THE RELATIONSHIP OF FAT DEPOSITION TO ZUGUNRUHE AND MIGRATION

By James R. King and Donald S. Farner

The accumulation of fat in subcutaneous and visceral reserves during premigratory and intramigratory periods has been observed widely among migratory species of birds and has been related to the energy requirements of migratory flight. (For reviews, discussions, and examples, see Wachs, 1926; Zedlitz, 1926; Putzig, 1939; Hagen, 1942; Wolfson, 1945, 1959*a*, 1959*b*, 1960; Farner, 1955, 1960; Farner *et al.*, 1961; King, 1961*a*; Odum and Perkinson, 1951; Odum, Connell, and Stoddard, 1961; Merkel, 1938, 1958; Helms, 1959; Helms and Drury, 1960; Weise, 1956, 1962; Dolnik, 1961.) It should be emphasized that the accumulation of such reserves is not necessarily an essential prerequisite for migration, at least in some species which migrate only short distances or by short flights (Putzig, 1939; Nice, 1946; Helms, 1959; Johnston, 1962; Millar, MS). Despite the extensive investigation of the quantitative aspects of premigratory fat deposition, little attention has been directed to identifying the temporal and causal relationships between fat deposition and the initiation of migration. These relationships have been investigated recently by Kendeigh, West, and Cox (1960) in studies with caged Tree Sparrows (*Spizella arborea*) under natural conditions of temperature and photoperiod. In these birds it appeared that *Zugunruhe* developed before the accumulation of fat reserves. From this and from the results of experiments on the interaction of temperature and photoperiod in the induction of migration, it was suggested for birds wintering north of the tropics that *Zugunruhe* is the primary response to increasing temperature and photoperiod and that the increased locomotor activity in turn causes an increased rate of energy intake which exceeds the existence requirements, thus resulting in the deposition of fat. This hypothesis has stimulated us to analyze carefully our data on the development of *Zugunruhe* in relation to fat deposition in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii* and *Z. l. pugetensis*), the Golden-crowned Sparrow (*Zonotrichia atricapilla*), and the Harris Sparrow (*Zonotrichia querula*). The function of this paper is to present the results of these analyses as they bear on the relationship between fat deposition and the development of *Zugunruhe*.

ACKNOWLEDGMENTS

This investigation was supported by funds provided for biological and medical research by State of Washington Initiative Measure No. 171 and by a grant (G 9872) from the National Science Foundation. Some of the data were obtained as by-products from the experiments conducted for other purposes and supported by a contract with the Office of Naval Research, Nonr–1520(00). We are sincerely grateful to Mr. Lloyd Tevis, Jr. for supplying *Zonotrichia leucophrys gambelii* from Rancho Mirage, California; to Dr. L. R. Mewaldt for the stocks of *Z. l. gambelii*, *Z. l. nuttalli*, *Z. l. pugetensis*, and *Zonotrichia atricapilla* from San Jose, California; and to Dr. Harrison B. Tordoff for *Zonotrichia querula* from Lawrence, Kansas. We are indebted to Dr. A. C. Wilson, Mr. Donald A. Wells, Mr. Kenneth Gallagher, Mr. Donald Forsyth, and Dr. William Brown for invaluable technical assistance. Dr. Conrad Donovan performed the castrations. This investigation has been the subject of a previous preliminary report (King and Farner, 1961). Some of the data have been used previously to illustrate the temporal coincidence of the beginning of *Zugunruhe* and the beginning of natural migration (Farner, King, and Wilson, 1957; Farner, 1960).

MATERIAL AND METHODS

The *Zonotrichia leucophrys gambelii* used in these investigations were obtained chiefly by netting from overwintering populations in the Snake River Canyon near Pullman, Washington. This area is the northernmost boundary of the winter range of this race. Other *Z. l. gambelii* were captured at southerly (Rancho Mirage, California) and intermediate (San Jose, California) localities in the winter range. *Zonotrichia leucophrys nuttalli* were obtained from postbreeding populations near Santa Cruz, California, and *Zonotrichia leucophrys pugetensis* from wintering populations near San Jose. *Zonotrichia querula* were obtained near Lawrence, Kansas, and *Zonotrichia atricapilla* were captured at San Jose. With the exception of *Z. l. gambelii*, southeastern Washington is outside the major wintering range of these taxa. However, *Z. querula* and *Z. atricapilla* winter at similar latitudes east of the Rocky Mountains and west of the Cascades, respectively, and are found occasionally in flocks of *Z. l. gambelii* near Pullman.

Captive stocks of birds were held in large outdoor aviaries at Pullman until required in the experiments. They were maintained in excellent physical condition on a diet of chick-starter mash supplemented initially by millet seed.

For recording locomotor activity the birds were confined individually in cages ($23 \times 36 \times 28$ cm.) in which a central, spring-loaded perch-microswitch assembly served to detect the movements of the bird (Farner and Mewaldt, 1953*a*). Each movement of the perch releases a unit discharge from a condenser into the read-out device. In 1952 and 1953, the latter consisted of a signal marker recording on a uniformly moving paper tape. In 1955 the apparatus was modified to provide simultaneous graphic and digital read-out integrated by one-hour intervals. As we have previously emphasized (Farner and Mewaldt, 1953*a*; Farner, Mewaldt, and King, 1954; King, 1961*a*) this apparatus provides an index of activity as a fraction of the total activity. Because each bird, soon after confinement in the activity cage, develops a stable, individualistic exercise pattern, the fraction of the total activity sampled by the system may be different for each individual. For this reason quantitative comparison of the intensity of activity among different birds is not appropriate. In the present investigation, where we are concerned with qualitative changes in the seasonal patterns of activity and with seasonal variations in the intensity of activity for a given individual, this is not a significant limitation.

In the investigation of birds exposed to natural weather and photoperiod, the activity cages were placed in a walled enclosure on a roof four floors above the street level. The cages were protected from precipitation by an overhanging roof, but the birds were otherwise fully exposed to the weather. Municipal light and noise were negligible in the enclosure. Food and water were freely available to the birds except in the experiments designed to suppress fat deposition in the spring. In this case, an amount of food calculated to maintain the body weight at a premigratory level was supplied daily. The birds were weighed daily in 1960, at 4-day intervals in 1956, and at 7-day intervals during the other years. All weighings were made at a uniform time during the midday within each year. During each examination of the birds, the extent of molt was also recorded. In the expression of the activity data obtained from birds exposed to the natural photoperiod, the nocturnal phase is defined as the interval between the end of civil twilight in the evening and its beginning in the morning.

In experiments conducted indoors, the activity cages were placed in constant-condition rooms in which light from incandescent lamps was so adjusted that the minimum intensity at the floor-level of the cages was 375 lux. The change between the dark phase and the light phase of the daily cycle was abrupt, without artificial twilight. During the dark phase the rooms were entirely without light. In the experiment with a fractionated photoperiod (table 4), the birds were given 9 hours of continuous light per day followed by an additional 9 hours during which the lights were automatically switched on for exactly one minute every 20 minutes. Although this program exposed the birds to only 9 hours and 27 minutes of light per day, which is essentially subliminal if given as a single continuous photoperiod, it produced testicular and metabolic responses approximately equivalent to an 18-hour daily photoperiod. This is a manifestation of the "carry-over" phenomenon (Farner, Mewaldt, and Irving, 1953; Farner and Wilson, 1959; Farner, 1959). Other laboratory routine was the same as that already described for birds held outdoors.

The castration of experimental birds was performed under sodium pentobarbital anesthesia via a paralumbar incision, essentially as described by Bailey (1953). Following completion of the experiments the dorsal body wall from all castrates was preserved in an alcohol-formaldehyde-acetic acid fixation fluid for subsequent histologic confirmation of the success of castration.

RESULTS AND DISCUSSION

The primary data are records of more than 20,000 bird-hours of activity for 74 individuals, and body weights taken at intervals of one week or less. The changes in body weight are used as indicators of changes of fat reserves, a relationship which has been adequately established for *Zonotrichia leucophrys gambelii* (McGreal and Farner, 1956; King and Farner, 1959). The mean weights for the individuals of the four taxa held under outdoor conditions of light and temperature are summarized in figure 1. In the four migratory taxa there is a close temporal relationship between the deposition of fat reserves, as indicated by body weights, and the beginning of natural vernal migration (Farner, 1960); a similar, although less precise relationship exists also for autumnal migration. In the nonmigratory race *Zonotrichia leucophrys nuttalli* neither vernal fat deposition nor typical *Zugunruhe* occurred.

An adequate presentation of the data on activity is difficult. Because of differences among individuals and differences from day to day in the activity patterns of each individual, there is no obvious scheme by which such a mass of data can be reduced to a completely satisfactory, simple form of presentation. Since our attention in this paper is focused on the temporal and functional relationships between fat deposition and the beginning of *Zugunruhe*, we have devised what appears to be the most effective scheme for summarizing these relationships. On the basis of calculations that show nocturnal activity as a fraction of total activity, for intervals of one week or less, we have ascertained the time at which *Zugunruhe* began for each bird. By comparing this with the body-weight curve we then reached a decision concerning the temporal relationship between the beginning of *Zugunruhe* and the deposition of fat reserves. We have categorized these temporal relationships into four groups (tables 1, 2, and 3): (1) FAT DEPOSITION BEFORE ZUGUNRUHE. In this category we have included only those birds in which there was a very evident increase in weight before the beginning of *Zugunruhe*. Typical cases for vernal *Zugunruhe* are those of *Zonotrichia leucophrys gambelii*, nos. 29–139124 ♂ (fig. 2), 29–195428 ♂ (fig. 3), 24–199093 ♂ (fig. 5); *Zonotrichia atricapilla*, nos. 50–156353 ♂ (fig. 6), 50–156346 ♂ (fig. 8B); and *Zonotrichia querula*, no. 24–119279 ♂ (fig. 7). Typical cases for autumnal *Zugunruhe* are those of *Z. atricapilla*, nos. 50–156349 ♂ (fig. 11), 50-156327 ♂ (fig. 13A); *Z. querula*, no. 24–119280 ♀ (fig. 13D). A typical experimental case of photoperiodically induced fat deposition and *Zugunruhe* is that of *Z. l. gambelii*, no. 25–139121 ♂ (fig. 14). (2) FAT

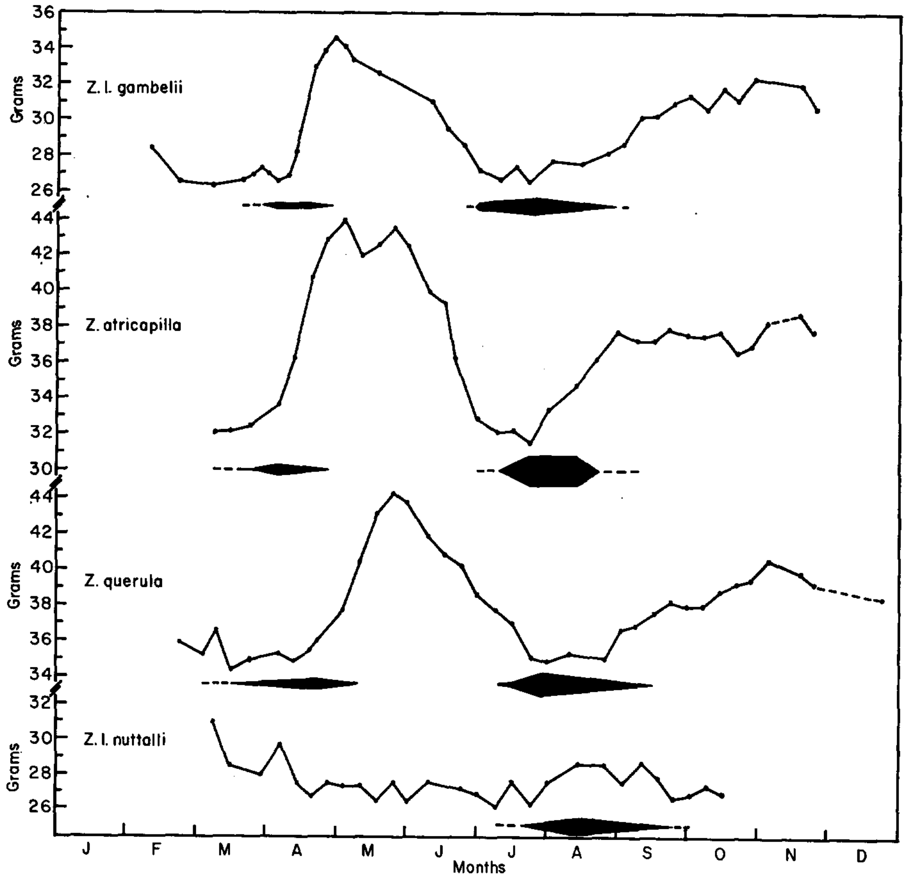

Fig. 1. Annual variation in mean body weight and the occurrence of molt in four taxa of *Zonotrichia* (see text) in 1956. Black polygons depict the duration and relative intensity of molt. Sample sizes (n): *Zonotrichia leucophrys gambelii*, n=7; *Z. atricapilla*, *Z. querula*, n=5; *Z. l. nuttalli*, n=4.

DEPOSITION SIMULTANEOUS WITH DEVELOPMENT OF ZUGUNRUHE. This category is illustrated here by *Z. l. gambelii*, no. 24–119087 ♂ (fig. 4). Obviously such cases are difficult to detect. It is reasonably certain that some of the cases referred to category 4 belong more properly in this category. (3) FAT DEPOSITION AFTER THE BEGINNING OF ZUGUNRUHE. Illustrative are *Z. l. gambelii*, no. 23–170439 ♀ (fig. 8C), and 24–119087 ♂ (fig. 9); *Z. querula*, no. 24–119280 ♀ (fig. 13C). (4) EQUIVOCAL CASES. These are cases in which failure of the recording apparatus has made a categorization impossible or in which the performance of the birds does not conform clearly with one of the other categories. Examples of the latter include *Z. l. gambelii*, nos 27–195508 ♂ (fig. 15) and 24–119382 ♂ (fig. 10).

In figures 2 to 7, 9 to 12, and 14 to 15 we have shown detailed distributions of activity for three selected 48-hour periods for each of the birds. In each case one of these periods represents activity before the development of *Zugunruhe* and one is typical of the distribution of activity during the period of *Zugunruhe*. Generally the development of *Zugunruhe* is characterized by a reduction of late-afternoon activity, often with the disappearance of a late-afternoon maximum, and the development of intensive nocturnal activity with a maximum at midnight or shortly thereafter and a marked reduction or total cessation of activity before sunrise (see also Palmgren, 1944; Farner, Mewaldt, and King, 1954). Figures 2, 4 to 6, 10, and 14 are most typical. Careful examination of the daily distribution of activity, as illustrated in these figures, is of importance in reaching a decision concerning the time at which *Zugunruhe* begins. Thus it was clear that the nocturnal activity of *Z. querula*, no. 24–119280♀ (fig. 8A) in March was not typical *Zugunruhe* but simply the result of a post-sunset continuation of late-afternoon activity and a predawn beginning of the period of morning activity.

Zonotrichia leucophrys gambelii in outdoor cages in spring.—Examples of the vernal development of *Zugunruhe* in this race are given in figures 2 to 5, and 8C to D. The results for all birds of this race in spring are summarized in table 1. Obviously the typical pattern involves deposition of fat before vernal migration, a relationship contrary to the hypothesis of Kendeigh, West, and Cox (1960). Indeed, only two birds clearly conformed to this generalization; even if all eight of the equivocal cases were actually cases in which fat was deposited after the beginning of *Zugunruhe*, there would be conformance in only 22 per cent of the cases. Certainly in this species *Zugunruhe* cannot be regarded as a cause of fat deposition. Although the numbers of birds in which fat deposition follows the beginning of *Zugunruhe* is small (see tables 2, 3, and 4), they are of significance as a converse indication that fat deposition is not an immediate cause of *Zugunruhe*.

TABLE 1

RELATIONSHIP OF FAT DEPOSITION AND *Zugunruhe* IN *Zonotrichia leucophrys gambelii*[1]

		Temporal relationship of fat deposition to the beginning of *Zugunruhe*				
Year	Number of birds	Before	Simultaneous	After	Equivocal	Initial dates of *Zugunruhe*
1952	4	2	....	....	2	April 21–29
1953	6	4	....	....	2	April 26–May 3
1955	6	4	2	....	....	April 19–28
1956[2]	4	1	2	....	1	April 9–21
1957[3]	11	4	3	2	2	April 10–26
1958	5	5	....	....	....	April 27–28
1960	9	8	....	....	1	April 24–May 6
Totals	45	28	7	2	8	

[1] Birds kept in outdoor recording cages in spring under natural conditions of day length and temperature.
[2] Included also in table 3.
[3] Included also in table 2.

With data on the beginning of fat deposition and *Zugunruhe* in *Z. l. gambelii* for seven vernal migratory seasons, it has been possible to make tentative generalizations concerning the role of environmental temperature. The complex, irregular patterns of environmental temperature in southeastern Washington in spring make this a formidable task. Satisfactory general correlations with mean maximal and minimal daily temperatures for all years are elusive. It is significant that *Zugunruhe* began earliest (April 10 to 20) in the warmest spring, 1956, and latest (April 27 to 28) in the coldest spring, 1958 (fig. 16). This is consistent with our limited observations on the effect of environmental temperature on *Zugunruhe* in indoor aviaries (Farner and Mewaldt, 1953*b*, 1955*a*).

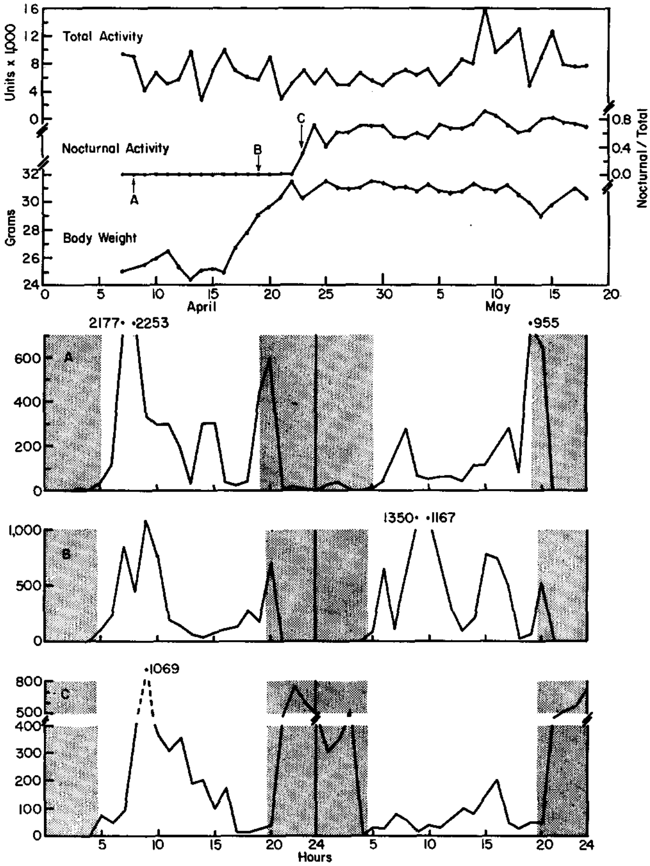

Fig. 2. Activity and body weight in *Zonotrichia leucophrys gambelii*, first-year male no. 29–139124, exposed outdoors to natural weather and photoperiod, spring, 1960. Upper panel: total activity is total switch-movements per day; nocturnal activity is represented as a fraction (right ordinate) of total activity. Lower panels, A, B, and C: daily activity patterns for pertinent 48-hour intervals beginning on the dates indicated by arrows in the upper panel; ordinate indicates total switch-movements per hour. Shaded areas indicate the duration of darkness, including civil twilight.

Zonotrichia leucophrys gambelii subjected to 16- and 20-hour daily photoperiods in indoor aviaries.—As we have previously demonstrated, both under outdoor and indoor conditions (Farner, 1960; King, 1961*a*, 1961*b*), an artificial increase in daily photoperiod in winter causes fat deposition and the development of *Zugunruhe* (figs. 14, 15; table 4). In the birds subjected to a 16-hour photoperiod, the deposition of fat definitely preceded the development of *Zugunruhe* in all cases except one (fig. 15). On the other hand, among the four subjected to a 20-hour photoperiod, in no case did fat deposition precede *Zugunruhe*. We have often observed that 20-hour photoperiods tend to cause a telescoping of photoperiodically induced vernal events. Thus under very long photoperiods there is a marked tendency for the "prenuptial" molt to occur during fat deposition and the beginning of *Zugunruhe* rather than to precede them (Farner and Me-

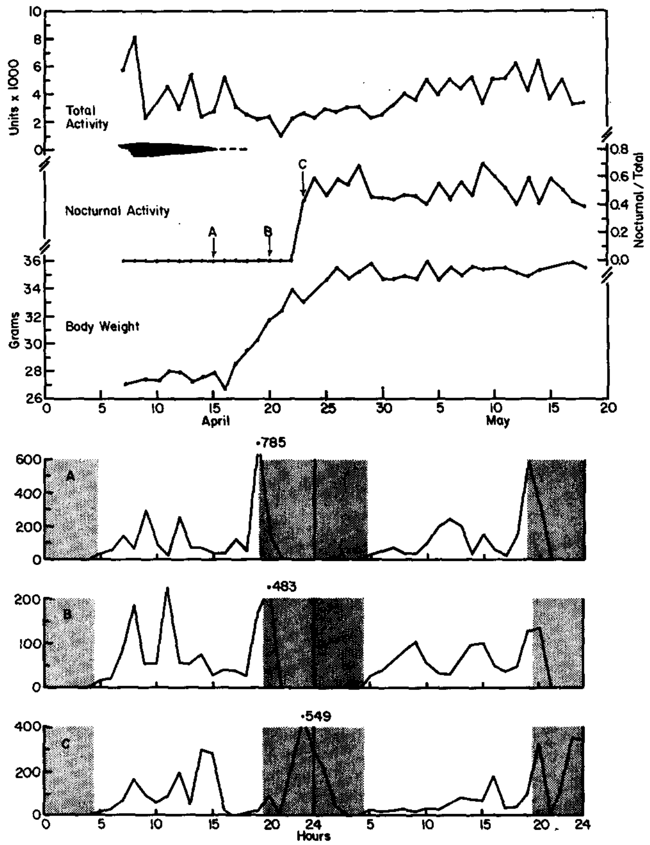

Fig. 3. Activity and body weight in *Zonotrichia leucophrys gambelii*, first-year male no. 27–195428, exposed outdoors to natural weather and photoperiod, spring, 1960. See figure 2. Black polygon indicates duration and relative intensity of molt.

waldt, 1955*b*; King, 1961*b*). The data in table 4 suggest that this "telescoping" may also occur with respect to the temporal relationship of fat deposition and the development of *Zugunruhe*.

TABLE 2

RELATIONSHIP OF FAT DEPOSITION AND *Zugunruhe* IN *Zonotrichia leucophrys gambelii* AND *Zonotrichia leucophrys pugetensis*[1]

			Temporal relationship of fat deposition to the beginning of *Zugunruhe*				
Race	Locality of capture	Number of birds	Before	Simultaneous	After	Equivocal	Initial dates of *Zugunruhe*
pugetensis	San Jose	4	1	2	1	....	April 10–15
gambelii[2]	Pullman	3	1	1	....	1	April 16–18
gambelii[2]	San Jose	4	2	2	....	....	April 10–24
gambelii[2]	Rancho Mirage	4	3	....	....	1	April 10–26
	Totals	15	7	5	1	2	

[1] Birds kept in outdoor recording cages in spring of 1957 under natural conditions of day length and temperature.
[2] Also in table 1.

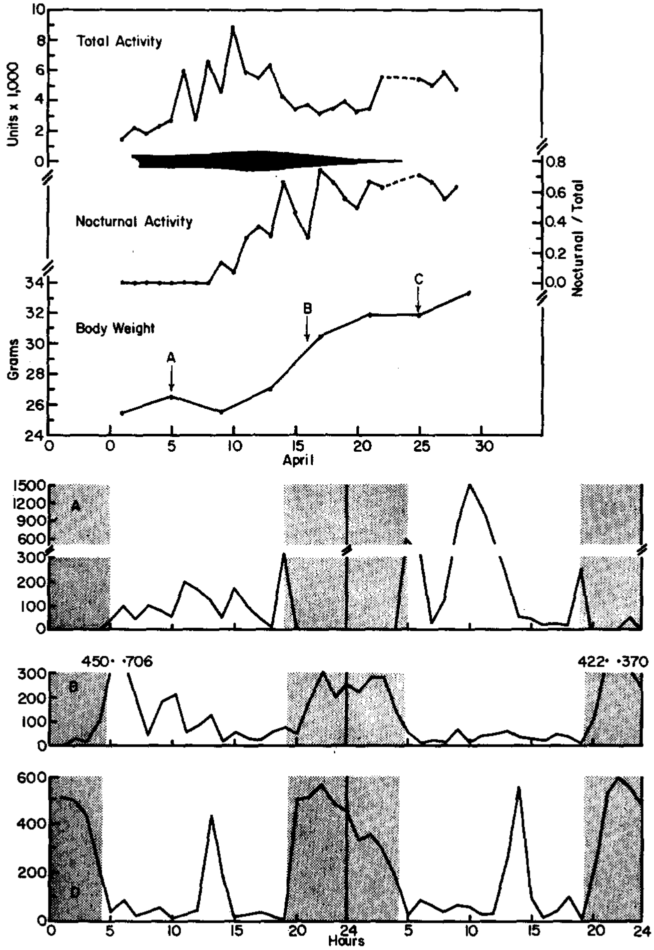

Fig. 4. Activity and body weight in *Zonotrichia leucophrys gambelii*, first-year male no. 24–119087, exposed outdoors to natural weather and photoperiod, spring, 1956. See figure 2.

Zonotrichia leucophrys gambelii subjected to fractionated light pattern.—(See page 202 and table 4). These are data from an experiment (King, 1961*b*) designed to ascertain, by use of short stimulatory flashes of light during which the birds remain inactive during the pre-*Zugunruhe* period, whether the long-day induction of fattening is simply the result of a longer period of daytime activity and feeding, or of a photostimulation of a hyperphagic mechanism. The results of the experiment show clearly that the latter is the case (King, *op. cit.*). In these it is evident also that fat deposition precedes the development of *Zugunruhe* (table 4).

Zonotrichia leucophrys pugetensis in outdoor cages in spring.—Because we obtained data from only four birds (table 2), no firm conclusions concerning this race are possible. Since shorter distances are involved in migration, it is not surprising that only one of the individuals deposited fat before the development of *Zugunruhe*. It is possible that this race approaches the situations observed in the Savannah Sparrow, *Passerculus sandwichensis* (Odum, Connell, and Stoddard, 1961), in the Tree Sparrow, *Spizella*

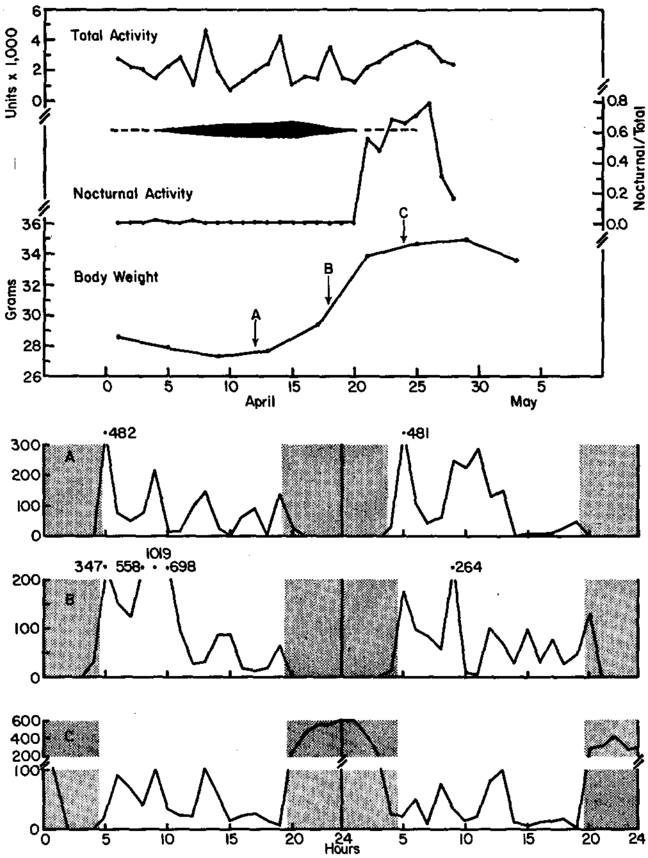

Fig. 5. Activity and body weight in *Zonotrichia leucophrys gambelii*, adult male no. 24–119093, exposed outdoors to natural weather and photoperiod, spring, 1956. See figure 2.

arborea (Helms and Drury, 1960), in the population of the Slate-colored Junco (*Junco hyemalis*) studied by Johnston (1962), and in the Gray-crowned Rosy Finch (*Leucosticte tephrocotis tephrocotis* and *L. t. littoralis*), and in the Black Rosy Finch, *Leucosticte atrata* (King, MS), in which there is no fat deposition before the beginning of migration.

TABLE 3

RELATIONSHIP OF FAT DEPOSITION AND *Zugunruhe* IN THREE SPECIES OF *Zonotrichia*[1]

		Temporal relationship of fat deposition to the beginning of *Zugunruhe*				
Species	Number of birds	Before	Simultaneous	After	Equivocal	Initial dates of *Zugunruhe*
leucophrys gambelii[2]	4	1	2	....	1	April 16–26
atricapilla	5	4	....	1	....	April 16–24
querula	5	5	....	....	....	May 6–14
Totals	14	10	2	1	1	

[1] Birds kept in outdoor recording cages during spring migratory season, 1956, under natural conditions of day length and temperature.
[2] From table 1.

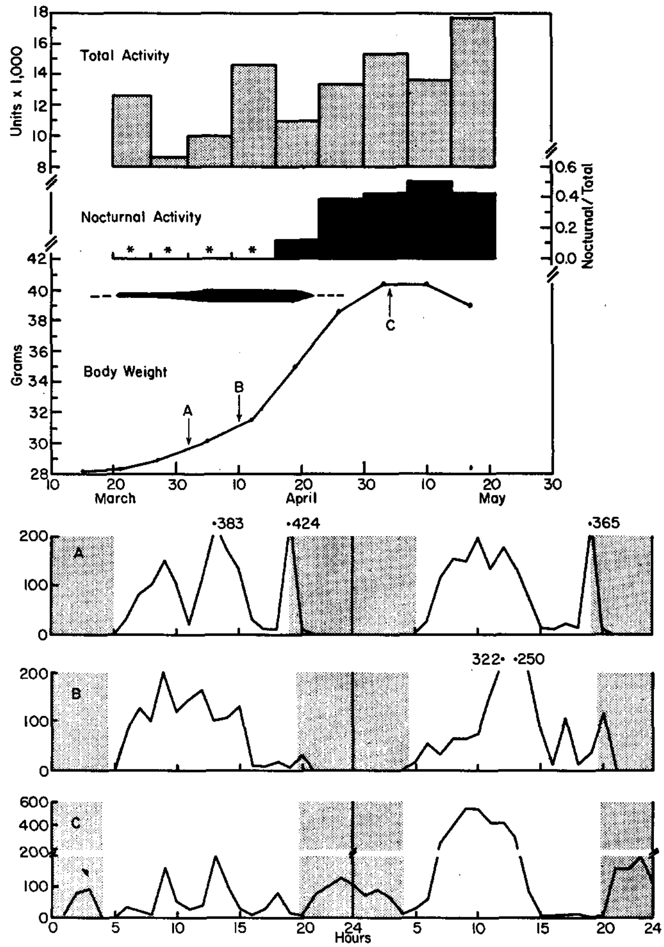

Fig. 6. Activity and body weight in *Zonotrichia atricapilla*, first-year male no. 50–156353, exposed outdoors to natural weather and photoperiod, spring, 1956. Asterisks indicate that activity was monitored for the period shown, but was zero (nocturnal activity) or less than the minimum value on the ordinate (total activity). See figure 2.

TABLE 4

RELATIONSHIP OF FAT DEPOSITION AND *Zugunruhe* IN *Zonotrichia leucophrys gambelii*[1]

Experimental photoperiod	Ambient temperature	Time of year	Number of birds	Temporal relationship of fat deposition to the beginning of *Zugunruhe*: Before	Simultaneous	After	Equivocal
20 hours/day	*ca.* 12°	Jan.-Mar.	4	....	3	1	....
Fractionated[2]	*ca.* 12°	Jan.-Feb.	4	3	....	....	1
16 hours/day	*ca.* 10°	Feb.-Mar.	7	6	....	....	1
Totals			15	9	3	1	2

[1] Experiments with birds in indoor recording cages.
[2] Daily light treatment: 9 hours continuous light followed by 9 hours with one 1-minute flash per 20 minutes and then by six hours of darkness. (See text.)

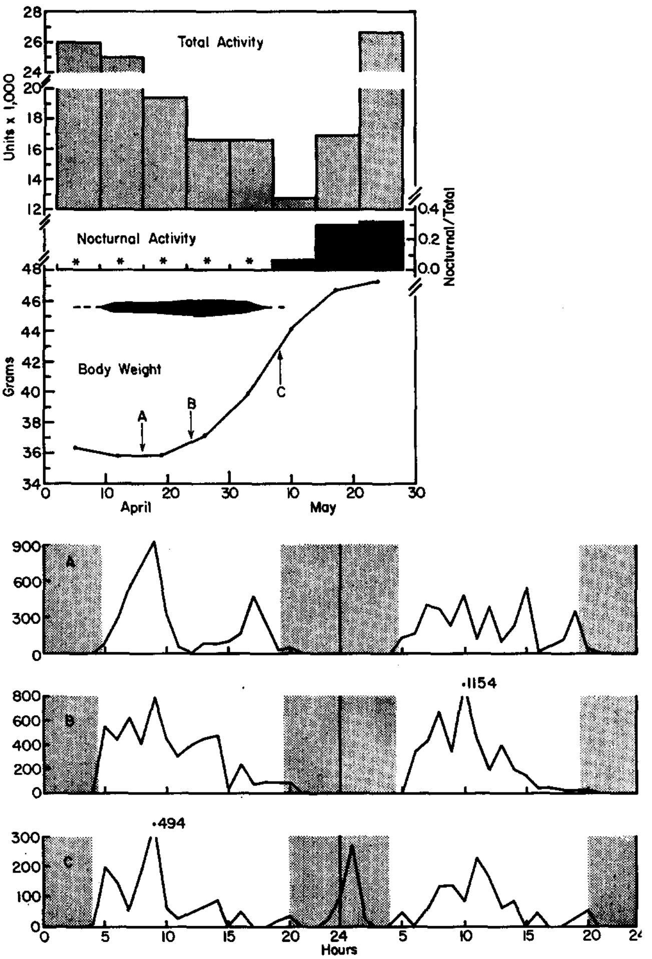

Fig. 7. Activity and body weight in *Zonotrichia querula*, first-year male no. 24–119279, exposed outdoors to natural weather and photoperiod, spring, 1956. See figures 2 and 6.

Zonotrichia atricapilla and Zonotrichia querula in outdoor cages in spring.—The data on these two species come from an investigation designed to study the correlation between the development of *Zugunruhe* and the natural period of migration. These birds, together with four *Z. leucophrys gambelii* and five *Z. l. nuttalli*, were maintained in recording cages in random order in an outdoor aviary. The fidelity of the relationship between the development of *Zugunruhe* and the natural migratory period is evident in table 3. (See also, Farner, 1960.) The *Z. l. nuttalli* showed no appreciable nocturnal activity. Of primary importance here, however, is the deposition of fat before *Zugunruhe* in four out of five *atricapilla*, and in all five *querula*. Thus it seems evident that these species also fail to support the hypothesis of Kendeigh, West, and Cox (1960).

Zonotrichia spp. in outdoor cages in autumn.—Four *Zonotrichia leucophrys gambelii*, five *Z. atricapilla*, and five *Z. querula* were kept in activity cages continuously during the late summer and autumn of 1956. Responses of representative individuals are shown in figures 9 to 13. In comparison with the vernal migratory period, the events of the autumn season are characterized by conspicuous quantitative and temporal variability. Because of the slow development of autumnal premigratory fattening, often without a clear-cut increase from week to week (cf. fig. 1) we have not emphasized in tabular form the temporal relationship between fat deposition and *Zugunruhe.* An inspection of figures 9 to 13, however, will reveal representatives of each of the various classes of relationship described above for the spring. In the 14 individuals studied, the apparent onset of fat deposition preceded *Zugunruhe* in eight, was apparently concurrent with it in one case, occurred after the beginning of *Zugunruhe* in two cases, and was equivocal in three cases.

Like premigratory fat deposition, the beginning of *Zugunruhe* is much less precisely timed in the autumn in comparison with the spring. Thus in *Z. l. gambelii* the first clear manifestations of *Zugunruhe* extended from August 6 to August 24 in the four individuals, in *Z. atricapilla* from August 14 to September 20, and in *Z. querula* from August 22 to September 12 for four individuals, and to October 3 in a fifth, especially fractious bird in which the postnuptial molt was abnormally prolonged probably as a consequence of persistent feather loss in handling. As a perusal of figures 9 to 13 will indicate, these dates of first *Zugunruhe* are closely correlated with the termination of the postnuptial molt. *Zugunruhe* did not begin in any individual until the molt was substantially or entirely complete. This correlation is much less frequent in the spring, in which the less

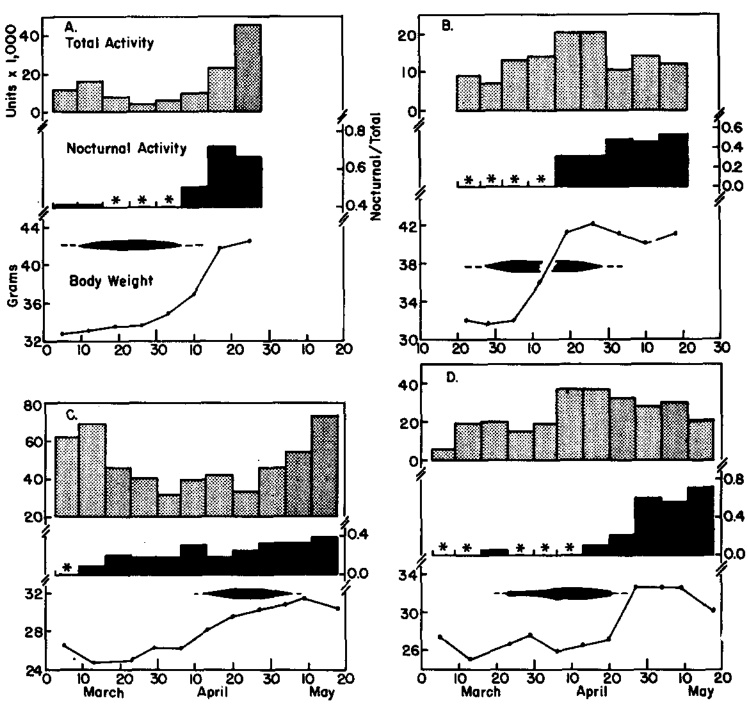

Fig. 8. Birds exposed outdoors to natural weather and photoperiod, spring, 1956. A, *Zonotrichia querula*, adult female no. 24–119280; B, *Z. atricapilla*, adult male no. 50–156346; C, *Z. l. gambelii*, adult female no. 23–170439, captured at San Jose, California; D, *Z. l. gambelii*, adult female no. 23–170440, captured at San Jose, California.

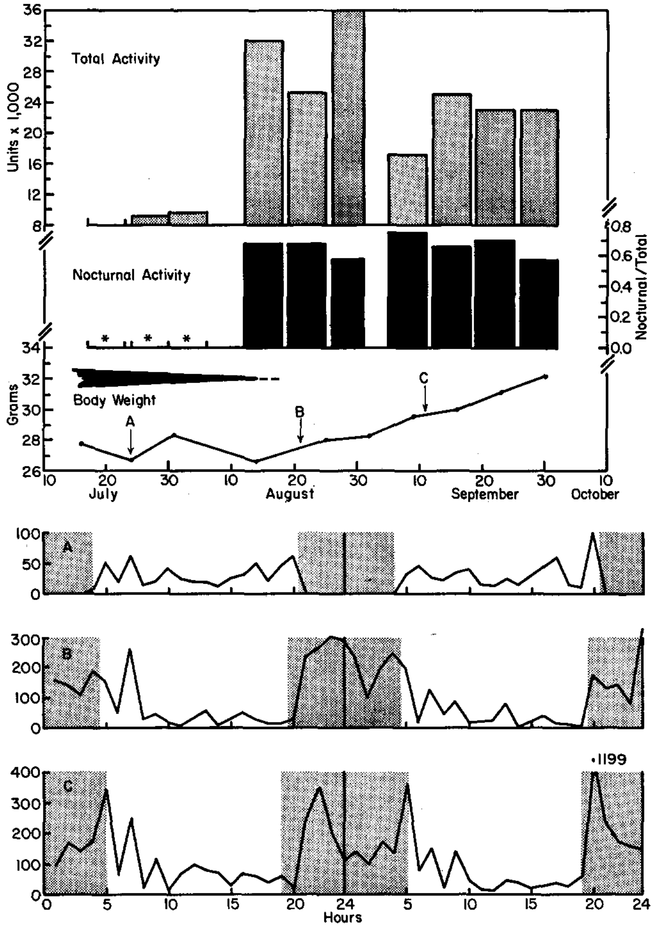

Fig. 9. Activity and body weight in *Zonotrichia leucophrys gambelii*, adult male no. 24–119087, exposed outdoors to natural weather and photoperiod, autumn, 1956. See figures 2 and 6.

intense prenuptial molt, involving mainly the contour feathers, often continues into the period of *Zugunruhe*.

That this decreased intensity and/or temporal precision of fat deposition and *Zugunruhe* in autumn is not simply the accumulated result of captivity is shown by our observations that captive *Zonotrichia* develop fat reserves at the normal time and of typical magnitude during the second spring of captivity. Furthermore the autumnal pattern in the captives conforms with the much smaller fat reserves of feral autumn migrants and the comparatively variable and prolonged period of autumn migration (King, Barker, and Farner, 1963).

The effects of restricted caloric intake.—The fact that fat deposition normally precedes or accompanies the development of vernal *Zugunruhe* or migration has led some investigators to the viewpoint that the presence of fat reserves somehow releases migratory behavior or at least permits it to occur. (For review see Farner, 1955:216.) Although this hypothesis is seriously weakened by the observation that many species begin

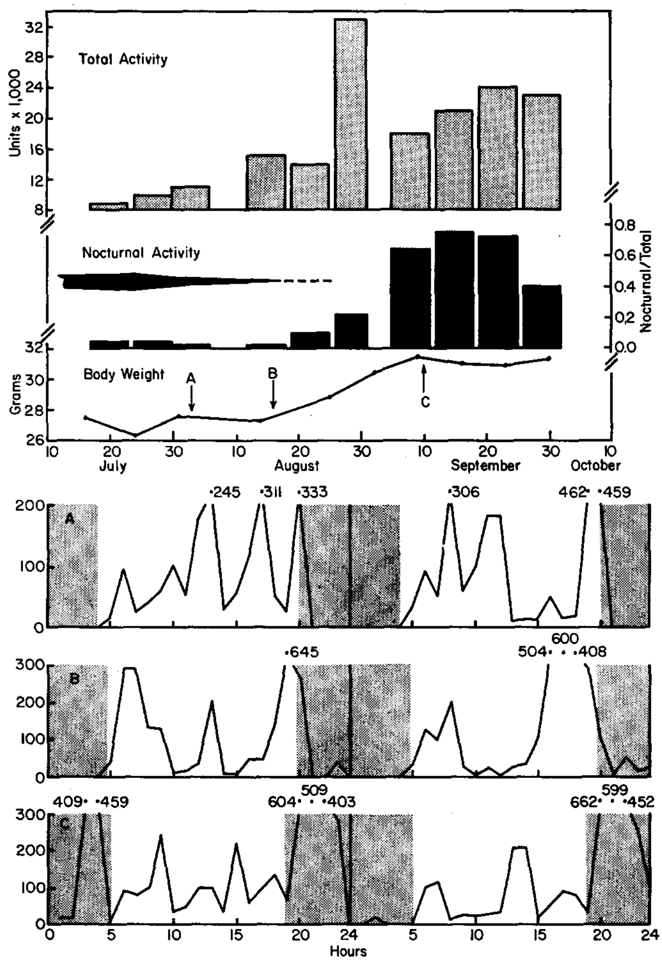

Fig. 10. Activity and body weight in *Zonotrichia leucophrys gambelii*, adult male no. 24–119382, exposed outdoors to natural weather and photoperiod, autumn, 1956. See figures 2 and 6.

or continue migration without conspicuously increased adipose reserves, and particularly by the quantitative evidence to this effect (Millar, MS; Odum, 1960; Odum, Connell, and Stoddard, 1961), critical experimental evidence on the permissive relationship between adipose reserves and *Zugunruhe* is still lacking. Anticipating the suggestion of Lofts and Marshall (1960), we investigated the *Zugunruhe* and changes in body weight of two groups of *Zonotrichia leucophrys gambelii* confined outdoors during the late winter and spring of 1960. In the control group the birds were permitted to feed freely. In the experimental group, food was provided daily in an amount calculated to hold the body weight at a premigratory level. The results of the experiment are summarized as mean values in figure 17. Because we could not anticipate fluctuations in the ambient temperature, and hence the energy demand of thermoregulation, the body weights of the experimental birds were not controlled at a perfectly stable day-to-day level (for example, note the increase during an unexpected warm period in mid-April). Nevertheless, they were maintained in all cases within the normal premigratory limits (cf. fig. 1). The

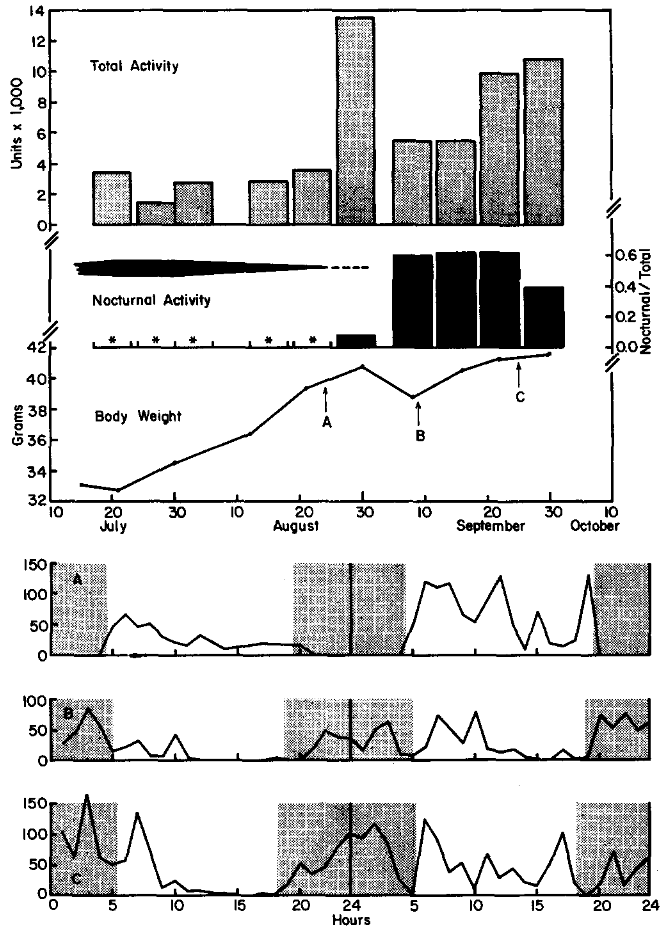

Fig. 11. Activity and body weight in *Zonotrichia atricapilla*, adult male no. 50–156349, exposed outdoors to natural weather and photoperiod, autumn, 1956. See figures 2 and 6.

records of locomotor activity (fig. 17) indicate that *Zugunruhe* began concurrently in the experimental and control groups, although the mean intensity of nocturnal activity was clearly less in the experimental group. Extrapolated to free-living birds, these data suggest that prevention of accumulation of fat reserves by caloric restriction will diminish the intensity of the migratory drive but will not abolish it or delay its onset. This conclusion is basically concordant with the results of a similar investigation of *Fringilla montifringilla* by Lofts, Marshall, and Wolfson (1963), except that the intensity of nocturnal activity in their investigation was not significantly different between the experimental and control groups. These observations support our thesis that fat deposition and *Zugunruhe*, although functionally interactive, develop through essentially separate regulatory systems.

Zugunruhe in castrated sparrows.—The hypothesis formalized by Rowan (1926, 1929, 1932, 1946) that migration is a sex-oriented activity dependent upon gonadal stimulation has been challenged by several recent investigations. With few exceptions,

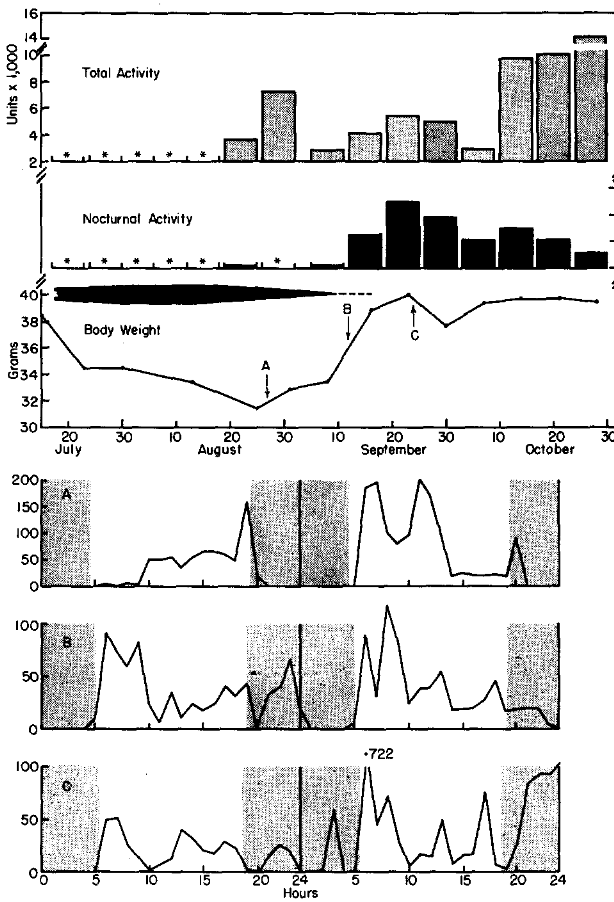

Fig. 12. Activity and body weight in *Zonotrichia querula*, adult female no. 24–119267, exposed outdoors to natural weather and photoperiod, autumn, 1956. See figures 2 and 6.

the results of these investigations indicate that essentially normal *Zugunruhe* and fat deposition occur in captive castrated birds. Although Weise (MS) was unable to induce *Zugunruhe* by artificial photostimulation of three completely castrated *Zonotrichia albicollis,* Millar (MS) found *Zugunruhe* comparable in intensity to that of intact controls in seven complete castrates of this same species exposed to outdoor conditions in the spring. Lofts and Marshall (1961) report that *Zugunruhe* equal in intensity to that of intact controls developed in 15 completely castrated *Fringilla montifringilla* exposed to natural photoperiod in the spring. The seasonal onset of *Zugunruhe* in the castrates was about one week later than in the controls, and the peak of activity during the night was later in the castrates. Most recently, Morton and Mewaldt (1962) report the results of an investigation of 39 castrated *Zonotrichia atricapilla* confined outdoors during two successive vernal seasons. The results are essentially congruent with those of Lofts and Marshall (1961). During each year of the investigation, *Zugunruhe* began in the castrates approximately one week later than in the intact controls. Similarly, the nocturnal maximum in the castrates was attained at a later hour of the night

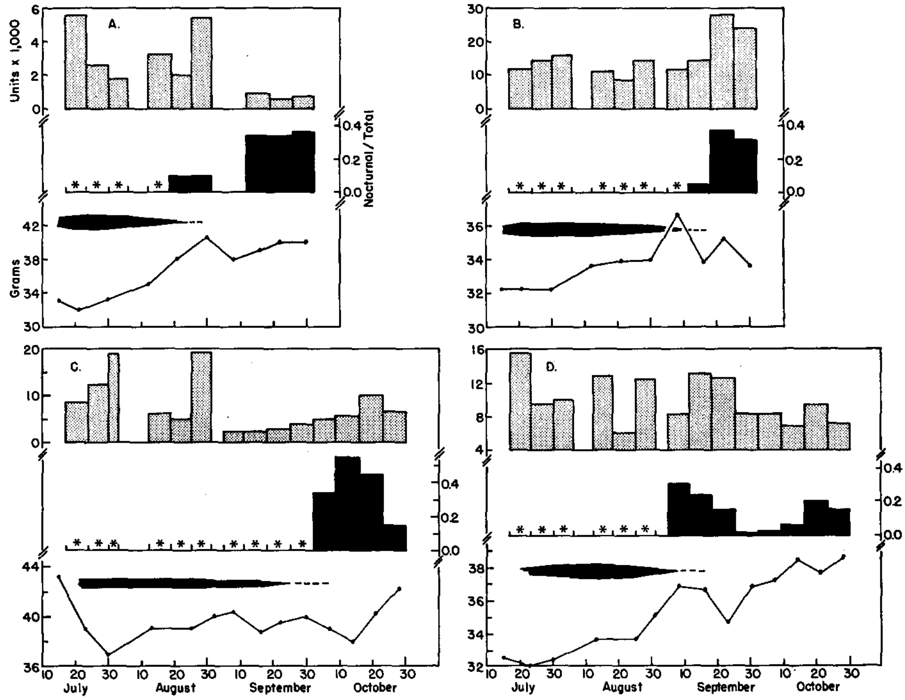

Fig. 13. Birds exposed outdoors to natural weather and photoperiod, autumn, 1956. A, *Zonotrichia atricapilla*, adult male no. 50–156327; B, *Z. atricapilla*, adult male no. 50–156346; C, *Z. querula*, adult male no. 24–119265; D, *Z. querula*, adult female no. 24–119280.

than in the controls. Migratory fat deposition was conspicuous and concurrent in both groups but attained a slightly lesser maximum in the castrates. Although our investigation has now been discontinued because of the conclusive results summarized above, pilot experiments with castrated *Zonotrichia leucophrys gambelii* in this laboratory are

Table 5

Résumé of Changes in Body Weight and Nocturnal Activity of Castrated and Intact Male *Zonotrichia leucophrys gambelii*, 1958

Item	25–139076	25–139039	Experimental birds 24–184982	24–184929	Control group mean (n = 5)
Increase in body weight, gm.	6.9	8.7	7.5	8.2	9.7
Beginning of body-weight increase	May 11–17	Apr. 20–26	Apr. 27-May 3	Apr. 20–26	Apr. 20–26
Beginning of body *Zugunruhe*	May 18	Apr. 29	May 6	Apr. 27	Apr. 27–28
Period of maximum *Zugunruhe*	May 18–24	Apr. 27-May 3	May 4–10	Apr. 27-May 3	Apr. 27-May 3
Testicular weight, mg. (June)	None	None	0.6	3.3	350

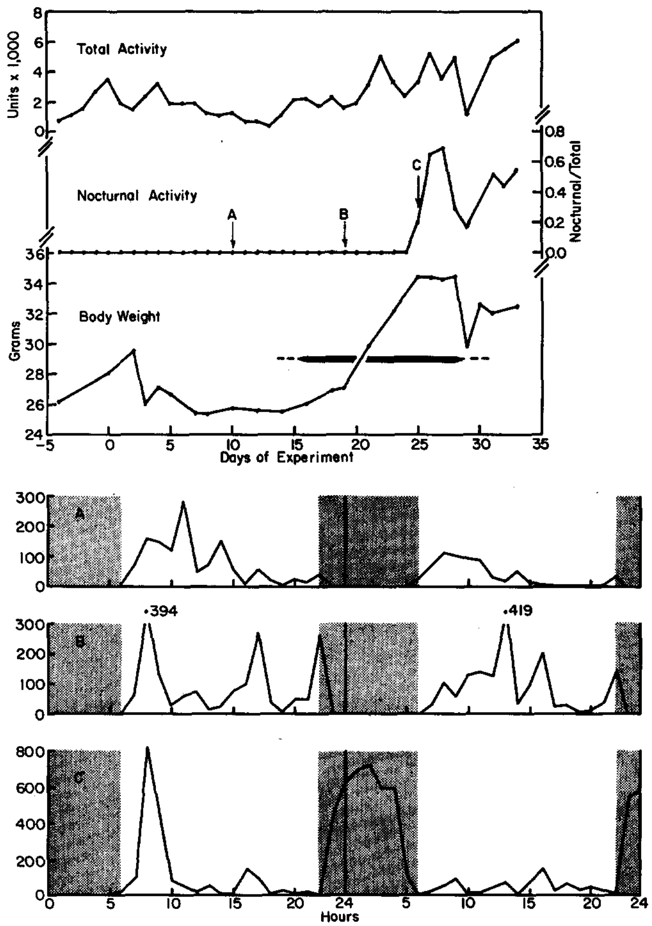

Fig. 14. *Zonotrichia leucophrys gambelii*, first-year male no. 25–139121. Experimental photoperiod changed from 8 hours of light per day to 16 hours per day on day zero. Ambient temperature constant at *ca.* 10° C. See figures 2 and 6.

basically concordant with these results. Our data for birds exposed to natural weather and photoperiod in the spring are shown in table 5. Although equivocal by themselves, these data indicate for *Z. l. gambelii* that the absence of testicular androgens does not necessarily disrupt the vernal response pattern (no. 25–139039), although it may delay its development (nos. 25–139076, 24–184982).

We thus conclude that, for the species discussed above, the metabolic and behavioral aspects of vernal migration are basically independent of endogenous sexual stimuli, although, as noted by Morton and Mewaldt (1962), the sex steroids may exert a potentiating effect on the rate and magnitude of the developing responses.

Possible functional relationships between vernal fat deposition and vernal Zugunruhe.—It is obvious from the summaries in tables 1 to 4 that *Zugunruhe* cannot be an essential causal factor in the development of premigratory fat deposition in *Zonotrichia leucophrys gambelii, Z. l. pugetensis, Z. querula,* and *Z. atricapilla.* We readily

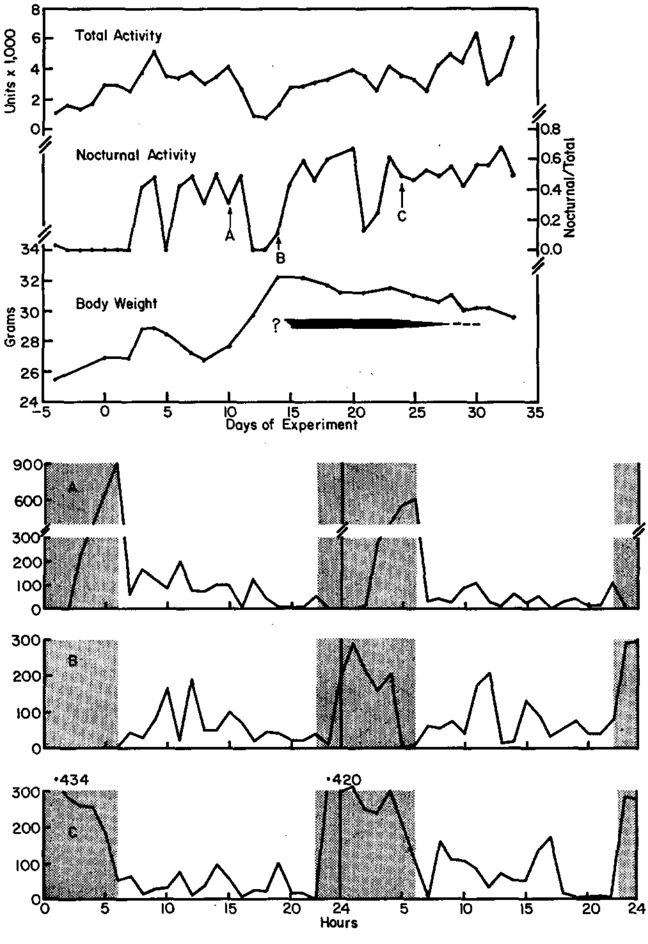

Fig. 15. *Zonotrichia leucophrys gambelii*, first-year male no. 27–195508. Experiment as in figure 14.

recognize that the hypothesis of Kendeigh, West, and Cox (1960) may hold for *Spizella arborea*, the species from which the primary data were obtained, although we feel that an alternative explanation is equally plausible at the present state of our knowledge. It is likewise obvious from the summaries in tables 1 to 4, and from the experiments on caloric restriction with *Z. l. gambelii*, that fat deposition *per se* is not the cause of *Zugunruhe*. Since these two alternative hypotheses of direct functional relationships must be discarded, at least in the species involved in this investigation, it seems necessary to assume that these two phenomena are controlled by divergent mechanisms using the same primary source of photoperiodic information, as in the lower scheme, figure 18. E, in this scheme, represents the environmental factors that cause and influence the development of vernal fat deposition and *Zugunruhe*. For both, the absolutely essential factor is the increasing daily photoperiod; environmental temperature, within natural limits, functions as an important modifier as indicated above. (See, also, Lack, 1960.) The characteristics of the two diverging mechanisms must be such that, although normally adjusted in *Z. l. gambelii* to cause fat deposition before *Zugunruhe* or the

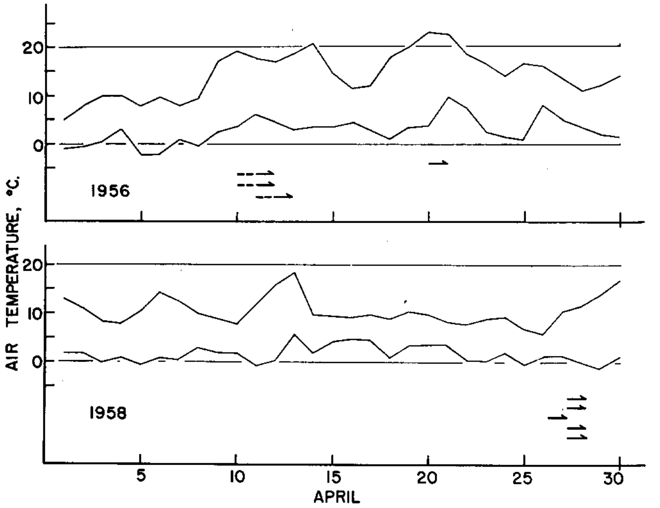

Fig. 16. Daily maximum and minimum air temperature in relation to the beginning of *Zugunruhe*. For individual *Zonotrichia leucophrys gambelii* the arrow points indicate the night when *Zugunruhe* began. In 1958, *Zugunruhe* was intense and continuous on the first night of occurrence; in 1956, it was weak and discontinuous on the first night (broken line) but intense thereafter.

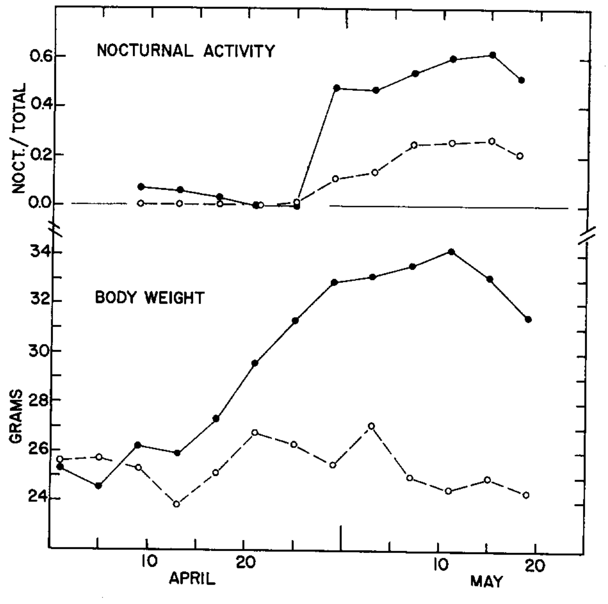

Fig. 17. Mean body weight and nocturnal activity in *Zonotrichia leucophrys gambelii* exposed outdoors to natural weather and photoperiod, 1960. Black dots: control group (n=8) feeding *ad libitum*; open circles: experimental group (n=9) with restricted food intake. See text.

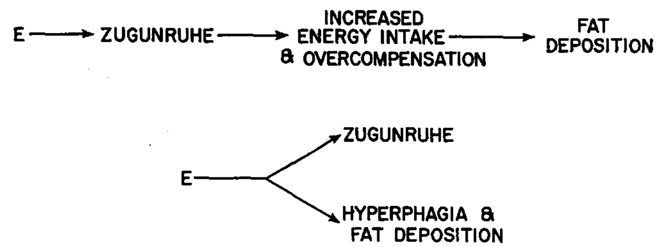

Fig. 18. Alternative hypotheses of the control sequence in the induction of the vernal migratory state in *Zonotrichia* spp. E symbolizes the environmental factors affecting the internal status of the bird.

beginning of vernal migration, the sequence may vary among individuals. Similar variations in the temporal relationships of these two mechanisms can be projected to the racial or species level. In *Z. l. gambelii*, which has a fairly rapid vernal migration, it appears probable that premigratory fat deposition has positive selective value as a source of fuel for migratory flight, although it is probably not sufficient for more than one or two nights, and as a reserve for inclement weather (Odum, Connell, and Stoddard, 1961; King, Barker, and Farner, 1963).

For the reasons outlined earlier (Farner, 1955), and more specifically because of the above-cited experiments with castrates, our scheme does not include the gonads as essential elements despite the fact that gonadal development is photoperiodically controlled in the species that we have studied. The essential differences between our hypothesis and that of Kendeigh, West, and Cox (1960) are shown in figure 18. It should be emphasized that in the present state of our knowledge, our hypothesis also could provide an ample explanation for the primary observations of Kendeigh, West, and Cox (*op. cit.*) on *Spizella arborea* and for other species which winter in temperate latitudes and begin spring migration with little or no increase in fat reserves. In consideration of the development of *Zugunruhe* and the initiation of migration in relation to the accumulation of fat reserves, it must be borne in mind that the latter phenomenon is probably extensively adaptive with respect to the nature of the migratory pattern of the species or population involved. It is therefore not surprising that there are populations, races, and species which begin migration without noticeable accumulation of fat reserves and that reserves are accumulated later when migration becomes more intense and the hazards of inclement weather have increased (Odum, Connell, and Stoddard, *op. cit.*), in contrast to those in which the full metabolic adjustment for maximum or near-maximum migratory effort is timed to occur before the initiation of migratory behavior.

SUMMARY

In *Zonotrichia leucophrys gambelii* the development of vernal *Zugunruhe* in birds in outdoor cages generally is preceded by the characteristic vernal fat deposition. This correlates well with the increase in fat reserves in natural populations prior to vernal migration. However, *Zugunruhe* does occur in some individuals before the deposition of additional fat reserves thus indicating clearly that fat deposition *per se* is not the direct cause of *Zugunruhe*. This is confirmed by the development of *Zugunruhe* in experiments in which photostimulated birds were prevented from accumulating fat reserves. It is therefore concluded that the mechanisms of development of *Zugunruhe* and fat deposition are essentially independent although both are dependent on a com-

mon source of information. The gonads apparently are not essential elements in either mechanism. Although our data are more limited, it seems apparent that this generalization holds also, at least in principle, for *Zonotrichia querula* and *Zonotrichia atricapilla*.

The basic and essential environmental factor in the development of vernal fat deposition and *Zugunruhe* (and also vernal migration) in *Zonotrichia leucophrys gambelii* is the vernal increase in day length. Environmental temperature, in an obviously complex manner, has an important modifying role with respect to the schedule and intensity of these phenomena.

LITERATURE CITED

Bailey, R. E.

1953. Surgery for sexing and observing gonad condition in birds. Auk, 70:497–499.

Dolnik, V. R.

1961. Mekhanizm energeticheskoi podgotovki ptits k pereletu i faktory, ee opredelyayushchie. *In* Ekologiya i migratsii ptits pribaltiki (Akademii Nauk Latviiskoi SSR, Riga) pp. 281–288.

Farner, D. S.

1955. The annual stimulus for migration: Experimental and physiolcgic aspects. *In* Recent Studies in Avian Biology, edited by A. Wolfson (Univ. Illinois Press, Urbana), pp. 198–237.

1959. Photoperiodic control of annual gonadal cycles in birds. *In* Photoperiodism and Related Phenomena in Plants and Animals (A.A.A.S. Publ. No. 55), pp. 717–750.

1960. Metabolic adaptations in migration. Proc. XII Intern. Ornithol. Congr., Helsinki, 1958, pp. 197–208.

Farner, D. S., King, J. R., and Wilson, A. C.

1957. The development of vernal migratory behavior in caged individuals of several taxa of *Zonotrichia*. Anat. Rec., 128:546.

Farner, D. S., and Mewaldt, L. R.

1953*a*. The recording of diurnal activity patterns in caged birds. Bird-Banding, 24:55–65.

1953*b*. The relative roles of diurnal periods of activity and diurnal photoperiods in gonadal activation in male *Zonotrichia leucophrys gambelii* (Nuttall). Experientia, 9:219–221.

1955*a*. Is increased activity or wakefulness an essential element in the mechanism of the photoperiodic responses of avian gonads? Northwest Sci., 29:53-65.

1955*b*. The natural termination of the refractory period in the white-crowned sparrow. Condor, 57:112–116.

Farner, D. S., Mewaldt, L. R., and Irving, S. D.

1953. The roles of darkness and light in the photoperiodic response of the testes of white-crowned sparrows. Biol. Bull., 105:434-441.

Farner, D. S., Mewaldt, L. R., and King, J. R.

1954. The diurnal activity patterns of caged migratory white-crowned sparrows in late winter and spring. Jour. Comp. Physiol. Psych., 47:148–153.

Farner, D. S., Oksche, A., Kamemoto, F. I., King, J. R., and Cheyney, H. E.

1961. A comparison of the effect of long daily photoperiods on the pattern of energy storage in migratory and non-migratory finches. Comp. Biochem. Physiol., 2:125–142.

Farner, D. S., and Wilson, A. C.

1957. A quantitative examination of testicular growth in the white-crowned sparrow. Biol. Bull., 113:254–267.

1959. The relation of single daily photoperiods to numerous short repeated photoperiods in testicular development in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). Atti del 2° Congresso Internazionale di Fotobiologia, 400.

Hagen, Y.
1942. Totalgewichts-Studien bei norwegischen Vogelarten. Arch. Naturgeschichte, N. F., 11:1–173.

Helms, C.W.
1959. Song and tree sparrow weight and fat before and after a night of migration. Wilson Bull., 71:244–253.

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

Johnston, D. W.
1962. Lipid deposition and gonadal recrudescence in response to photoperiodic manipulations in the slate-colored junco. Auk, 79:387–398.

Kendeigh, S. C., West, G. C., and Cox, G. W.
1960. Annual stimulus for spring migration in birds. Animal Behaviour, 8:180–185.

King, J. R.
1961*a*. The bioenergetics of vernal premigratory fat deposition in the white-crowned sparrow. Condor, 63:128–142.
1961*b*. On the regulation of vernal premigratory fattening in the white-crowned sparrow. Physiol. Zool., 34:145–157.

King, J. R., Barker, S., and Farner, D. S.
1963. A comparison of energy reserves during the autumnal and vernal migratory periods in the white-crowned sparrow, *Zonotrichia leucophrys gambelii*. Ecology, in press.

King, J. R., and Farner, D. S.
1959. Premigratory changes in body weight and fat in wild and captive male white-crowned sparrows. Condor, 61:315–324.
1961. The relationship of fat deposition and vernal migratory behavior as indicated by *Zugunruhe* in *Zonotrichia leucophrys gambelii*. Amer. Zool., 1:365.

Lack, D.
1960. The influence of weather on passerine migration. A review. Auk, 77:171–209.

Lofts, B., and Marshall, A. J.
1960. The experimental regulation of *Zugunruhe* and the sexual cycle in the brambling *Fringilla montifringilla*. Ibis, 102:209–214.
1961. *Zugunruhe* activity in castrated bramblings *Fringilla montifringilla*. Ibis, 103a:189-194.

McGreal, R. D., and Farner, D. S.
1956. Premigratory fat deposition in the Gambel white-crowned sparrow: some morphologic and chemical observations. Northwest Sci., 30:12–23.

Merkel, F. W.
1938. Zur Physiologie der Zugunruhe bei Vögeln. Ber. Ver. Schles. Ornith. 25 (Sonderheft):1–72.
1958. Untersuchungen über tages- und jahresperiodische Änderungen im Energiehaushalt gekäfigter Zugvögel. Zeits. f. vergl. Physiol., 41:154–178.

Morton, M. L., and Mewaldt, L. R.
1962. Some effects of castration on a migratory sparrow (*Zonotrichia atricapilla*). Physiol. Zool., 35:237–247.

Nice, M. M.
1946. Weights of resident and winter visitant song sparrows in central Ohio. Condor, 48:41–42.

Odum, E. P.
1960. Premigratory hyperphagia in birds. Amer. Jour. Clin. Nutrition, 8:622–629.

Odum, E. P., Connell, C. E., and Stoddard, H. L.
1961. Flight energy and estimated flight ranges of some migratory birds. Auk, 78:515–527.

Odum, E. P., Connell, C. E., and Stoddard, H. L.
1951. Relation of lipid metabolism to migration in birds: seasonal variation in body lipids of the migratory white-throated sparrow. Physiol. Zool., 24:216–230.

Palmgren, P.
1944. Studien über die Tagesrhythmik gekäfigter Zugvögel. Zeits. f. Tierpsychol., 6:44–86.

Putzig, P.
1939. Beiträge zur Stoffwechselphysiologie des Zugvogels. Vogelzug, 10:139–154.

Rowan, W.
1926. On photoperiodism, reproductive periodicity, and the annual migrations of birds and certain fishes. Proc. Boston Soc. Nat. Hist., 38:147–189.
1929. Experiments in bird migration. I. Manipulation of the reproductive cycle: seasonal histological changes in the gonads. Proc. Boston Soc. Nat. Hist., 39:151–208.
1932. Experiments in bird migration. III. The effects of artificial light, castration and certain extracts on the autumn movements of the American crow (*Corvus brachyrhynchos*). Proc. Nat. Acad. Sci., 18:639–654.
1946. Experiments in bird migration. Trans. Royal Soc. Canada, Ser. 3, Sect. V, 40:123–135.

Wachs, H.
1926. Die Wanderungen der Vögel. Ergeb. Biol., 1:478–637.

Weise, C. M.
1956. Nightly unrest in caged migratory sparrows under outdoor conditions. Ecology, 37:275–287.
1962. Migratory and gonadal responses of birds on long-continued short day-lengths. Auk, 79:161–172.

Wolfson, A.
1945. The role of the pituitary, fat deposition, and body weight in bird migration. Condor, 47:95–127.
1959*a*. Ecologic and physiologic factors in the regulation of spring migration and reproductive cycles in birds. *In* Comparative Endocrinology, Proceedings of the Columbia University Symposium on Comparative Endocrinology (John Wiley, New York), pp. 38–70.
1959*b*. The role of light and dark in the regulation of spring migration and reproductive cycles in birds. *In* Photoperiodism and Related Phenomena in Plants and Animals (A.A.A.S. Publ. No. 55), pp. 679–716.
1960. Role of light and darkness in the regulation of the annual stimulus for spring migration and reproductive cycles. Proc. XII Intern. Ornith. Congr., Helsinki, 1958, pp. 758–789.

Zedlitz, O.
1926. Vogelgewichte als Hilfsmittel für biologische Forschung. Jour. f. Ornith., 74:296–308.

Department of Zoology, Washington State University, Pullman, Washington, October 3, 1962.