MIGRATORY AND GONADAL RESPONSES OF BIRDS ON LONG-CONTINUED SHORT DAY-LENGTHS

CHARLES M. WEISE

IN the experimental investigation of the annual stimuli for migration, reproduction, and molt, it would often be desirable to suspend the annual cycle at some point, preferably in the inactive winter condition. Recent experiments involving birds that have been held at constant short day-lengths after the winter solstice indicate that this may not be possible, the cycles being merely suppressed or retarded to some degree but not completely suspended. Nonmigratory birds under such conditions have exhibited testicular recrudescence ranging from partial in the Starling (*Sturnus vulgaris*) (Burger, 1953) to "complete" in the House Sparrow (*Passer domesticus*) (Threadgold, 1960) and White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*) (Miller, 1955). In migratory forms Winn (1950) found some testicular development in the Slate-colored Junco (*Junco hyemalis*) after nearly a year at nine hours. Miller (*op. cit.*), however, found only slight development, followed by regression, in the Golden-crowned Sparrow (*Zonotrichia atricapilla*) after six–eight months at a 10-hour photoperiod, while Laws and Farner (Farner, 1959) found no testicular enlargement in *Zonotrichia leucophrys gambelii* held at eight hours for 10 months. In regard to the development of the spring migratory condition, Winn's (*op. cit.*) short photoperiod Juncos underwent typical premigratory fat deposition in May and June, about 40 days later than normal. Miller's (*op. cit.*) Golden-crowned Sparrows exhibited subcutaneous fat from June to September. Wolfson (1959a) held Slate-colored Juncos and White-throated Sparrows (*Zonotrichia albicollis*) at 9L-15D from December until June and then released them to determine if they would migrate. Fat condition at the time of release showed "considerable variation," but "about 60 per cent of the birds left the area and presumably migrated" (p. 44).

The experiment to be reported here was undertaken to determine the migratory responses of White-throated Sparrows held at a nine-hour photoperiod, which represents about the minimum winter day-length to which the species is exposed in nature. A few Slate-colored Juncos and Fox Sparrows (*Passerella iliaca*) were also included in the experiment. In effect the experiment repeated the nine-hour photoperiod experiments of Winn and Wolfson, previously cited, with the essential difference that nightly unrest or *Zugunruhe* was used as an additional and (it is believed) more reliable criterion of the migratory condition. *Zugunruhe* is believed to be a manifestation of the behavior that in wild birds is expressed in nocturnal migratory flight, and it has been found to be closely restricted

to the normal migratory seasons in White-throated Sparrows and Slate-colored Juncos under outdoor conditions (Weise, 1956, and unpublished). Although concentration was on the migratory cycle, some gonadal and molt data were obtained.

DESCRIPTION OF THE EXPERIMENT AND METHODS

The experiment was conducted in two photoperiod chambers lacking temperature control. The aviary temperatures fluctuated daily and seasonally but with much less range than outdoor temperatures. The lowest temperature recorded (by thermograph) was 0° C and the highest, 34°. Monthly mean temperatures are shown in Figure 2. Lighting was provided by two 100-watt incandescent bulbs in each chamber, with intensity of 30–50 foot candles at cage level.

The experiment began on 21 December 1957 when the birds (12 White-throated Sparrows, four Slate-colored Juncos, and three Fox Sparrows) were moved from a naturally lighted room to one of the photoperiod chambers with a lighting program of 9L-15D. Until April 1958 the birds remained in large holding cages and no regular examinations were conducted, although casual observations of fat and molt were made during the weekly cage cleanings. On 8 April 1958 all the birds were placed in individual activity-recording cages in the same chamber. Subsequently activity was recorded continuously, and all birds were examined at weekly or biweekly intervals for weight, fat, molt, and cloacal condition. There was a four-week gap between examinations of some birds in May 1958, and another in October 1958. On 10 December 1958 after nearly 12 months at 9L-15D, the birds (except for a few killed earlier for gonadal examination) were divided at random into two groups. Group A, consisting of five White-throated Sparrows, one Junco, and one Fox Sparrow, remained in the original chamber while the lighting was changed to 15L-9D to test whether the birds were actually responsive. Most of these birds were killed for autopsy in February and March 1959. Group B, consisting also of five White-throated Sparrows, one Junco, and one Fox Sparrow, was moved to the adjacent chamber and kept on the 9L-15D regime. Two of the White-throated Sparrows were killed in February, and the Junco and Fox Sparrow in June 1959. The three remaining White-throated Sparrows were finally changed to 16L-8D on 21 June 1959, 18 months after the beginning of the experiment. These were killed for autopsy on 13 July 1959.

Another group of 13 White-throated Sparrows was kept in the same photoperiod chamber at 9L-15D from 21 December 1959 through June 1960. Although these were kept for another purpose, they provided corroboratory and supplementary evidence for the 1957–1959 experiment.

The activity cages used in this experiment were improved versions of those described in an earlier paper (Weise, 1956). A high proportion of locomotor movement was registered; the cages were adjusted so that when the birds were disturbed, as when someone was in the chamber, an essentially solid line of marks appeared on the record chart. Recording was by means of an Esterline-Angus recorder, chart speed three inches per hour. In analyzing the records, each hour was divided into 20 equal intervals, and the number of intervals containing activity marks was counted. Such intervals are referred to in this paper as activity units. In a 15-hour dark period the maximum possible number of activity units is 300. Outdoor birds in the spring migratory condition usually exhibit between 50 and 150 units in a nine- or 10-hour night.

Body weight and fat class were determined as previously described (Weise, *op. cit.*). Fat classes ranged from 0 (none) to 4 (very heavy). The cloacal protuberance was used as an indication of advanced and sustained testicular recrudescence, the degree of protuberance being rated from 0 to 3. The value 3 was assigned only when the whitish, sperm-filled tubules of the seminal vesicle were visible through the skin of the protuberance.

At autopsy the gonads were measured crudely with calipers, and the fresh weights of testes, seminal vesicles, ovary, and oviduct were obtained with a torsion balance. The original plan of the experiment was to kill birds for gonadal examination after they had begun to show migratory responses or such gonadal responses as the cloacal protuberance. This plan was carried out with the few Juncos involved. But since such responses did not occur in the White-throated Sparrows, only a few gonadal samples were obtained for this species.

RESULTS

Weight and fat. Desultory observations during the period from 21 December 1957 to 8 April 1958 indicated that many of the White-throated Sparrows were in fat classes 2–4 in midwinter, while the Juncos and Fox Sparrows were in classes 1 or 2. By March the fat deposits were diminishing, and on 8 April when the birds were placed in the activity cages none of the Fox Sparrows or Juncos and only three of the White-throated Sparrows were in class 2 or higher. These trends of weight and fat during the December–April period were confirmed by the 1959–1960 group of White-throated Sparrows. All but two of the 13 birds in this latter group exhibited fat class 2 or 3 during the winter months, with weight peaks of 29–33 g in February or early March (Figure 2).

In the original experiment, as shown in Figures 1 and 2, the White-throated Sparrows continued a slow decline in weight and fat until August,

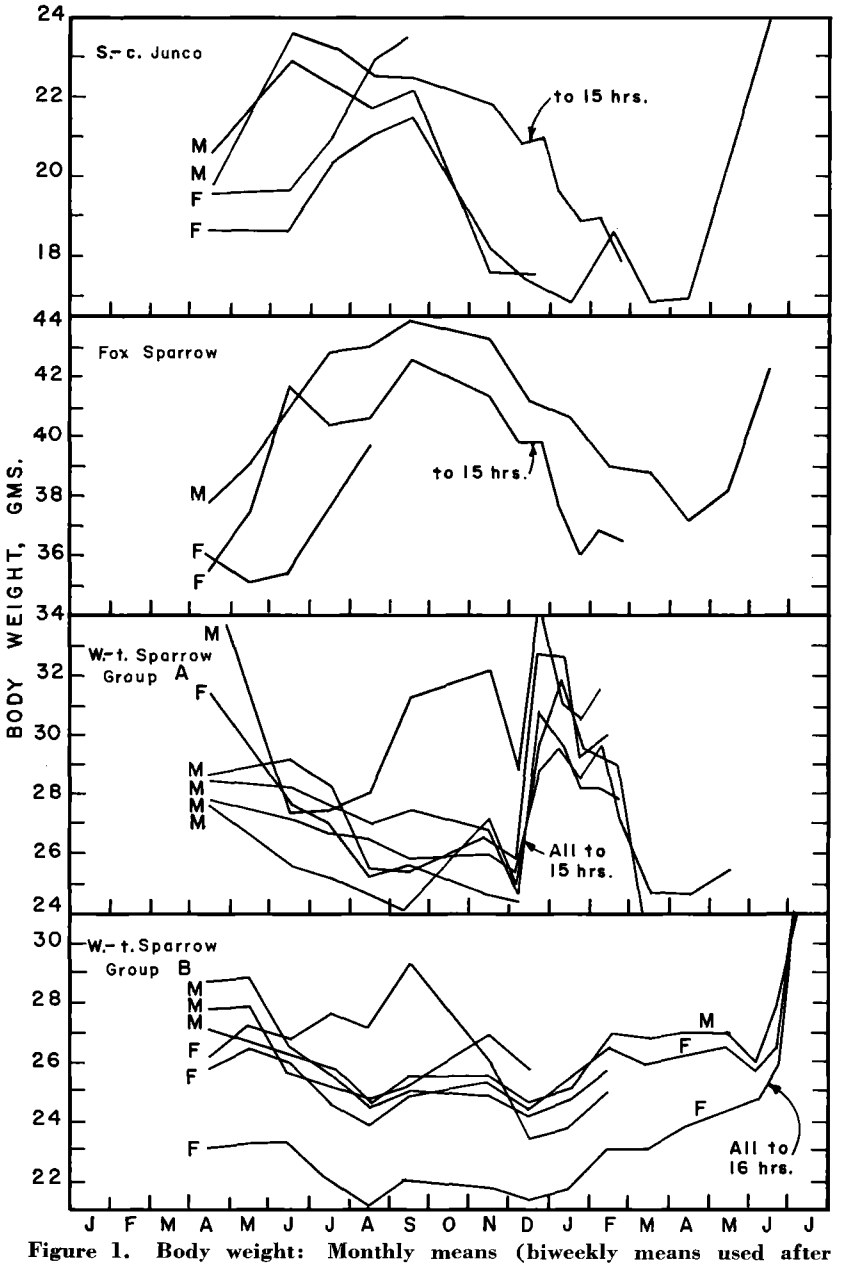

Figure 1. Body weight: Monthly means (biweekly means used after photoperiod increase) for individual birds. Each point based on two to four weighings determined in midafternoon except during December 1958 and January 1959, when birds were weighed in midmorning. Sex indicated by M and F.

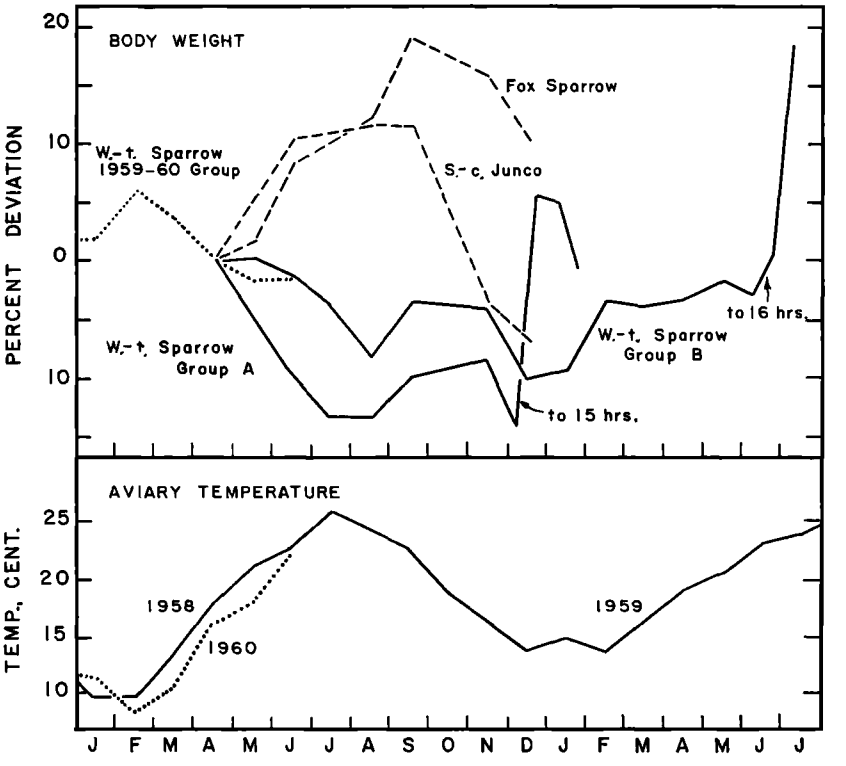

Figure 2. Upper. Body weight: Monthly or biweekly means for all groups, expressed as per cent deviation from April mean weight. Lower. Monthly mean temperatures in aviary.

when an upswing began. Two of the White-throated Sparrows increased markedly in weight and fat in September. In the 1959–1960 group three of the 13 birds showed a moderate gain in weight and fat in June.

The Slate-colored Juncos and Fox Sparrows had a completely different weight picture during this first year of the experiment. All the birds showed pronounced weight and fat gains during the summer months, although there were some differences in the timing. All achieved fat class 3 or 4 during this period. After September a gradual decline set in, but three of five birds were still quite high in weight in December.

The White-throated Sparrows of group B increased slightly in weight and fat during the first half of 1959, but remained well below the levels characteristic of the migratory condition. In contrast the one Junco and the one Fox Sparrow of this group again showed significant weight and fat increases in May and June as they had in the previous year. In short, most of the White-throated Sparrows exhibited no marked weight or fat

increases during up to 18 months on a short day-length, while the Juncos and Fox Sparrows (judging by the admittedly meager evidence presented above) exhibited two periods of fat deposition and body weight increase, the first in the summer of 1958 and the second in the early summer of 1959.

Nightly unrest. Curves showing the intensity of *Zugunruhe* are shown in Figure 3. All the Juncos and Fox Sparrows exhibited nightly unrest at some time during the July–November period of 1958. This was generally of the typical pattern (see Weise, 1956), but was of low intensity, the maxima for a single night ranging only up to 66 units in the Juncos and to 94 units in the Fox Sparrows. The periods of unrest were variable. One Junco was active at night from July through November, another only for a few weeks in July, and two for several weeks in August and September. All the Fox Sparrows exhibited *Zugunruhe* in July and August; of the two remaining thereafter, one ceased in September while the other showed declining activity until January when there was a temporary resurgence followed by cessation.

Among the White-throated Sparrows there was no nightly unrest during this time except in one aberrant case. This was a bird that exhibited an atypical pattern of activity (intense movement for the last hour or so of the dark period), following the moving of its cage to a new position in the aviary. This activity occurred on nine nights between 29 July and 14 August 1958 with a maximum intensity for one night of 36 units, and an average of 11 units. It is unlikely that this should be considered a migratory response.

In the 1959–1960 group of White-throated Sparrows no *Zugunruhe* occurred in any of the birds at any time between December and the end of June, despite the presence of moderate or heavy fat deposits during the winter months.

None of the White-throated Sparrows of group B became active at night during their second year on the short photoperiod. The Fox Sparrow and Junco, however, initiated second periods of nightly unrest in May 1959. These coincided with the weight increases mentioned above.

Molt. All the White-throated Sparrows and Juncos went through a molt of the prenuptial type in the spring and early summer of the first year, and those kept for 18 months underwent a similar molt at the same time of the second year. This molt involved only a few inter-ramal feathers in the Juncos. In the White-throated Sparrows it differed from the normal prenuptial molt in being irregular in pattern, confined to parts of the trunk and not including the head at all, and of long duration. The molt began at about the normal time each year (March) but continued until June, July, or even August in one case.

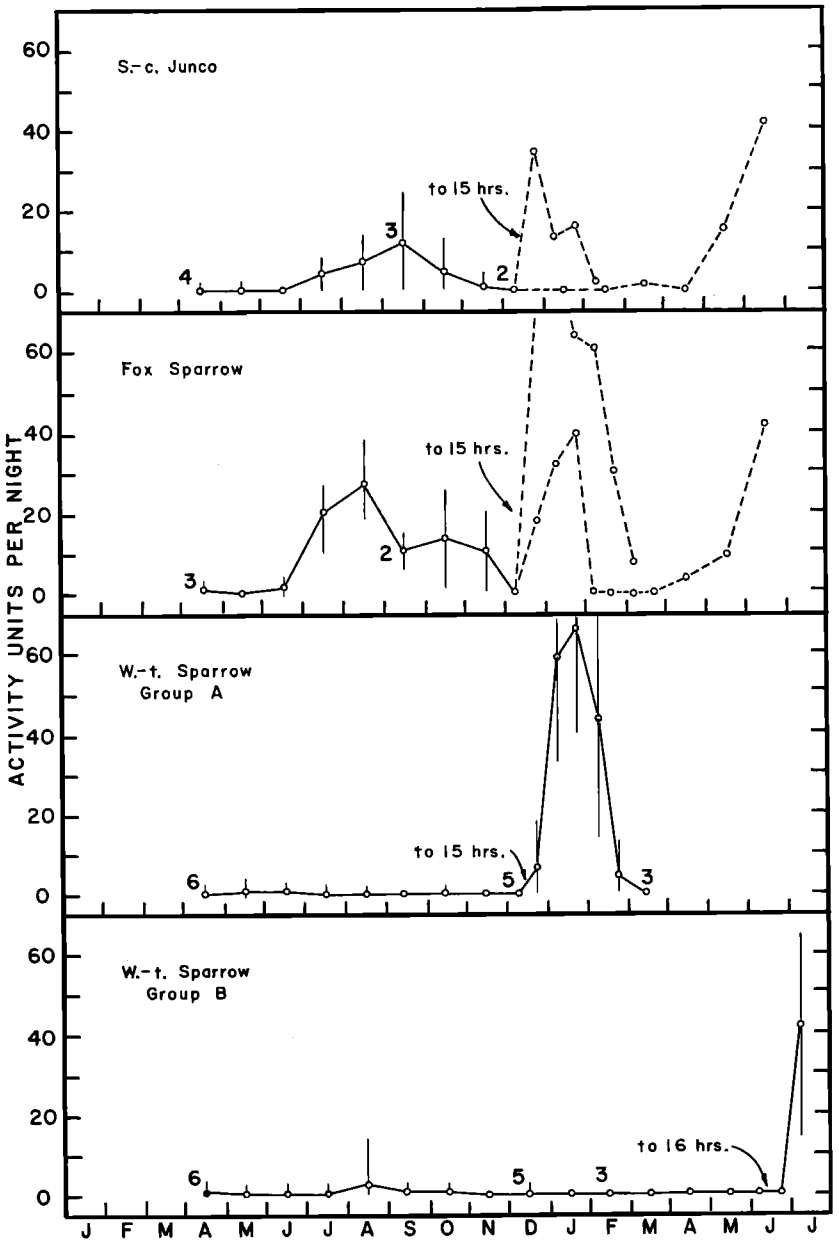

Figure 3. Nightly unrest or *Zugunruhe:* Monthly or biweekly means for groups. Vertical lines indicate the range of means for individuals. Numbers indicate number of birds. Broken lines represent single birds.

TABLE 1
GONADAL CONDITION FOLLOWING LONG EXPOSURE TO NINE-HOUR DAYS

	Date of autopsy	*Days at nine hours*	*Migratory condition at time of death*	*Testis stage (Wolfson, 1942)*	*Weights in mg*			
					Largest testis	*Largest seminal vesicle*	*Ovary*	*Oviduct*
White-throated Sparrow								
5754	2 Dec. 1958	346	–	3	2.4	0.7		
5711	2 Dec. 1958	346	–				8.9	10.2
5758	3 Feb. 1959	409	–	3	7.0	0.7		
5774	3 Feb. 1959	409	–				11.2	13.3
Slate-colored Junco								
5768	9 Sept. 1958	262	+				9.0	small
5756	2 Dec. 1958	346	–	2	1.7	small		
5752	10 June 1959	536	+				13.6	6.4
Fox Sparrow								
5773	22 Aug. 1958	244	+				12.2	small
5772	10 June 1959	536	+	3	6.4	1.5		

Gonadal condition. Table 1 sets forth the gonadal conditions of the birds killed while at 9L-15D. In these species single testes in the minimum condition vary from about 0.5 to 2 mg in weight, while ovaries range from less than 3 to about 8 mg. Fully active testes are on the order of 200–300 mg, and ovaries vary from 30–50 mg ordinarily to over 300 mg when approaching ovulation.

Four White-throated Sparrows examined after exposure to the short photoperiod for 12 or 14 months had gonads only slightly above the normal minimum. Histologically the testes were in stage 3 of Wolfson (1942). The gonads of Juncos and Fox Sparrows after exposure for eight or 18 months were in a similar condition, suggesting low-level gonadal development like that observed by Winn (1950) and Miller (1955). The single Junco examined after 12 months had gonads near the minimum size.

Obviously, none of the birds examined had gonads anywhere near the breeding condition, and there was no outward manifestation of such condition at any time during the experiment. None of the birds exhibited a cloacal protuberance, song, or other sexual behavior, while at 9L-15D.

Results of exposure to 15L-9D or 16L-8D. Group A was placed on 15L-9D on 10 December 1958, 354 days after the beginning of the experiment. All five of the White-throated Sparrows exhibited unmistakable migratory and gonadal responses (weight and fat increase, nightly unrest,

cloacal protuberance ratings of 3) during late December and January, as shown in Figures 1–3. Single testis weights varied from 248 to 306 mg. The Fox Sparrow and Junco did not exhibit a weight or fat increase at this time, but rather showed a continued gradual decline from the high values of the previous summer. However, they did become strongly active at night, and the Junco developed a moderate cloacal protuberance (the Fox Sparrow was a female). Neither bird was killed for autopsy at this time.

The White-throated Sparrows of group B, which were placed at 16L-8D on 20 June 1959, exhibited strong migratory responses (Figures 1–3) and had somewhat enlarged gonads when killed on 13 July (largest testis, 87 mg; ovaries, 31 and 37 mg).

DISCUSSION

The present experiment is directly comparable with the nine-hour photoperiod experiments of Winn (1950) and Wolfson (1959a) referred to in the introduction. The Slate-colored Juncos of this experiment deposited fat to the same extent and at about the same time as those of Winn. That this was premigratory fat is confirmed by the occurrence of *Zugunruhe* in all four Juncos, but perhaps its rather low intensity and its variability in timing and duration indicate some degree of suppression of the migratory response. The present data differ from those of Winn in respect to the duration of the migratory condition. My Juncos had lost or were losing their fat by the end of the first year (and had long since ceased nightly activity), while three of the four birds kept by Winn longer than 10 months maintained their fat deposits. Furthermore, the single Junco in this experiment that was kept for 18 months initiated a second migratory response, manifested by both fat deposition and *Zugunruhe,* in May and June of the second year.

The Fox Sparrows exhibited migratory responses similar to those of the Juncos, but stronger and less variable.

On the other hand, the White-throated Sparrows at 9L-15D utterly failed to develop *Zugunruhe* or the migratory physiological condition, unless the moderate weight and fat gains of a few of the birds represented a tendency toward the latter. Wolfson's (*op. cit.*) release experiment, which included White-throated Sparrows, has not been published in detail, but the disappearance of 60 per cent of the birds, which he attributed to migration, could as easily have been due to simple wandering and the potentially high mortality of such birds.

In nature the Slate-colored Junco migrates in the spring several weeks before the White-throated Sparrow. In captive birds in outdoor cages this is reflected by a three weeks' difference between the two species in the timing of fat deposition and in the onset of *Zugunruhe* (Weise, 1956,

corroborated by recent unpublished data). These differences, combined with the results of the present experiment, indicate an important difference in the photoperiodic response mechanism during the "progressive phase" (Wolfson, 1958) of the cycle. This difference could be due to (1) a different rate of response to photoperiod per se or a different minimum photoperiod threshold, (2) a difference in the role played by temperature, or (3) a more complex difference in the endocrine and metabolic mechanisms involved.

Each of these possibilities has some argument in its favor. Wolfson's extensive experiments, as well as unpublished experiments in this laboratory, indicate essentially identical rates of response to stimulatory photoperiods, but the results of the present experiment could be explained on the basis of a different photoperiod threshold—below nine hours in the Slate-colored Junco, above nine hours in the White-throated Sparrow.

That temperature might play an important augmentative role in the photoperiod response is suggested by the experiments of Kendeigh, *et al.* (1960) with the Tree Sparrow (*Spizella arborea*), which migrates at about the same time as the Junco in the spring. In the Tree Sparrow longer photoperiods were needed to induce *Zugunruhe* at −4° C than at +6° C. Nightly unrest could not be induced in short photoperiod birds by raising the temperature, but the experiment was perhaps too short (20 days) to be conclusive. At any rate an interaction between photoperiod and temperature in the induction of *Zugunruhe* was clearly shown. Farner and Mewaldt (1953) observed nightly unrest in White-crowned Sparrows held on short days but at a high temperature (21° C). In the present experiment the decline of the migratory condition in the Junco and Fox Sparrow in the fall and its renewal the following spring suggest a correlation with temperature, since this environmental cue was varying in a nearly natural way. The influence of temperature on the development of the spring migratory condition requires more careful study than it has received. It is unwarranted to assume that its role here is as slight as it has been shown to be in gonadal development (Farner and Wilson, 1957), particularly in the earlier migrants like the Tree Sparrow, Fox Sparrow, and Slate-colored Junco.

Endocrine and/or metabolic differences between the Junco and the White-throated Sparrow are suggested by the apparently more extensive deposition of "winter fat" and the much more intense prenuptial molt in the latter. Just how these are related to the development of the migratory condition is not clear.

With regard to the gonadal response there appeared to be no differences among the three species involved, despite the differences in migratory response. None of the male birds at 9L-15D attained the full breeding con-

dition as indicated by the cloacal protuberance, song, or other sexual behavior. However, the autopsy data, collected from birds that had been at the short photoperiod for 8–18 months, revealed that the gonads of both sexes had developed beyond the minimum winter condition. This is in agreement with the findings of Winn (1950) for the Slate-colored Junco. Miller's (1955) Golden-crowned Sparrows exhibited a corresponding degree of development within six–eight months but had regressed to the minimum condition by 10 months. However, he used a slightly longer photoperiod so that the experiments are not strictly comparable.

My interpretation of these results differs somewhat from that of Wolfson (1959a, 1959b, 1960), who stresses the positive fact that some gonadal development did occur at nine hours and regards this as a "response." I would stress the negative aspect, that the weight of the evidence is against the occurrence of an ecologically effective response involving complete spermatogenesis and sufficient secretion of sex hormones to bring about reproductive behavior. It appears that a photoperiod above nine hours is necessary for such a response in these migratory species (cf. Miller, 1955), notwithstanding the demonstrated fact that even lower photoperiods can induce such responses in certain early breeding, nonmigratory birds, as Farner (1959) has pointed out.

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SUMMARY

White-throated Sparrows, Slate-colored Juncos, and Fox Sparrows were kept on nine-hour days for up to 18 months, beginning 21 December 1957 and 21 December 1959. Aviary temperatures were uncontrolled and fluctuated with day and season. The Juncos and Fox Sparrows exhibited a migratory response (fat deposition and *Zugunruhe*), retarded by about two months and possibly somewhat suppressed. This migratory condition declined and disappeared in the following autumn and winter. In one bird of each species kept for 18 months, the migratory condition developed anew in the second spring of the experiment. White-throated Sparrows, on the other hand, completely failed to exhibit migratory responses under these conditions, although the prenuptial molt was initiated at about the normal time in both the first and second years of the experiment. Thus the White-throated Sparrow differs from the Fox Sparrow and Slate-colored Junco in some way in regard to the mechanisms regulating the development of the migratory condition.

None of the three species came into the full breeding condition while at nine hours. However, birds killed after 8–18 months had gonads advanced beyond the minimum condition. Granting that some gonadal development occurs, the evidence from this experiment and from others in the literature indicates that a nine-hour photoperiod is too short for an ecologically effective gonadal response in these temperate-zone migratory species.

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Department of Zoology, University of Wisconsin–Milwaukee, Milwaukee, Wisconsin.