns of the experimental group for the 10 days previous to the

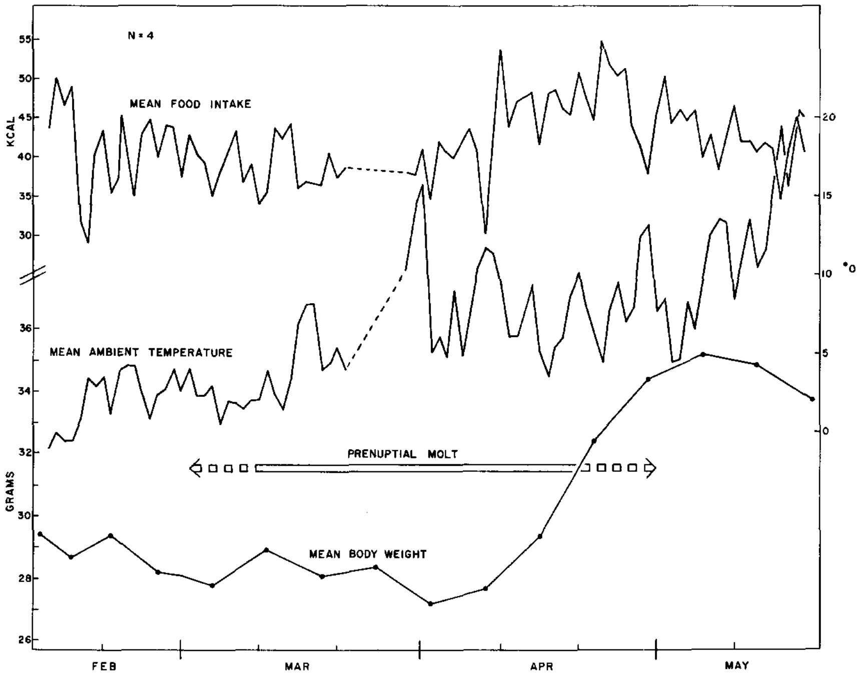

Figure 7. Relationship of mean ambient temperature to mean daily food intake in *Zonotrichia leucophrys gambelii* caged outdoors. Seasonal variation in body weight and course of prenuptial molt are also shown.

increase in daily photoperiod, days 1 to 10, and selected three-day intervals thereafter are shown in figure 8. On day 11 the experimental birds were exposed to the lengthened photoperiod, and they showed an immediate increase in food intake as they kept eating during the added light period. Within a week food intake during the first hours of light had declined, and the feeding pattern was permanently altered to a parabolic form similar to that of hyperphagic birds held outdoors (compare fig. 5). Doubtless it is not diagnostic of the hyperphagic condition because the parabolic pattern seems to be typical of birds on long photoperiods whether or not they are photostimulated (*i.e.*, not photorefractory).

The total daily intake of individual birds shows that a great increase in food intake occurred on the very first long day (fig. 9). This suggests that the abrupt doubling of the photoperiod has a permissive effect on total daily intake. In two birds this resulted in a detected weight increase, and in two it did not. Apparently this perturbation was corrected by the fifth long day. Subsequently, there was another, more extended, increase in food intake. This period of elevated intake undoubtedly represents the usual photoperiodically induced hyperphagia and accompanying increase in weight. The individual control birds maintained fairly stable body weights and food intake throughout the experiment.

FEEDING PATTERNS IN CONTINUOUS ILLUMINATION

The early termination of feeding in birds prepared for migration and the late-afternoon increase in feeding activity observed in wild flocks suggest that these birds

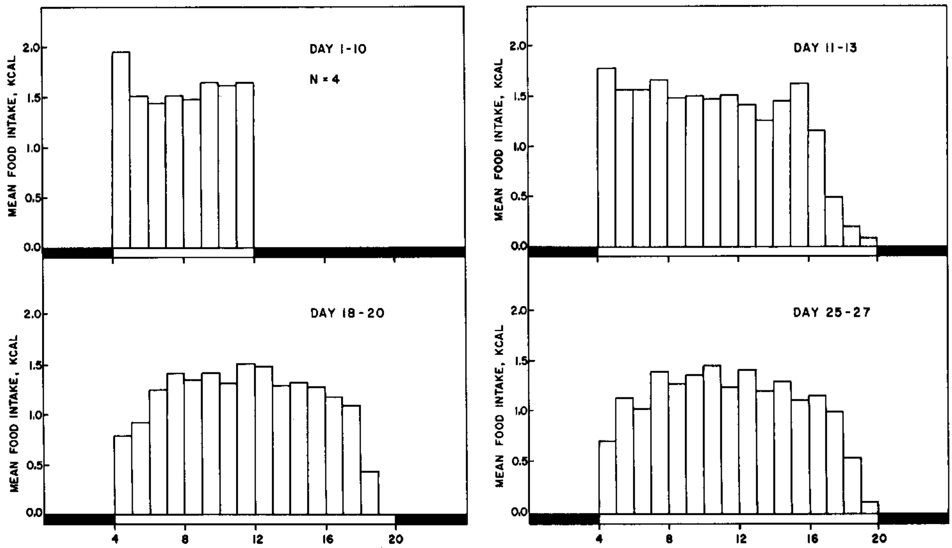

Figure 8. Feeding patterns of photosensitive *Zonotrichia leucophrys gambelii* caged indoors. Eight-hour photoperiod on days 1–10. Sixteen-hour photoperiod on days 11 and beyond.

may have a diurnal rhythm in appetite that is at least partially independent of thermal stimuli. To explore this possibility photorefractory birds were held individually in isolation chambers and entrained for at least 14 days on a 12L 12D schedule before being placed on continuous light (LL). Food intake and locomotor activity were measured continuously. Air temperature was held constant at 19° C.

The time and amount of each food withdrawal by an isolated bird is shown in fig. 10. Although the onset and termination of feeding on LL were not perfectly abrupt, the terminations appear to occur about every 22.9 hours. This bird had been exhibiting intense locomotor activity in the dark, but when LL conditions were imposed it tended to hop about much less in the cage, and its movements tended to show a periodicity about like that of feeding. It is interesting that this bird ate only during the first 10 hours of the entraining photoperiod. The food intake of all four birds tested under free-run conditions had a circadian rhythm.

DISCUSSION

FACTORS AFFECTING THE DIURNAL FEEDING PATTERN

More than three decades ago Kendeigh (1934) emphasized the importance of microclimatic adaptation to the distribution of birds. More recently Johnson's (1957) observations on the microclimatic preferences of small arctic birds reveal that they utilize favorable microclimates when possible, but that their activities are dictated primarily by the location of their food supply. The same principle was found to apply in the present study. The wild birds did not restrict their foraging to a particular area except during high wind or heavy rain. At those times they tended to avoid open ground and foraged almost exclusively in sheltered spots such as in and around weed piles and brushy fencerows. Neither light rain nor intermittent snow seemed

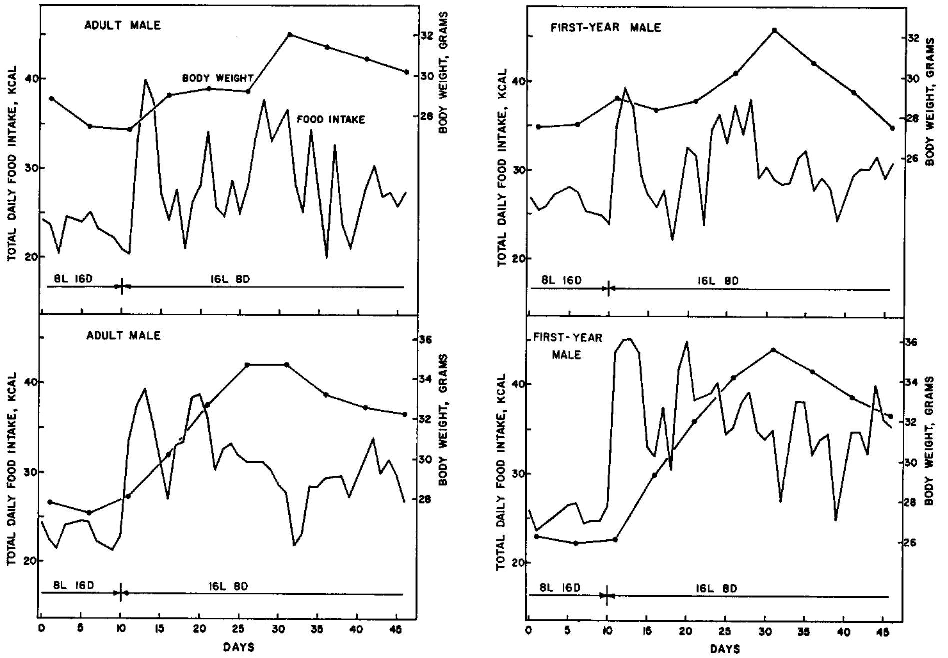

Figure 9. Total daily food intake and five-day body weights of photosensitive *Zonotrichia leucophrys gambelii* caged indoors. Eight-hour photoperiod on days 1–10. Sixteen-hour photoperiod on days 11 and beyond.

to affect their choice of foraging sites. Under no circumstances did the prevailing weather conditions appear to prevent them from obtaining food. During the most severe conditions of wind and rain the rate of food intake increased, if it changed at all, and the birds continued to forage effectively through the simple expedient of remaining in a favorable microclimate.

Food intake has been demonstrated repeatedly to be a function of environmental temperature. For example, field observations indicate that air temperature and feeding intensity are inversely related on a day-to-day basis (Gibb, 1954, 1956, 1960; Eber, 1956; Helms and Drury, 1960; Murton *et al.*, 1964; Inozemtsev, 1964; Verbeek, 1964; Pulliainen, 1965, 1966; Bailey, 1966). Laboratory studies have generally corroborated these observations (Kendeigh, 1949; Seibert, 1949; Davis, 1955; Rautenberg, 1957; Steen, 1957; West, 1960; Cox, 1961; King, 1964). However, Merkel (1958) and Hart (1962) found no consistent correlation between food intake and ambient temperature, suggesting that environmental factors other than air temperature may also affect the daily feeding pattern.

In the present study it was found that total daily food intake and ambient temperature were inversely correlated in captives held outdoors. However, the effect was usually subtly distributed throughout the day and was not detectable in a change in the diurnal pattern of food intake. Wild flocks exhibited more intensive feeding during midday on cold, cloudy days than on warm, sunny days, but this effect may be related primarily to levels of insolation.

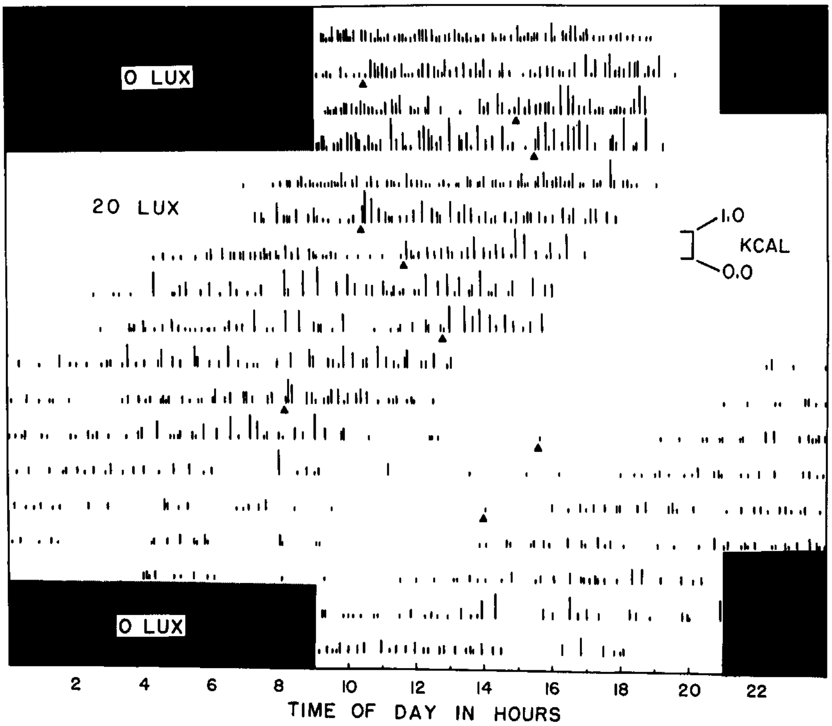

Figure 10. Circadian rhythm of feeding of an adult male *Zonotrichia leucophrys gambelii.* Vertical lines indicate time and amount (scale at right) of food withdrawals. Triangles indicate when food cup was refilled.

FACTORS INVOLVED IN PREMIGRATORY FATTENING

Buds and insects have a relatively high caloric value (Golley, 1961), and the inclusion of more of this type of food in the diet from late March onward may facilitate fat deposition in the wild birds during the period of premigratory hyperphagia. This has been suggested previously by Dolnik (1963) and by Dolnik and Blyumental (1964). They feel that the shift to a broader spectrum of foods just prior to migration may be characteristic of many migratory species.

It has been shown for a variety of migratory birds that vernal premigratory fattening is accompanied by a photoperiodically induced stimulation of appetite. Doubtless the increased time for feeding and the less severe environmental conditions which prevail during the lengthening days of spring are also important. These factors are essentially permissive with regard to the accumulation of energy reserves, and they, along with the broadened nutritional base at this time, undoubtedly contribute positively to the fattening response in natural populations. But they are not essential components (King and Farner, 1956, 1959, 1965; King, 1961a). That a photoperiodically induced hyperphagia is the cause of premigratory fattening is clear also from the present study. During the time of active vernal fattening the outdoor captives showed an average increase of 20.2 per cent in food intake in a time span when the photoperiod increased 8.6 per cent. King (1961b) also has shown that photostimulated *Z. l. gambelii* in cages will become fat even when their feeding time is drastically curtailed.

There was no detectable change in the diurnal feeding pattern as hyperphagia developed in the birds held outdoors (fig. 5). As usual, they ate at essentially a constant rate throughout the day. In the wild population there was a change in feeding pattern with season. At the time of vernal premigratory fattening their midday decrease in foraging disappeared, and, like the captives, they fed fairly steadily through the whole day. This change in feeding pattern would seem to provide good evidence for the primary mode by which hyperphagia leads to the attainment of a positive energy balance and subsequent premigratory fattening in the wild population.

It was not determined whether the extra intake by captives during hyperphagia occurred because the birds visited the feeders more often or whether they ate more at each visit. Moldenhauer (1965) found in *Z. l. gambelii* during vernal hyperphagia that "meal" size remained about the same whereas the frequency of food cup visits increased. This is true also for *Z. atricapilla* (Marsh, 1965).

THE EFFECTS OF FOOD DEPRIVATION

It has been frequently demonstrated that animals become hyperactive when deprived of food (Wald and Jackson, 1944), although this is not always the case (Rozin, 1964); hyperactivity may be related to an increased sensitivity to normal environmental changes (Campbell and Sheffield, 1953) or to the maintenance of body temperature (Stevenson and Rixon, 1957). Eyster (1954) noted hyperactivity in *Z. leucophrys* and *Z. albicollis* under conditions of food or water shortage. But during deprivation periods of a few hours or less, small birds, especially when they are fat, may not show an increase in activity (Blyumental and Dolnik, 1962). In the present study the deprived birds were all fat, and there was no significant hyperactivity except during the 570-minute period of deprivation. It is interesting that the deprived birds did not eat in a compensatory manner when refed, but this point cannot be emphasized until data are obtained concurrently on changes in body weight. Bare (1959) has shown that the amount of food ingested by deprived rats upon refeeding is a function of the time of day at which deprivation occurs. Subsequently, this phenomenon was interpreted in terms of a conflict between the tendency to explore or rest and the tendency to eat (Bare and Cicala, 1960). A logical but perhaps faulty assumption made in this case is that locomotor and feeding activities are inseparable. Although they must be closely related under normal circumstances, they do not seem to be absolutely interdependent. This is exemplified further by the absence in outdoor captives of a diurnal feeding pattern that coincides with the bimodal locomotor rhythm (compare figs. 3, 4, and 5). It should be reemphasized that deprivations were performed in the present study only during the period of migratory readiness.

THE RHYTHMICITY OF FEEDING

Captive *Fringilla* spp. feed in bursts (Blyumental and Dolnik, 1962), as do captive and feral *Spizella arborea* (Helms and Drury, 1960) and captive *Z. l. gambelii*; however, the flocks of *Z. l. gambelii* in the Snake River Canyon did not conspicuously alternate eating and resting periods except at the lower foraging intensities. Usually (FI of 6 to 10) these birds were foraging and eating almost continuously. Since this population resides at the northern edge of the intermountain winter range of the race, this nearly constant feeding may be related to relatively severe environmental conditions in the Snake River Canyon, to a relatively low density of suitable food, or to both. A comparable study of a southern wintering population might resolve this question.

It should be emphasized that only a small portion of a wild flock was usually disengaged from foraging activities, even when the actual rate of food intake was low. Apparently the birds were motivated to perform the locomotor patterns involved in hunting for food even when they were satiated. Lorenz (1937) has suggested that eating and hunting must be satisfied independently in predators. Hinde (1953) found that Great Tits (*Parus major*) confined to an aviary with a plethora of food still spent considerable time performing food-searching movements. He postulated that there might be separate neural centers controlling hunting and eating.

Some data in the present study suggest that there is a diurnal rhythm in food intake that is independent of obvious exogenous stimuli. For example, indoor captives on 12- or 16-hour photoperiods always exhibited a decrease in food intake during the latter portion of the photoperiod. The same was true of the outdoor captives. Also the onset of the increase in foraging intensity of wild flocks in the afternoon did not seem to be associated with concurrent changes in environmental conditions that called for increased energy intake. The evening maximum in foraging coincided approximately with sunset, but the increase in foraging had begun several hours earlier when insolation and air temperature were near maximal. This does not rule out the possible importance of other environmental cues such as light intensity, which decreases rapidly in late afternoon (von Haartman, 1949). The data on the early termination of feeding prior to migration also suggest the presence of important endogenous stimuli that regulate appetite.

There is ample evidence that some activities of birds have a circadian periodicity. This has been most clearly demonstrated with respect to locomotor activity (Aschoff, 1961; Aschoff *et al.*, 1962). There is also some evidence that feeding behavior of birds has a circadian periodicity when tested under suitable conditions (compare Vaugien and Vaugien, 1962, 1963; Adler, 1963b). Admittedly, the data for *Z. l. gambelii* here presented are scant, but they are consistent with the emerging picture, and the presence of a circadian feeding rhythm in constant ambient conditions is clearly indicated.

The feeding patterns of wild and captive *Z. l. gambelii* are clearly dissimilar except during the period of hyperphagia. These differences may derive from a number of variables. For example, captives were usually not exposed to the microclimatic fluctuations experienced by feral birds, nor could they indulge in the broad spectrum of social activities that pervade the everyday existence of the wild flocks. Other variables include inter- and intraspecific facilitation of feeding (Turner, 1961), the density and kinds of suitable food, and the assessment of feeding rates through greatly different methods.

THE EARLY TERMINATION OF FEEDING AND ITS POSSIBLE REGULATION

The locomotor pattern of captive *Z. l. gambelii* during the daylight hours is altered somewhat with the beginning of nocturnal migratory restlessness (*Zugunruhe*). It can be seen (fig. 4, lower) that the early-morning peak in activity is lower and that the birds become essentially inactive during the evening twilight. During this quiescent period the birds do not eat. The periods of food deprivation (fig. 6) strongly indicate that this cessation of feeding is closely controlled. They also indicate that an empty gut in itself is not a time cue for the beginning of *Zugunruhe*. This does not preclude the possibility that these two events operate under natural conditions in an advantageous temporal arrangement.

It has been shown that food is evacuated from the gut of small birds 90 to 150 minutes after ingestion (Stevenson, 1933; Wallgren, 1954; Blyumental and Dolnik, 1962). At the end of the experiment with the outdoor captives the birds were killed within two to four minutes after the beginning of *Zugunruhe*, and, except for a small amount of material in the large intestine, the digestive tracts were completely empty.

It is significant that a premature termination of feeding also occurred just prior to a movement by wild flocks during the migration period. These observations, together with the laboratory data, suggest that the early termination of feeding is another adaptation that contributes to the ability of migratory birds to perform prolonged flights. Presumably such termination tends to minimize weight by insuring that the gut contents will be digested and absorbed by the time migratory flight begins. This is consistent with the observation that birds killed during migratory flight usually have an empty digestive tract (Odum, 1965). Merkel (1958) noted a similar cessation in feeding prior to *Zugunruhe* in *Sylvia communis* and argued that the period that is allowed for eliminating excess ballast is an advantage of nocturnal migration.

The relative stability of the termination of feeding in *Z. l. gambelii* prior to migratory activity, and its occurrence at a time when the light intensity is still relatively high, raises provocative questions regarding its physiological control. Logically one might assume that 24-hour rhythms in food intake might be related directly and concurrently to such functions as arteriovenous differences in blood glucose or to levels of nonesterified fatty acids (Van Itallie and Hashim, 1960). These data are not yet available, but it is known that diurnal changes in blood glucose levels occur in wild birds (Bergman, 1950; Dolnik *et al.*, 1963; King, pers. comm.), as does a rhythm in liver fat and glycogen (Fisher and Bartlett, 1957; Farner *et al.*, 1960). It is also known that the diurnal cycle in liver glycogen of baby chicks is phased by the light cycle (Petrén, 1955), and that this rhythm persists under continuous illumination (Elfvin *et al.*, 1955; Sollberger, 1955). Of further interest is the observation of Blyumental and Dolnik (1962) that fat birds eat less in the first hours of feeding than do emaciated birds. The same phenomenon was observed in the present study. Dolnik and Blyumental (1964) have suggested that a negative feedback exists between fat reserves and appetite. This concept is supported by recent data which indicate that adipose tissue is an effector organ (Morgane, 1962; Correll, 1963; Liebelt, 1963; Liebelt *et al.*, 1965).

The exact relationship between depot fat and appetite in migratory birds is still unknown, but it is intriguing that the early termination of feeding in captive *Z. l. gambelii* occurs at maximum body weight. Also migrants do not exhibit an early cessation of feeding until they have spent several days replenishing their reserves. Presumably, they have attained a condition of obesity by the time further migratory flight is only one or two nights away. It seems possible that the stimulus for the early termination of feeding is the accumulation of fat reserves above a certain level. Ultimately, selective pressure for this response may occur because it is adaptive to the migratory condition.

SUMMARY AND CONCLUSIONS

The diurnal pattern of food intake of a migratory finch, *Zonotrichia leucophrys gambelii*, was investigated under various field and laboratory conditions. Food intake

was measured continuously in the laboratory with a strain-gage apparatus and in the field by direct observation. An attempt was made to relate the feeding patterns to the possible effects of daily and seasonal changes in the environment and in physiological state, and to the characteristics of premigratory and intramigratory fattening.

In winter, captive birds held outdoors begin feeding at about the onset of civil twilight, feed steadily throughout the day, and stop feeding during civil twilight in the evening. Wild flocks in the winter exhibit a feeding pattern with morning and evening maxima. The midday minimum is greater on warm, sunny days than on cold, cloudy days.

At times of low food intake wild *Z. l. gambelii* continue to perform nearly continuously the locomotor patterns associated with foraging. Birds caged outdoors display a bimodal pattern of locomotor activity, typical of small birds, that does not conform to their feeding pattern. These two lines of evidence enforce Hinde's assertion that feeding and locomotor activity are motivated separately.

A photoperiodically induced hyperphagia occurs in *Z. l. gambelii* prior to vernal migration (King and Farner, 1956). The rate of food intake increases during hyperphagia in birds caged outdoors, but there is no change in the form of their feeding pattern until they attain maximum lipid reserves. At about that time they begin to exhibit *Zugunruhe* and to discontinue feeding each day about 45 minutes earlier than usual. The birds will not eat during this 45-minute period even when they are deprived of food for 270 minutes previous to it. They do feed during the 45-minute period after 570 minutes of deprivation. However, the nightly onset of *Zugunruhe* is unaffected in either case. Captives held indoors on an 8-hour photoperiod feed at a constant rate throughout the light period except that intake is elevated during the first 30 minutes. When these birds are changed abruptly to a 16-hour photoperiod they overeat for the first few days, then regulate at the base level of intake until photostimulated hyperphagia develops. Within seven days after they are placed on a stimulatory photoperiod their diurnal feeding pattern takes a permanently retained parabolic form.

An alteration in the feeding pattern of wild flocks occurs on cold, cloudy winter days and during premigratory and intramigratory hyperphagia. The bimodality of the pattern tends to disappear because the birds feed rather intently throughout the day. It is suggested that this increase in the rate of food intake during midday is the primary source of the extra energy accumulated as fat stores. One or two nights before wild flocks migrate, they stop feeding about 20 to 30 minutes earlier than usual. The actual time when migratory flight begins is not known, but it does occur after the end of civil twilight. It is hypothesized that the advance in the termination of feeding in birds showing a physiological readiness to migrate involves a negative feedback of lipid reserves on appetite. It is also hypothesized that the early termination of feeding is adaptive because it provides a time for emptying the digestive tract prior to migratory flight.

Field data indicate that air temperature may have an effect on the diurnal feeding pattern, but the laboratory data do not corroborate this. The total daily intake of caged birds outdoors is inversely correlated with the mean daily air temperature both before and during hyperphagia, but the pattern of intake is usually not altered concurrently with the daily cycle in air temperature. The level of solar radiation, on the other hand, seems to be directly involved with changes in the diurnal feeding pattern in the field and in the laboratory. Its importance is analyzed more completely in another report (Morton, 1967).

Feral *Z. l. gambelii* and captives on long photoperiods show changes in their feeding patterns that do not seem to be related in a direct causal manner to their thermal environment. In addition, birds in isolation entrained by a 12L 12D light schedule exhibit a circadian periodicity in their feeding when placed on an LL schedule. These data suggest that the neural centers regulating caloric intake may have a light-entrained circadian periodicity in sensitivity to the complement of endogenous and exogenous stimuli normally utilized in the control of food intake.

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