# Endogenous Timing Factors in Bird Migration

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MIGRATORY BIRDS, in addition to being confronted with problems of spatial orientation, have to solve various problems of orientation with respect to time. The success of their migrations depends, among other factors, upon proper timing of the onset and end of their daily and seasonal migratory activity. The question of which factors are responsible for the initiation of spring and fall migration at the appropriate and specific time of the year has particularly challenged naturalists from the early days of research in this field, and, from the very beginning, opinions were divided between those holding environmental factors responsible and those postulating endogenous factors as principal releasers of bird migrations (e.g., refs. 1 to 7). The former group received strong impetus from Rowan's (ref. 8) discovery that environmental changes in daylength are of overwhelming significance for the timing of migrations in birds. As a result, interest has focussed on this rewarding aspect of the problem, and many bird species have been shown subsequently to depend strongly on environmental changes in photoperiod for the

timing of their migratory activities (reviews in refs. 9 to 16).

Photoperiodic induction, however, cannot be the only mechanism, and Rowan himself (ref. 17) in his early papers stressed the fact that the applicability of this concept is obviously limited. Many bird species breeding in the temperate zones migrate to regions close to the equator and thus winter in environments in which seasonal changes in photoperiod are of small magnitude. Nevertheless, these birds depart in spring very precisely at the appropriate time for their homeward migration. Factors other than photoperiod seem to induce migratory behavior in these birds. However, in many equatorial regions, none of the more obvious environmental factors, such as temperature or precipitation, is likely to be the releaser of spring migration because these factors either vary within a narrow range or so irregular that they could not account for the very precise departure of the birds. It has been speculated, therefore, by Rowan and others that these birds may be equipped with an endogenous timing mechanism that makes their temporal orientation independent of environmental information (e.g. refs. 18 to 22). This paper reports experiments carried out to test this hypothesis. The results revealed that en-

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dogenous stimuli are, in fact, essential timing factors in warbler migration, not only for the initiation of migrations at the appropriate times of the season, but possibly also for the termination of migration at the appropriate places.

## GENERAL EXPERIMENTAL PROCEDURE

The subjects of most of the experiments summarized in this paper are two closely related species of the old-world warbler genus *Phylloscopus*. The willow warbler (*P. trochilus*) is a long-distance migrant with breeding grounds throughout most of the palaearctic region and winter quarters in equatorial and southern Africa. Its sibling species, the chiff-

chaff (*P. collybita*), on the other hand, is a short-distance migrant, breeding in the more southwesterly parts of the palaearctic and wintering in the Mediterranean area. Only a few individuals of the western races seem to cross the Sahara on their migrations. (These migrations are covered later in detail.)

All the birds employed in this study were taken from their nests in southwestern Germany and in northern Sweden and raised by hand. After they had reached independence they were housed individually in 42 × 28 × 23 cm registration cages in which their locomotor activity was recorded on event recorders by means of miniature switches mounted underneath one of the perches. By this method it was possible to obtain a continuous record on "Zugunruhe," the nocturnal activ-
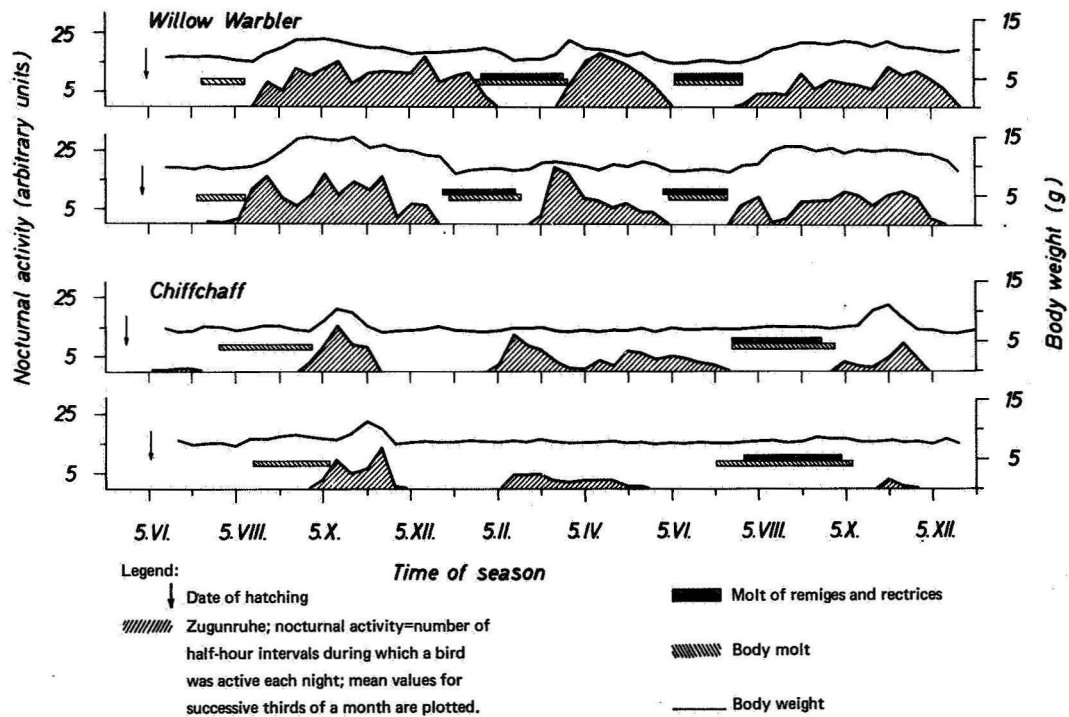


FIGURE 1. Variations in Zugunruhe, body weight and molt in two willow warblers and two chiffchaffs kept under natural photoperiodic conditions of their southwest German breeding grounds.

ity, typically shown by nocturnal migrants during the migratory seasons (ref. 23). In addition, body weights and data on molting were taken at regular intervals, usually twice a week (for details see refs. 24 and 25). Birds were kept in the following experimental conditions:

(1) ENi: Natural photoperiodic conditions of the southwest German breeding grounds in Erling (48°N, 11°11'E), in a temperature-regulated room (21° ±2°C)

(2) B: Natural photoperiodic conditions of the central African wintering area of the willow warbler in Bukavu, Congo (2°4'S, 28°39'E), either outdoors or indoors in a temperature-regulated room (23° ± 2°C) with large windows

(3) LD 12:12 and LD 18:6: Constant artificial photoperiodic conditions with 12 and 18 hr of light, respectively, in 24 hr (200: 0.02 lux unless otherwise noted), in temperature-regulated chambers (20° ± 1°C or 23° ± 1°C)

The usefulness as well as the limitations of this indirect approach can be illustrated by results obtained from willow warblers and chiffchaffs kept for a period of about 9 months under natural photoperiodic conditions of their breeding grounds. The representative examples, depicted in figure 1, show that the behavior of the caged birds reflects fairly accurately the normal annual cycle of the two species. The birds perform nocturnal activity during the migratory seasons, accompanied at least in autumn by an increase in body weight typical for most migratory birds. Periods of Zugunruhe and obesity are separated by periods of molt. As in freeliving birds, postnuptial molt is complete in both species; prenuptial molt, on the other hand, is complete only in the willow warbler, whereas only a few of the chiffchaffs replace parts of their body plumage.

Despite this harmony in general features

between the behavior of caged birds with that of freeliving conspecifics (some other characteristic differences between the species will be discussed below), discrepancies appear in some important details. For instance, obesity, typical for both species during autumn Zugunruhe, is nearly absent in spring, whereas freeliving individuals apparently become as fat in spring as in autumn. More importantly, spring Zugunruhe is extended in both species beyond the date at which actual migration stops, continuing until the onset of postnuptial molt. While we can only speculate on the reasons for such discrepancies, these findings indicate obvious weaknesses of the method employed and thus suggest caution in the interpretation of the results.

## RESULTS

### Initiation of Zugunruhe in Seasonally Constant Conditions

*Spring.*—A first series of experiments was carried out to investigate whether or not spring Zugunruhe would develop despite the absence of seasonal changes in the environment. Twenty-five willow warblers from southwestern Germany were hand raised in the springs of 1966 and 1967, respectively, and kept until autumn under the natural photoperiodic conditions of their breeding grounds. Between September 18 and 21, when most individuals had started to exhibit autumn Zugunruhe, they were divided into four groups and transferred to the following experimental regimes: Group I remained under the natural photoperiodic conditions of their breeding grounds; group II was displaced by air to a location in central Africa within the winter range of the species; groups III and IV were transferred to constant photoperiodic conditions with 12 and 18 hr of daylight, respectively, per 24 hr.

Figure 2 shows that Zugenruhe develops in the birds of all experimental groups. It is preceded, in all birds, by prenuptial molt and followed by postnuptial molt in those birds kept long enough under experimental conditions.
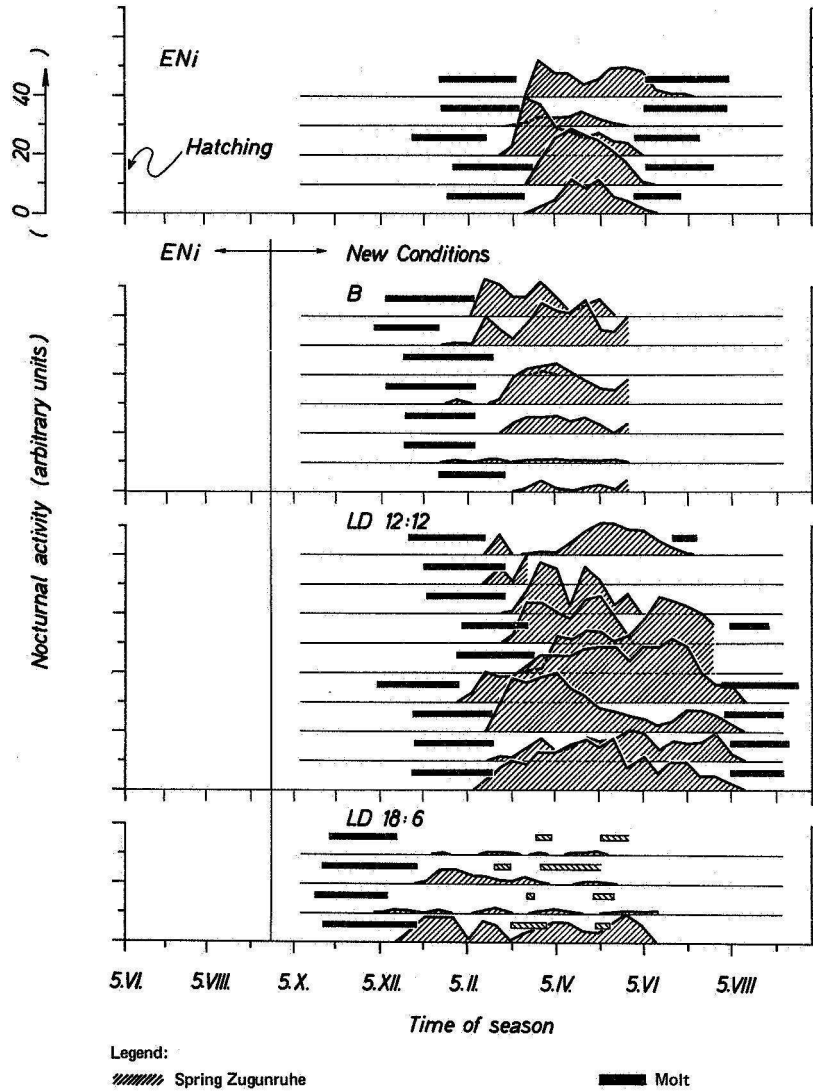


**Legend:**

▨▨▨ Spring Zugunruhe          ▅▅▅ Molt

**FIGURE 2.** Spring Zugunruhe and molt of willow warblers kept under natural photoperiodic conditions of their southwest-German breeding grounds (ENi, upper graph) and from birds transferred between September 15 and 20 from such conditions to either of the following schedules: LD *12*:12, LD *18*:6 = constant 12-hr photoperiod or 18-hr photoperiod, respectively. B = natural photoperiodic conditions of a location (Bukavu) within range of central African wintering grounds of the species (either outdoors—upper 3 birds—or indoors). For further explanations, see figure 1.

Apart from differences in timing, no major differences in the behavior of the birds kept in *LD 12*:12 and those living in natural light conditions can be detected. The willow warblers kept in *LD 18*:6, on the other hand, behave abnormally in at least two respects. Zugunruhe is weak in most subjects and is frequently interrupted or superimposed by short periods of body molt.

These results clearly demonstrate that spring Zugunruhe as well as pre- and postnuptial molt can occur independently of seasonal changes in photoperiod and temperature. Furthermore, the fact that the events investigated occur at different times of the season, depending on the experimental conditions, suggests that these processes are governed by endogenous factors rather than by uncontrolled environmental stimuli penetrating the experimental chambers.

*Autumn.*—A second set of experiments was conducted to test whether the same behavior pattern would hold for fall Zugunruhe and the events preceding and following it. Twenty-four willow warblers were taken from the nest at an age of 6 to 11 days and transferred immediately to a constant 12-hour day and 18-hour day, respectively. They were kept there until January of the subsequent year. The behavior of these birds was compared to that of a control group living under the natural light conditions of their breeding grounds.

Figure 3 summarizes the essential results. It is obvious that Zugunruhe develops in an orderly manner in all birds, regardless of the conditions under which they are kept. Similarly, postjuvenile molt is carried out by all individuals. Prenuptial molt, on the other hand, can be observed only in the birds kept under natural light conditions or in *LD 12*:12, but not in the long-day group. Since the long-day conditions delay postjuvenile molt as well as Zugunruhe, the experimental



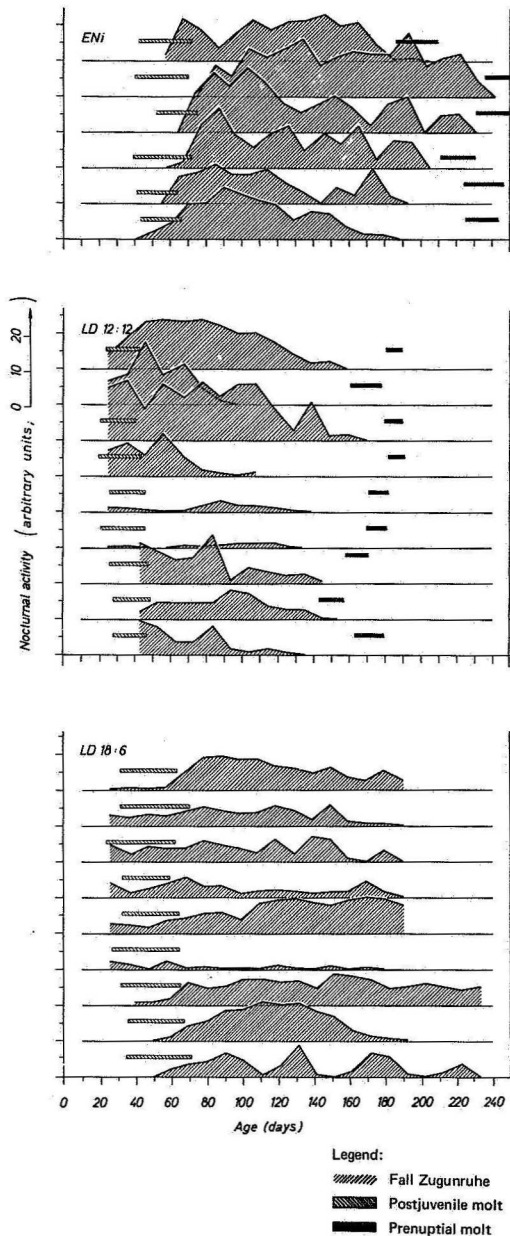Legend:
▨ Fall Zugunruhe
▧ Postjuvenile molt
■ Prenuptial molt

FIGURE 3. Fall Zugunruhe, postjuvenile molt, and prenuptial molt of birds raised from an average of 9 days either indoors under natural photoperiodic conditions of their breeding grounds (ENi) or in a constant 12-hr or 18-hr photoperiod. For further explanations see figure 1.

period may have been too short for prenuptial molt to occur.

In birds kept under natural light conditions, intense nocturnal activity usually sets in when postjuvenile molt is almost completed. Therefore, I did not start to record activity in the experimental bird until they had begun to molt. As it turned out, however, Zugunruhe was already intense in most of the birds kept under constant light conditions at that time. For that reason the exact times of onset of nocturnal activity are unknown in most of these birds.

Even though the results described in this section are not as unequivocal as those obtained from the experiments described before, the conclusion is justified that one group of factors controlling the onset and end of pre- and postnuptial molt as well as of the onset and end of Zugunruhe is within the bird.

*The nature of the time measuring mechanism.*—The results discussed so far are not sufficient to come to any definite conclusions about the nature of the postulated endogenous mechanism. Theoretically, two possibilities have to be considered:

(1) An hourglass type mechanism, i.e., a time measuring device which has to be set at least once a year by environmental stimuli

(2) A rhythmical process with a period of about one year which continues to oscillate for at least several periods even in the absence of periodic environmental stimuli. To decide between these two alternatives it was necessary to keep warblers for more than one year in seasonally constant conditions.

Results of such experiments have been described in detail elsewhere (refs. 24 and 25).[2] They all clearly favor the endogenous rhythm hypothesis. As an example, figure 4 illustrates

the behavior of two willow warblers during a 28-month period in LD *12*:12. It can be seen that both birds continue to molt twice a year; in between the molts they develop Zugunruhe. Moreover, the phases of the molt and Zugunruhe cycle in bird *a* (left) shift progressively forward, thus expressing a freerunning rhythmicity with a period length of about 10 months. In bird *b*, which is a sibling of bird *a* and which was kept in a cage adjacent to that of bird *a*, the average period length is close to 12 months. This deviation of the period length from the 12-month periodicity in the environment definitely excludes the possibility that uncontrolled exogenous stimuli may have caused the rhythm; it must be endogenous.

The results presented in the last three sections provide answers to our initial questions. Zugunruhe and molt in the willow warbler are controlled by an endogenous annual rhythmicity which may persist for at least three cycles under constant environmental conditions. As in the few other animals for which the existence of such circannual rhythms has been demonstrated (refs. 26 to 33),[2] its most obvious function is that of the timing of biological events. The following sections show, however, that circannual rhythms might be much more basically involved in the control of migratory behaviour in warblers.

### Experiments on the Termination of Zugunruhe in Autumn

A substantial body of circumstantial and experimental evidence suggests that birds travelling to their winter quarters for at least the second time in their lives find their goal through goal orientation. Some inexperienced first-year birds, on the other hand, have been demonstrated to be capable of direction orientation only (reviews in refs. 34 and 35).

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[2] BERTHOLD, P.; GWINNER, E.; AND KLEIN, H.: Circannuale Periodik bei Grasmücken (*Sylvia*). Experientia, vol. 27, p. 399.
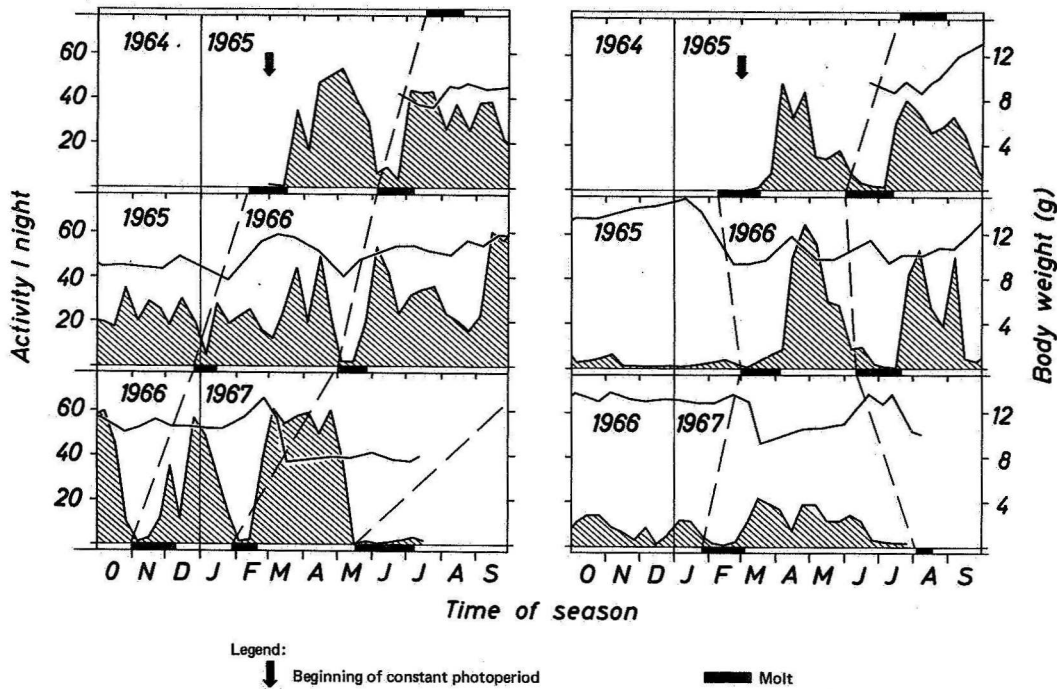
FIGURE 4. Variations in Zugunruhe, body weight and molt in two willow warblers kept from late February 1965 for 27 months in constant 12-hr photoperiod (200 : 0.2 lux) Successive years are displayed below each other. Dashed lines connect onsets of corresponding molts in successive years. Activity per night = number of 10-min intervals during which a bird was active each night; mean values for successive thirds of a month are plotted. Other symbols as in figure 1 (ref. 24).

While, in the case of goal orientation, the orientation mechanism by definition contains a component that guarantees termination of migration upon arrival, such a component is lacking in the case of direction orientation. This poses the problem of what factors are responsible for the termination of autumn migration in birds capable only of maintaining a given direction. At least three mechanisms are conceivable:

(1) The birds may have an innate knowledge of the environmental features of their winter quarters.

(2) The birds may have an innate knowledge of the distance they have to travel.

(3) The birds could have an innate

knowledge of the time they have to travel with a given average speed.

There is little evidence on which to decide which one of these mechanisms might be involved. Results of some experiments (refs. 36 and 37) have been interpreted as supporting (1), but in no case is this conclusion convincing (refs. 24 and 37 to 39). Other findings suggest that endogenous mechanisms, (2) or (3) above, are involved (e.g., refs. 40 and 41). The following sections summarize some pertinent experimental results.

*Autumnal displacement of willow warblers to central Africa.*—The main objective of the autumnal displacement of young willow warblers directly into the central African
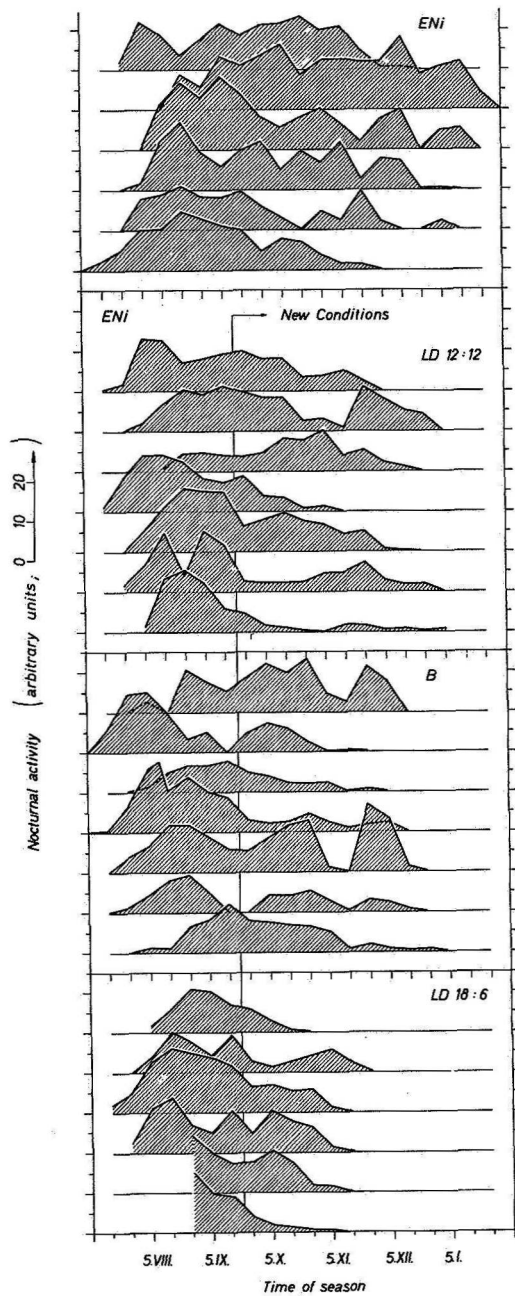
FIGURE 5. Fall Zugunruhe in willow warblers kept under natural photoperiodic conditions of their southwest-German breeding grounds (ENi,

winter quarters of this species (B in fig. 2) was to test whether environmental factors are involved in the termination of autumn Zugunruhe. On September 18, the date of the displacement, most of the birds had already passed the maximum of their autumn Zugunruhe. By that time, the bulk of free-living willow warblers appears in Africa in regions adjacent to the southern border of the Sahara desert (ref. 24).

Figure 5 and table 1 show that Zugunruhe in all displaced birds continues well beyond the time of displacement. No differences in the pattern, the total amount or the duration of Zugunruhe can be detected, either between the indoor and the outdoor subgroup, or between all of these birds and the controls that had been transferred at the same date to a constant $12:12$ hr day (i.e., to a photoperiod simulating that experienced by the displaced birds). On the other hand, both experimentals and controls differ from the birds transferred to long-day conditions as well as from those retained under the natural light conditions of their breeding grounds. Zugunruhe of the birds of the long-day group tends to cease earlier and to be less intense than that of the experimentals or controls. In contrast, Zugunruhe in the birds kept in natural light conditions of their breeding grounds tends to last longer and to be more intense. Thus, whereas we find no effect of other environmental conditions on duration and intensity of Zugunruhe, we find an effect of photoperiod on these parameters.

upper graph) and from birds transferred between September 15 and 20 from these conditions to either of the following experimental schedules: LD 12:12, LD 18:6 = constant 12-hr and 18-hr photo-period; B = natural photoperiod conditions of a location (Bukavu) within the range of the central African wintering grounds of the species (either outdoors: upper three birds, or indoors). For further explanations see figure 1.

TABLE 1.—*Duration and Total Amount of Zugunruhe in Willow Warblers and Chiffchaffs During Their First Autumnal Migratory Season Under the Natural Photoperiod of the Breeding Area (ENi) and After Transfer to Either Artificial Photoperiods (LD) or to the Natural Photoperiod of the Wintering Area (B)*

| | | Willow warbler | | | Chiffchaff | |
|---|---|---|---|---|---|---|
| | $n^a$ | Duration of Zugunruhe (days) | Amount of Zugunruhe$^b$ | $n^a$ | Duration of Zugunruhe (days) | Amount of Zugunruhe$^b$ |
| ENi | 6 | $137 \pm 17.1$ | $1255 \pm 342$ | 6 | $51 \pm 22.5$ | $431 \pm 272$ |
| LD 12:12 | 7 | $131 \pm 13.7$ | $869 \pm 185$ | 8 | $82 \pm 15.2$ | $564 \pm 309$ |
| B | 7 | $138 \pm 11.2$ | $804 \pm 268$ | | | |
| LD 18:6 | 6 | $85 \pm 17.2$ | $675 \pm 260$ | | | |

Legend:
◄———► $p < 0.001$
◄——► $p < 0.01$
◄·······► $p < 0.05$

$^a$Number of individuals
$^b$Total number of half-hour intervals with nocturnal activity during the migratory season

It is clear that these results do not support any hypothesis postulating environmental factors as principal stimuli for the termination of fall migration in willow warblers. On the other hand, they do not exclude such a possibility. Among various possible objections to such a conclusion are the following:

(1) Since it is unknown where the different populations of the willow warbler spend the winter, we cannot be sure whether or not the experimental animals had been displaced to an area in which the critical stimuli prevail.

(2) Even if the birds had been displaced to their population-specific winter quarters, the restrictions of cage life may have prevented them from receiving the appropriate stimuli.

(3) The birds did receive the appropriate stimuli, but cage conditions prevented them from terminating Zugunruhe.

Despite these reservations, it seemed justified and reasonable to look for evidence that might favor one of the alternative hypotheses.

*Coincidence between the temporal pattern of Zugunruhe and actual migration.* Inspection of figure 5 suggests a rather similar temporal pattern of Zugunruhe in willow warblers exposed to photoperiods of similar duration (i.e., in all birds excluding those of the long-day group). This becomes even clearer if one plots the individual Zugunruhe curves of all these birds on the same graph. Figure 6 indicates a common trend in the temporal course of nocturnal activity. Zugunruhe first increases sharply to reach a maxi-
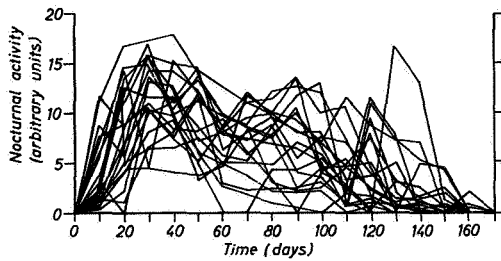
**FIGURE 6.** Individual Zugunruhe curves of the three groups of willow warblers depicted in upper three graphs of figure 5, drawn over one another. All curves are normalized with regard to onset of Zugunruhe so that they all start at the same point, day 0, on the abscissa.

mum in about 30 to 40 days. Then it steadily wanes and ceases 2 to 4 months later.

This pattern seems to correspond, at least grossly, with the actual pattern of migration. A review of the limited literature on the autumnal passage of willow warblers through southern Europe and Africa reveals that migratory speed is apparently high when the birds cross Europe and northern Africa. The maximal numbers of willow warblers pass through countries just beyond the Sahara only about 4 weeks after peak migration occurs in Europe. Then migration slows down. Rhodesia is reached not before the second half of October and the southern tip of Africa apparently as late as the end of November (ref. 24).

This similarity between the temporal pattern of Zugunruhe in caged willow warblers and the temporal pattern of actual migration suggested the following hypothesis:

(1) It is proposed that the nocturnal activity measured as Zugunruhe in the caged willow warblers is the expression of an endogenous temporal program which determines duration and temporal variations in migratory activity. If this is true then the nocturnal activity displayed by cag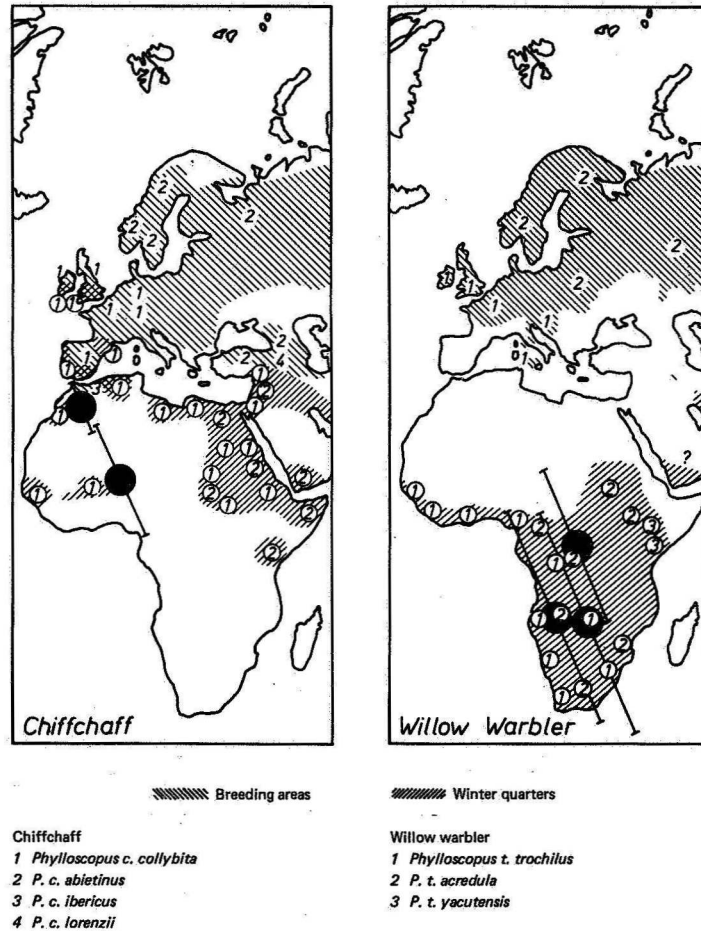ed birds should be equivalent to a given amount of actual migratory activity, i.e., a given distance travelled by freeliving individuals during the same time.

(2) Furthermore, it is proposed that this temporal program is organized in such a way that it produces just enough migratory activity during the migratory season as is required to reach the goal; that is, the bird will have reached the vicinity of its winter quarters when this program tapers and ends.

The following sections present evidence that indirectly supports this hypothesis.

*Comparison of Zugunruhe in closely-related species.*—The hypothesis implies that related species or races, travelling different distances on fall migration, develop different total quantities of Zugunruhe during the migratory season. We have tested this prediction by comparing migratory restlessness of the willow warbler with that of its sibling species, the chiffchaff. From the distribution map (fig. 7), one should expect willow warblers to develop at least twice as much migratory activity as chiffchaffs. Figure 8 and table 1 show that this prediction is, in fact, verified. Both in birds kept under natural photoperiodic conditions of their breeding grounds and in birds transferred in mid-September to a constant $12:12$ hr day the willow warblers stay much longer in migratory condition and develop much more migratory activity as the chiffchaffs.

*Calculation of the distance equivalent to Zugunruhe.*—The hypothesis implies that the amount of Zugunruhe displayed by a caged bird within any given time interval $(U_i)$ is equivalent to the distance $D_i$ traveled during this interval by freeliving conspecifics. The ratio $U_i/D_i$ should then equal the ratio $U_g/D_g$, where $U_g$ is the total amount of Zugunruhe of the caged bird and $D_g$ the total distance travelled by freeliving conspecifics. $U_i$ and $U_g$ are known. If, in addition, we

Chiffchaff

Willow Warbler

▧▧▧ Breeding areas          ▨▨▨ Winter quarters

Chiffchaff
1  Phylloscopus c. collybita
2  P. c. abietinus
3  P. c. ibericus
4  P. c. lorenzii

Willow warbler
1  Phylloscopus t. trochilus
2  P. t. acredula
3  P. t. yacutensis

FIGURE 7. Breeding areas and winter quarters of chiffchaff and willow warbler (as in ref. 42). Numbers refer to various races of either species (numbers encircled represent winter quarters). Large solid circles are calculated endpoints of migration (with standard errors) for chiffchaffs and willow warblers kept in three different experimental conditions (as in figure 8. In addition, compare in figure 5 the group of willow warblers displaced to central Africa.).

knew $D_i$, we could calculate the theoretical distance which is equivalent to the total amount of Zugunruhe of the caged birds using the following formula:

$$D_g = \frac{U_g \cdot D_i}{U_i}$$

If the hypothesis proposed here is correct, this theoretical distance should be approximately that normally covered by the species during migration.

Fortunately such information is available from recoveries of banded birds. While almost no banded *Phylloscopus* warblers have been recovered beyond the Mediterranean Sea, we could get 24 cases of willow warblers and 20 cases of chiffchaffs that had been banded dur-
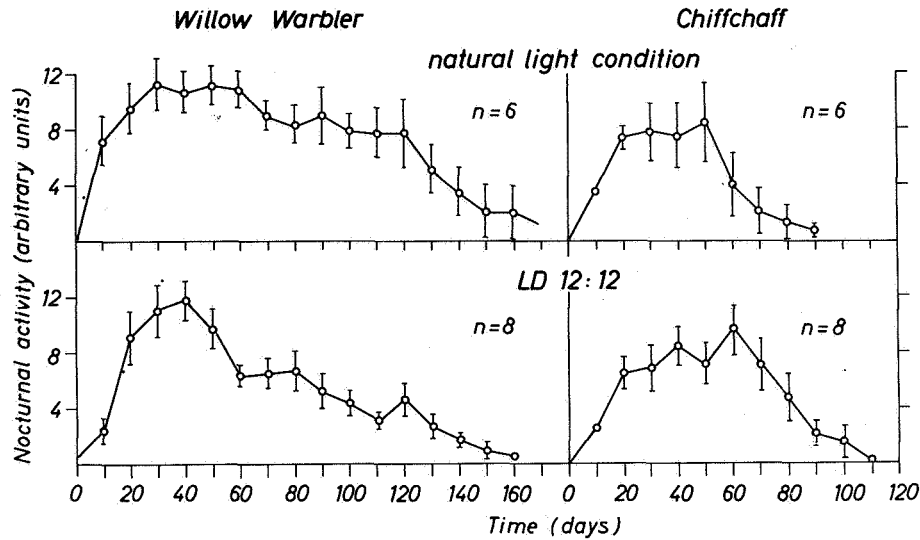
FIGURE 8. Variations in fall Zugunruhe in two groups of willow warblers and chiffchaffs, respectively. Birds were kept either in natural photoperiodic conditions of their breeding grounds over whole period of observation or they were transferred from such conditions' to a 12-hr photoperiod. Time of transfer for willow warblers was between days 50 and 80; for chiffchaffs between day 0 and 30. Vertical bars represent standard errors. For further explanations see figure 1 (ref. 43).

ing autumn migration in northern Europe and had been recovered during the same migratory season in southern Europe. From these birds we know, therefore, the distances they have travelled over a given period of time. Using these data, 20 and 24 $D_g$ values, respectively, have been calculated for individual willow warblers and chiffchaffs according to the 20 and 24 $D_i$ values available from banding recoveries. From these, a mean value was calculated for each caged bird. These mean distance values have been averaged again for the 6 to 8 birds of five experimental groups. Then the distance each experimental group would have migrated was plotted on a map under the assumption that the birds would have travelled along the normal migratory route from southwestern Germany to Gibraltar and then south-south-east towards the southern tip of South Africa.

Figure 7 shows that the birds would have ended up in their winter quarters.

A better agreement between these calculated distances with those covered during actual migration can hardly be expected since many assumptions had to be made. For instance, the computed distance depends on the time relationship between the onset of migratory restlessness in caged birds and the onset of migration in those freeliving birds from which the distance values have been obtained. For the calculation it has been assumed that both freeliving and caged birds started migratory activity at the same time of the season, but it is not clear to what extent this is true. In addition most of the wild birds which were compared with the caged birds belonged to northern European populations whose migratory pattern might differ from that of birds from southwestern Germany.

*Conclusion.*—The results and considerations presented so far support the hypothesis that endogenous factors are involved in the termination of fall migration in first-year migrant warblers. Is there evidence that such a mechanism may be significant in other species as well?

Results from displacement experiments with freeliving young autumnal migrants are at least compatible with such an assumption. Rüpell and Shüz (ref. 44) caught first-year carrion-crows (*Corvus corone cornix*) halfway along their migration from the Baltic breeding area to their winter quarters in northern Germany. Birds displaced to a location beyond the actual winter quarters of this population continued to migrate in their original direction. Banded birds were recovered at distances from the point of release not exceeding that which separated them at the point of capture from the southwestern boundaries of their actual winter quarters. Similar results were obtained by Perdeck (ref. 40). He caught starlings (*Sturnus vulgaris*) in Holland on their first fall migration from northeastern Europen to the canal area and displaced them southward to Switzerland and northeastern Spain. Those birds that had started migration comparatively recently continued to travel in their original direction, even if the environment at the release point was favorable for wintering. Only those birds which at the time of capture had already almost terminated fall migration stayed in the vicinity of the release site, provided the release site was in a favorable environment. Perdeck himself (ref. 41) considers endogenous temporal factors as possibly responsible for the continuation of migration in the first group of birds.

Results of a detention experiment conducted by Bellrose (ref. 45) are also compatible with the hypothesis proposed here. Bellrose caught blue-winged teals (*Anas discors*) in Illinois on their first fall migration from Canada to southeastern United States and northeastern South America and detained them until all the adults had passed through. When released, they continued to migrate in the appropriate south-southeasterly direction. An analysis of the data published by Bellrose revealed that recoveries of detained birds were, on the average, from shorter distances than recoveries of birds that had been caught in Illinois but had been released immediately after banding. While about 50 percent of the latter birds were recovered at distances greater than 2000 km from the release site, only about 10 percent of the former were found as far away.

Results from comparative Zugunruhe studies with other birds also confirm the predictions of the hypothesis, at least qualitatively. The upper graph of figure 9 depicts autumnal Zugunruhe curves from two closely related warblers of the genus *Sylvia*. The winter quarters of the garden warbler (*S. borin*) coincide approximately with those of the willow warbler, and those of the blackcap (*S. atricapilla*) are nearly congruent with those of the chiffchaff. Birds were taken as nestlings from the same locations as the *Phylloscopus* warblers and treated the same way. Kept in natural photoperiodic conditions of their breeding grounds, differences similar to those observed in the *Phylloscopus* warblers are found with regard to both amount and duration of Zugunruhe.[3] The autumnal Zugunruhe curves shown in the lower graphs of figure 9 are from members of three races of the White-crowned Sparrow (*Zonotrichia leucophrys*) (Gwinner, Farner and Mewaldt, unpublished data). The birds were caught in their winter quarters and, starting in August, kept in a constant 12-hour photope-

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[3] BERTHOLD; GWINNER; KLEIN; AND WESTRIUCK: Unpublished data.

riod. *Zonotrichia leucophrys nutalli* is a year-round resident of California. *Z. l. pugetensis* breeds essentially in western Washington and Oregon but winters in California. *Z. l. gambelii* breeds predominantly in western Canada and Alaska and migrates mainly to the southwestern United States and northern Mexico. On the average, therefore, *Z. l. gambelii* travels a greater distance than *Z. l. pugentensis; Z. l. nutalli* is a nonmigrant.

Since these birds have not been recorded to the end of their Zugunruhe period, no quantitative comparison of duration and amount of Zugunruhe is possible. However, there is a clear tendency in the maximal values of Zugunruhe to increase parallel with the increase of migratory distance.

While in the two *Sylvia* warblers, as in *Phylloscopus*, the temporal pattern of Zugunruhe coincides approximately with the temporal pattern of actual migration, this is surely not the case in the white-crowned sparrows. Even though recording was terminated before the end of fall Zugunruhe, it is clear that it exceeds the time these birds spend on actual migration. Since this is also the case in other short-distance migrants (e.g., refs. 46 and 47), it seems possible that these differences indicate differences in the mechanisms controlling migratory activity in long- and short-distance migrants. In the latter, Zugunruhe may express only vaguely the general readiness of a bird to migrate; the actual time course of its migration may then be molded largely by external factors.

Such a view is supported by the finding, among others, that Zugunruhe in the chiffchaff, the species migrating the shorter distance, is much less rigidly endogenously controlled and probably more susceptible to exogenous stimuli than that of the willow warbler (ref. 48). A stronger dependence on external stimuli of Zugunruhe in short-distance migrants is also suggested by experiments and

observations in other birds (e.g., refs. 49 to 52).

The endogenous temporal mechanism proposed here, therefore, may be of dominating significance only in long-distance migrants. Even in these migrants it is probably assisted by other mechanisms. The principal weakness is the mechanism's inaccuracy, and possibly it leads the migrating birds only grossly to the vicinity of their winter quarters where other factors, as yet unknown, determine more precisely where the birds actually terminate migration.

Despite these reservations the evidence presented here strongly suggests that circannual rhythms in warblers and possibly in other migratory birds may be of significance not only for the initiation of migration at the appropriate time but also for the termination of migration at the appropriate place.

## DISCUSSION

SLADEN: There is an overlap in your winter distribution. Could the chiffchaffs have exactly the same winter quarters as the willow warblers?

GWINNER: There is an overlap in the winter quarters of the chiffchaff and willow warbler, but apparently not in the winter quarters of the particular races studied (see fig. 7). Recent recoveries of banded warblers confirm such a conclusion.

EVANS: If a migrant normally made a long nonstop flight at some point in its migration, would you expect it to show in captivity, activity levels much greater than average during the appropriate time period? I am concerned particularly with trans-Saharan crossings.

GWINNER: Yes. My hypothesis implies that periods of intense migratory restlessness correspond with periods of intense migration.

EVANS: Are you proposing one synchronization per annual cycle or continual synchronization of the cycle?

GWINNER: I have some results indicating that the circannual rhythms of Zugunruhe, body weight, and molt can be affected by photoperiodic conditions during more than one phase of the cycle. The hypothesis that the annual rhythm of photoperiod
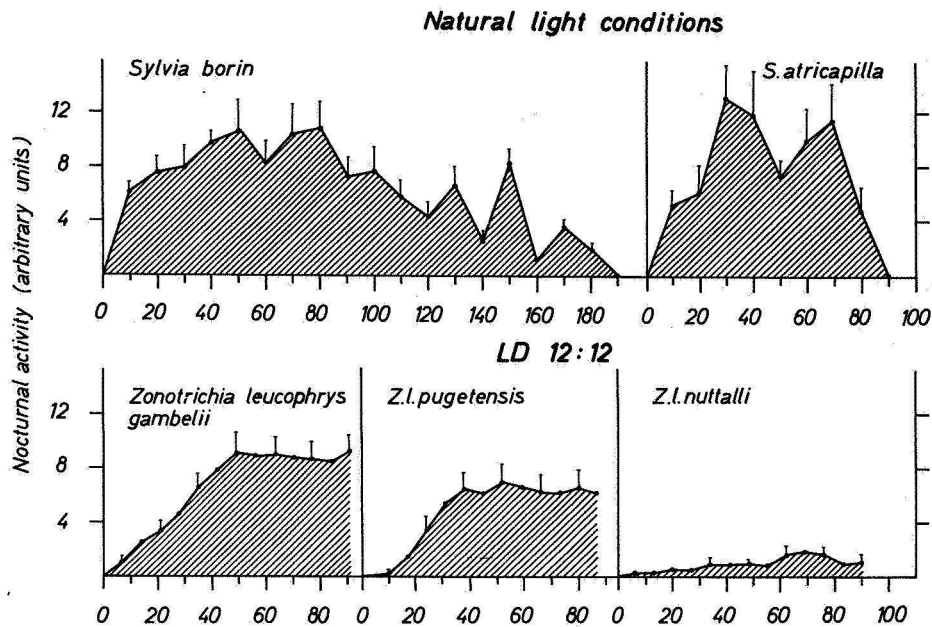
**FIGURE 9.** Variations in fall Zugunruhe of young garden warblers (*Sylvia borin*) and blackcaps (*S. atricapilla*) under natural photoperiodic conditions of their breeding grounds and of three races of the white-crowned sparrow (*Zonotrichia leucophrys*) kept over the whole period of observation in a constant 12-hr photoperiod (200 lux : 0 lux). Curves are based on mean values of seven garden warblers, seven blackcaps, 20 *Zonotrichia leucophrys gambelii*, 22 *Z. l. pugetensis* and 22 *Z. l. nutalli*. Vertical bars represent standard errors. For further explanations see figure 1.

provides essential stimuli for synchronization has not yet been thoroughly tested, however.

EVANS: Have you tried to determine the influence of food on the level of activity shown during Zugunruhe?

GWINNER: I have only some tentative results indicating that availability of food has little or no effect on Zugunruhe, within obvious physiological constraints, of course. This is in agreement with a variety of other results from experiments with long-distance migrants.

GAUTHREAUX: In your records of nocturnal restlessness do you find periodicity in multiples of 3 days, 4 days, 5 days?

GWINNER: We haven't analyzed the data, so far, under this aspect.

GAUTHREAUX: Have you measured weight changes after a night of very intense nocturnal restlessness?

GWINNER: No, I haven't done that yet. We

take body weights usually twice a week. I have no information about short-term fluctuations.

EMLEN: I have noticed that the seasonal sequence of Zugunruhe behavior in caged indigo buntings varies considerably depending upon the conditions of their captivity. In particular, buntings housed in small activity cages approximately 60 × 30 × 40 cm) continued their nocturnal activity long after the normal migration period, while individuals housed in large flight rooms (4 × 3½ × 3½ ft) displayed Zugunruhe activity for a period of only 6 to 8 weeks during the migration season and then such activity ceased. This might be of importance in interpreting your results since many of your graphs show nocturnal activity continuing long after the migration season—until the initiation of the next molt period.

I would also like to comment on the possible importance of seasonal Zeitgebers to circannual rhythms. I have conducted experiments in which

male indigo buntings were maintained for many months under conditions of constant 9- to 11-hr photoperiods. Experiments were initiated following the autumn migration season and results showed that the birds molted, deposited subcutaneous fat reserves, exhibited Zugunruhe, underwent characteristic bill color changes, and initiated song on schedule the following spring. However, the birds did not molt into the winter plumage the following autumn. Although these data are still being analyzed, they suggest an endogenous annual rhythmicity with the additional constraint that the birds require a seasonal Zeitgeber; furthermore, this synchronizing Zeitgeber occurs during the summer or early autumn. This species over-winters in southern Mexico and Central America (roughly 10° to 25° north latitude) where seasonal photoperiod changes are present but minimal. It will be interesting to see what new patterns of circannual rhythmicity emerge as more comparative studies are undertaken.

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