CIRCADIAN AND CIRCANNUAL PROGRAMMES IN AVIAN MIGRATION

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Summary

In migratory birds, endogenous daily (circadian) and annual (circannual) rhythms serve as biological clocks that provide the major basis for their temporal orientation. Circannual rhythms are responsible for the initiation of migration both in autumn and spring. This function of timing migrations is particularly important for birds that spend the winter close to the equator where the environment is too constant or irregular to provide accurate timing cues. In addition, circannual rhythms produce programmes that determine both the temporal and the spatial course of migration. In *Sylvia* warblers, the time programmes controlling autumn migration are organized in a species- or population-specific manner. It has been proposed that, in first-year migrants, the time programme for autumn migration plays a major role in determining migratory distance, thus providing the vector component in a mechanism of vector navigation. It is not yet clear, however, whether this programme does indeed determine migratory distance or whether it only provides the temporal framework within which other factors determine how far a bird flies. Evidence against the first alternative comes from findings indicating that migratory activity can be drastically modified by a constellation of rather specific, but highly relevant, factors and that the resulting changes in migratory activity are not compensated by subsequent increases or decreases of migratory activity.

In normally day-active but nocturnally migrating birds, circannual signals cause alterations in the circadian system leading to the development of nocturnal activity. Although the nature of these signals is unknown, there is evidence that changes in the diurnal pattern of melatonin secretion by the pineal gland are associated with, and possibly causally involved in, the waxing and waning of nocturnal activity. These changes in the melatonin pattern presumably also affect general synchronization properties of the circadian system to Zeitgebers in such a way that circadian rhythms adjust faster to new conditions after long transmeridian flights.

Key words: circadian rhythm, circannual rhythm, migration, birds.

Introduction

Migrations of birds are conspicuously rhythmic phenomena. As a rule, they occur at certain seasons and certain times of day and thus are manifestations of an approximately annual (circannual) as well as an approximately diurnal (circadian) rhythmicity. Both of these rhythms reflect basic adaptations to environmental cycles and serve as biological clocks to cope with the annual and daily fluctuations in external conditions (see reviews in Gwinner, 1990*b*, 1996; Berthold, 1993). Taken together, the annual and daily clocks of migratory birds provide the major basis for their 'orientation in time' supplementing their 'orientation in space'. These two categories of orientation mechanisms, although controlled by separate processes, interact at various levels to guide birds on their migrations. The present account summarizes some recent results on the temporal orientation of migratory birds, concentrating on areas in which mechanisms of orientation in time interact with mechanisms of orientation in space. Emphasis will be placed on defining open questions and clarifying some conceptual issues, rather than exhaustively reviewing the field.

The endogenous nature of annual and daily rhythms in migration

Many bird species, such as warblers, migrate exclusively at night. When kept in cages provided with an appropriate arrangement of perches, the birds' locomotor activity can be measured by means of microswitches mounted underneath the perches. With this widely used experimental method, it has been shown that locomotor activity in summer and winter is restricted to daytime, i.e. it occurs exclusively in the light portion of the light:dark (L:D) cycle. In autumn and spring, however, the seasons corresponding to natural migratory activity, the birds exhibit additional locomotor activity at night. Fig. 1 illustrates for two garden warblers (*Sylvia borin*; A and B) that even when the light:dark cycle is experimentally kept constant over the year – and can thus provide no cues about the season – the birds exhibit nocturnal activity (termed 'Zugunruhe' or migratory restlessness) in autumn and spring that approximately coincides with the actual migratory seasons of free-living birds of the same species. These and other experiments have shown that rhythmic waxing and waning of nocturnal activity indeed persists for many cycles in constant conditions. The rhythm is usually accompanied by variations in migratory fattening (indicated by an increase in body mass) and followed by a moult in winter and a phase of reproductive activity in summer (see Fig. 1). In the typical case, the period of the rhythm is longer or shorter than 12 months under such

constant conditions, attesting to its endogenous circannual nature (Berthold *et al.* 1972; Gwinner, 1986).

Similar to the annual repetition of migratory activity, its diurnal recurrence is also under the control of an endogenous – in this case circadian – clock. This can be demonstrated in experiments of the type shown in Fig. 2. Here, a blackcap (*Sylvia atricapilla*) that exhibited nocturnal migratory restlessness while held in an L:D cycle was transferred to constant conditions of light and temperature. The alternation of day and night activity persisted with a circadian period of about 25.5 h. These periodic alternations between normal daytime activity and nocturnal migratory restlessness have been shown to be associated with concomitant circadian changes, e.g. in preferred light intensity and vocal behaviour (Gwinner, 1975).

Taken together, these and many further results show that both the annual and the daily pattern of the 'migratory drive' that expresses itself in nocturnal activity and in a series of concomitant physiological and behavioural changes are primarily based on endogenous (circannual and circadian) clock mechanisms. In the following discussion, I shall concentrate on two questions: (1) what are the functions of circadian and circannual rhythms in the control of migrations and (2) how are these clock systems organized in order to fulfil these functions?

Circannual programmes for migration

Control of migratory onset and directional changes

Circannual rhythms have been convincingly shown to provide important stimuli triggering the onset of migration in both autumn and spring. This timing function of circannual
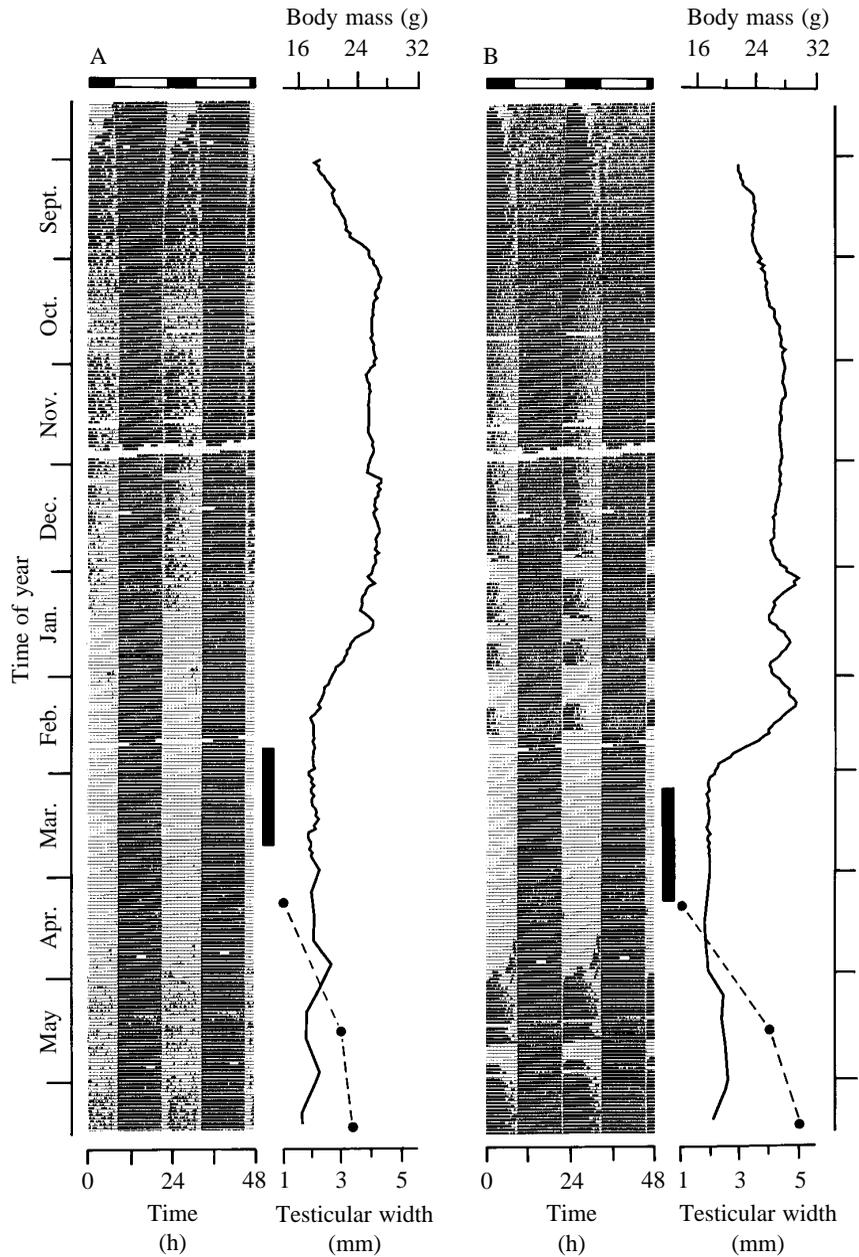

Fig. 1. Locomotor activity, changes in body mass (solid line) and testicular width (dashed line and filled circles) as well as the occurrence of the moult (black bar) in two garden warblers (*Sylvia borin*) kept from mid-August to mid-June under the light:dark (L:D) cycle indicated above the actograms. Initially, birds were held under the naturally changing L:D conditions, but from November onwards they were held under constant 12 h:12 h L:D. On the actograms, each horizontal line for 0–24 h represents the activity recording of 1 day. Recordings from successive days are mounted underneath each other in chronological sequence, and the original record has been repeated on the right (24–48 h).

rhythms is particularly evident and of high biological significance in birds wintering close to the equator. In these regions, photoperiod is constant over the year and other environmental factors such as temperature, precipitations and food abundance are too variable from one year to the next to be suitable for serving as external timing cues. In such birds with equatorial wintering grounds, processes preceding or accompanying spring migratory restlessness (e.g. winter moult and spring migratory fattening, respectively) are also under circannual control. These findings point to the important role of circannual rhythms not only in the timing itself but, in addition, in the timing of closely related processes that are very relevant to the success of migration (see Gwinner, 1986; Berthold, 1993, for reviews).

Circannual clocks affect not only migratory timing but also migratory direction. This dual role was first suggested by an experiment with garden warblers held for 1 year in a constant 12h:12h L:D. At regular intervals, birds were tested in orientation cages for the directional preferences of their nocturnal migratory restlessness relative to the earth's natural magnetic field. Birds preferred southerly directions during their subjective autumn and northerly directions during their subjective spring, grossly corresponding to the actual migratory directions of free-living conspecifics (Gwinner and Wiltschko, 1980). Moreover, in the course of autumn migratory restlessness, the directional preference of the birds shifted from a more southwesterly direction early in the season to a more southerly direction later in the season, which is again consistent with the actual directional shifts observed in the field (Gwinner and Wiltschko, 1978). Spontaneous directional shifts of a similar kind have more recently also been reported for blackcaps (Helbig *et al.* 1989) and pied flycatchers (*Ficedula hypoleuca*, Beck and Witschko, 1988), although in the latter species these changes seem to occur only if the earth's magnetic field is similar to the seasonally changing situation experienced by birds in nature.

Control of pattern and duration
A time programme for autumn migration
Circannual rhythms might control not only the timing of the onset of migration and the timing of changing migratory

direction (see above) but, in addition, the temporal course and the duration of the migratory flight (Gwinner, 1968). The internal clock may thereby provide the distance component required for 'vector navigation' (Jander, 1963), a process in which direction and distance are integrated such as to bring the animal to its specific goal. By endogenous control of flight duration, the birds would arrive at their wintering area even if they possessed no more than directional information.

Initial support for this hypothesis was provided by results showing that the duration and overall amount of autumn migratory restlessness developed by birds of a particular species or population in the cage are correlated with migratory distance: the further a species or population migrates in nature, the longer the duration and the larger the overall amount of migratory restlessness developed in the cage (see Gwinner, 1986; Berthold, 1988, for reviews). In the blackcap, population differences in the pattern of migratory restlessness have been shown to have a genetic basis (Berthold and Querner, 1982). Additional data supported the idea that the programme controlling autumn migratory restlessness is, indeed, a time programme that is little or not at all affected by the bird's metabolic state and/or energy turnover. For example, the pattern of Zugunruhe was not altered when garden warblers were put on a reduced diet, insufficient for the deposition of migratory fat (Berthold, 1976).

Is there compensation for interruptions?
The conclusion derived from these results, namely that the warblers' migratory time programmes are highly inflexible, is supported by results of other experiments indicating that there is no compensation for drastic reductions of migratory restlessness caused by severe interference, e.g. exposure to complete darkness at night (Gwinner, 1974), exposure to a combination of complete darkness at night, high humidity and rain (Schindler *et al.* 1981) or reduction of food intake to levels slightly below those required for the maintenance of fat-free body mass (Berthold, 1976). Although all of these treatments reduced nocturnal activity, the birds did not compensate for the reduced activity during the intervals following treatments.

These latter findings again support the idea that Zugunruhe is controlled by a time programme that is little affected by a
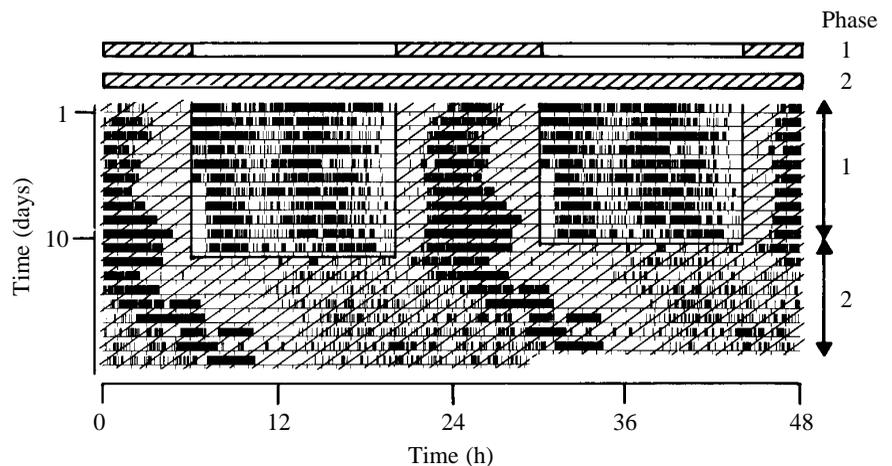

Fig. 2. Locomotor activity of a blackcap (*Sylvia atricapilla*) during the autumn migratory season. The bird was initially (phase 1) kept under an L:D cycle of 200 lx:0.5 lx (lights from 06:00 to 20:00 h on days 1–6; from 07:00 to 20:00 h on days 7–11) but subsequently (phase 2) under continuous dim light (0.5 lx). For explanation of the actogram see Fig. 1.

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bird's actual performance or its energy turnover. At the same time, however, they raise doubts about whether this time programme indeed leads the birds into their wintering grounds. A programme that does not compensate for interruptions should result in quite variable migratory distances depending on the conditions encountered by the birds during migration; for example, birds whose migration has frequently been interrupted, perhaps by adverse weather conditions, would end up in wintering areas closer to the breeding grounds than would birds whose flight has been interrupted less frequently or not at all (for a detailed discussion, see Gwinner, 1990a,b).

The findings described above raised the question of whether the experiments using activity-reducing conditions were adequate for investigating the hypothesis that an internal clock determines the duration of the migration flight. Some earlier results have suggested that, although complete darkness at night inhibits the intense perch-hopping used as a criterion for activity in these experiments, it does not necessarily inhibit other types of nocturnal activity such as 'whirring' (Czeschlik, 1977). Moreover, the reduction of body mass below fat-free levels that suppressed Zugunruhe in the experiments described above may, under natural conditions, be such a rare event that no compensation mechanisms have evolved to cope with it.

A more appropriate paradigm for reducing nocturnal activity is based on an effect that was first described by Biebach (1985) for spotted flycatchers (*Muscicapa striata*) and that was later also found to occur in other species (Gwinner *et al.* 1985).

When fat birds during the autumn migratory season were deprived of food and subsequently re-fed, migratory activity was abolished for one to several nights during the re-feeding phase, for example in the garden warbler (Fig. 3B). This food deprivation/re-feeding paradigm presumably simulates a field situation in which birds that have lost fat during their migratory flight arrive at resting areas suitable for restoring depleted fat reserves. It has, indeed, been found that lean migrants do interrupt migration upon arrival at resting places where feeding conditions are favourable but not at places where feeding conditions are unfavourable (Bairlein, 1985, 1987; Biebach *et al.* 1986).

We used this experimental design to interrupt repeatedly autumn migratory restlessness in a group of garden warblers and compared their overall migratory performance with that of an untreated control group (Gwinner *et al.* 1992). By starving and re-feeding the experimental birds throughout the season, the overall number of nights with nocturnal activity could be reduced by about 30 % compared with the control birds (Fig. 4A). By the end of the season, the experimental birds had a deficit of almost 20 % (in terms of time in 10 min intervals spent in nocturnal activity; Fig. 4B). This deficit corresponded quite closely to the amount of nocturnal activity that had been developed by the control birds during the times at which the experimentals experienced enforced interruptions (Fig. 4C). Moreover, the comparison among individual birds revealed that those experimental birds in which the treatment induced

Fig. 3. Variations of nocturnal migratory restlessness (expressed as the number of 10 min intervals with activity per night; hatched areas) and body mass (curves) as well as the occurrence of the moult (black bars) in three garden warblers (A, B, C) kept in the photoperiodic conditions indicated in Fig. 1. Day 0 corresponds to September 1 in Fig. 1. In B, the dotted segments of the curves show body mass changes during food deprivation, the dashed segments those during the subsequent re-feeding phase, during which the bird received 8 g of food per day. The unbroken segments show body mass changes during the subsequent *ad libitum* feeding phase. Birds in A and C received food *ad libitum* throughout (after Gwinner *et al.* 1992).
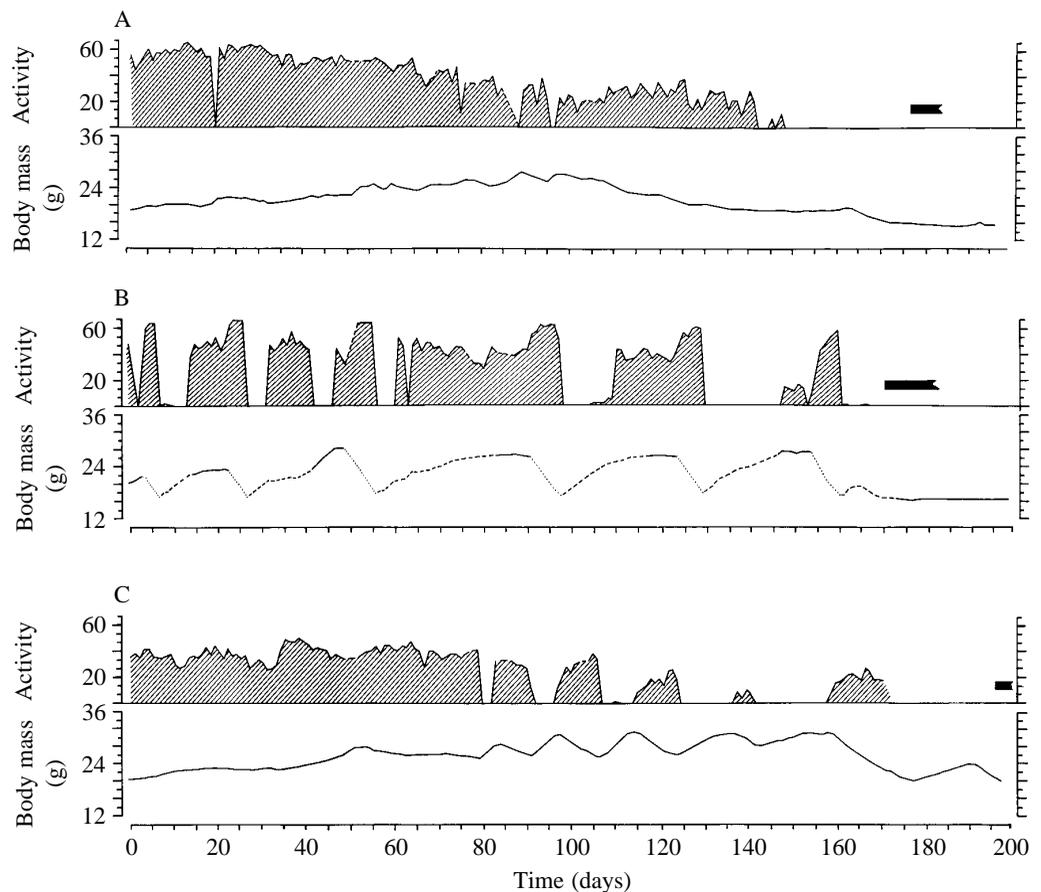
most interruptions showed the smallest amount of Zugunruhe over the total migratory season.

These results then clearly indicate that, even under the highly relevant simulation of a metabolic situation which leads
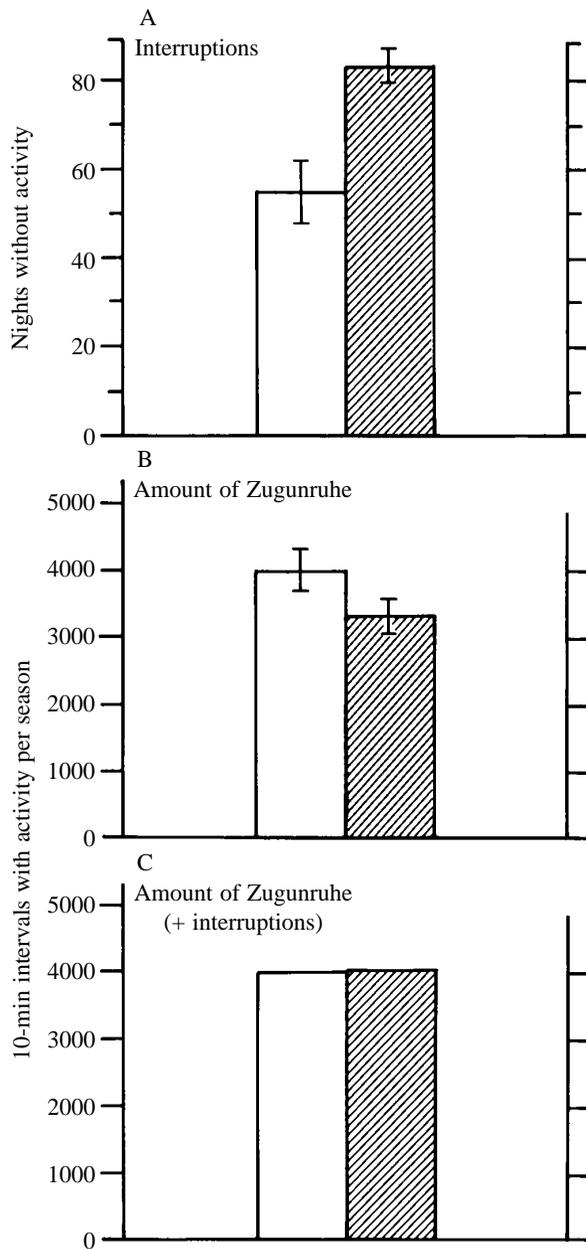

Fig. 4. Comparison of Zugunruhe parameters between control (white bars) and experimental (shaded bars) garden warblers whose migratory restlessness had been repeatedly interrupted by starvation/re-feeding schedules. This treatment of the experimental birds resulted in an increase in the total number of nights during which birds showed no nocturnal activity during the autumn migratory season (A). As a result, their total number of 10 min intervals with nocturnal activity (Amount of Zugunruhe) was reduced (B). (C) The amount of Zugunruhe of the experimental birds corrected for the amount of Zugunruhe developed by the control birds during the period in which Zugunruhe was interrupted in the experimentals (after Gwinner *et al.* 1992). Values are means ± S.E.M. (*N*=12 for controls; *N*=13 for experimentals).

to frequent interruptions of migratory activity in free-living birds, garden warblers show no tendency to compensate for these interruptions. Therefore, if the migratory distance of these birds were determined by a time programme, a considerable variability in the overall distance covered during autumn migration would be expected. This conclusion, in turn, suggests that a mechanism of vector navigation in which the length of the vector is determined by a circannual time programme is unlikely to be the only means by which first-year birds reach their wintering quarters. Instead, additional mechanisms must be more significantly involved in determining the actual migratory distance than was previously assumed.

The results of the experiments described here as well as those of previous studies (e.g. Biebach, 1985) also indicate that the initial hypothesis of an inflexible time programme for migration must be qualified. It is now clear that migratory restlessness can, indeed, be suppressed, although a highly specific and complex constellation of factors is required. The same studies have revealed that migratory activity may also become enhanced if energy reserves are lost as a result of food shortage (Fig. 3B). This effect is most conspicuous towards the end of the migratory season, when spontaneous migratory activity has almost ceased, and can no longer be seen once the birds have started to moult (Gwinner *et al.* 1988*b*, 1992). These findings indicate an adaptive responsiveness of the migratory time programme to the nutritional and/or energetic situation prevailing along the migratory route. The availability of food (or the resulting body mass increase) at resting places inhibits migratory activity in energy-depleted migrants, resulting in the restoration of energy reserves. In contrast, the absence of food (and the ensuing loss in body mass) enhances or reactivates migration, presumably enabling birds to leave unfavourable areas quickly.

Quite unexpectedly, our investigations (Gwinner *et al.* 1992) have also revealed that under certain, not yet defined, circumstances caged garden warblers may not only respond to food-dependent body mass changes with an increase or decrease of migratory activity but may even go spontaneously and repeatedly through these two states (see also Bairlein, 1986). Figs 1B and 3C show that the body mass of garden warblers fed *ad libitum* began to change rhythmically, starting in early January (Fig. 1) and at about day 70 (Fig. 3C), respectively. Each time body mass increased, migratory restlessness was interrupted in just the same manner as in birds that had increased their body mass during experimentally induced re-feeding. Spontaneous cycles of this type were seen in about 50 % of our control birds. An interruption of Zugunruhe was also frequently observed when birds initiated a rapid increase in body mass at the beginning of a migratory season. These observations show that the state of Zugunruhe may be somehow incompatible with the state of body mass increase, perhaps reflecting a general principle of regulation of these two functions. It is not yet clear whether these cycles are artefacts resulting from living in cages or whether similar phenomena also cause variations of migratory activity in nature.
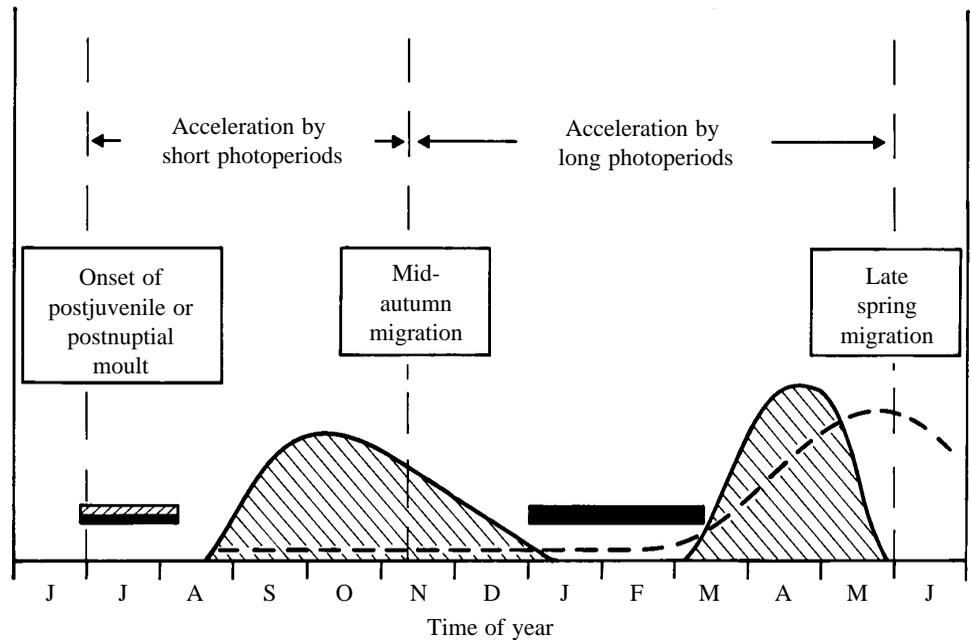
Fig. 5. Diagram showing some of the seasonal activities in long-distance migrating garden warblers and two principle effects of photoperiod on them. Hatched areas, migration; bars, moult; dashed curve, changes in gonadal size.

These results, like the ones reported at the beginning of this section, strongly suggest that it would be worthwhile to look more closely at the factors and mechanisms that modify Zugunruhe within the framework of the migratory time programme provided by the circannual oscillation. The analysis of these processes is not only a prerequisite for the definite evaluation of the time-based vector navigation hypothesis, it is also of great importance for understanding the strategies used by migrants in their day-to-day decisions about whether and at what rate migration should proceed.

Adaptive modifications of the migratory time programmes by photoperiod

In the previous section, some of the factors and mechanisms that are involved in modifying Zugunruhe have been discussed within the framework provided by the endogenous temporal programme for migration. While these factors are, indeed, capable of modifying the intensity of Zugunruhe, all available evidence suggests that they do not modify the temporal course and the limits of the programme as such. This kind of conclusion is indicated, for example, by the observation that the timing of the winter moult that follows autumn migration in many long-distance migrating species, or of any of the subsequent seasonal events, is not affected by the manipulations described above.

The only environmental factor known to be capable of changing the time course of the programme is photoperiod. Photoperiod synchronizes the circannual rhythms and, by doing so, it also affects the programmes that depend upon the basic clockwork. The circannual mechanism frequently responds to photoperiod in a functionally adaptive way. Two major effects have been described for the long-distance migrating garden warbler (reviewed in Gwinner, 1989a, 1996; Fig. 5). (1) The onset and the end of the post-juvenile moult and the onset of autumn migratory restlessness are advanced

by short photoperiods. This accelerating effect of short photoperiods in summer is important for young birds that have hatched from late clutches and, hence, grow up under shorter photoperiods than young hatched from earlier clutches. To be able to leave the breeding grounds in time, the birds from late clutches must start migration and complete the preceding processes of development at an earlier age. (2) The end of autumn migratory restlessness, the onset and end of the winter moult and the onset of spring migratory restlessness are advanced by long photoperiods. This accelerating effect of long photoperiods in winter is of high adaptive value because it truncates autumn migration in individuals that happen to have been carried too far into the southern hemisphere by their endogenous time programme. At the same time, it enables these birds to initiate spring migration earlier. This is probably necessary for them to reach their breeding grounds in time, i.e. not later than conspecifics that have spent the winter further north.

Detailed investigations of the dynamics of the changing responsiveness of the garden warbler's circannual rhythmicity to photoperiod have revealed rather subtle adjustments of the response system to prevailing photoperiodic conditions. Thus, while long photoperiods advance the onset of spring migratory restlessness and the associated onset of gonadal recrudescence, the acceleration is usually relatively small (Gwinner et al. 1988a). This slow response to long photoperiods guarantees that the reproductive system of warblers that have crossed the equator during their autumn migration is not instantaneously activated by the increasing photoperiod of the southern hemisphere spring (Gwinner, 1987). Reproduction in the southern hemisphere is further prevented by the particular way in which the circannual system is internally organized: long photoperiods accelerate both the onset of spring migratory restlessness and the onset of gonadal growth. However, since migratory restlessness is internally timed such that it starts
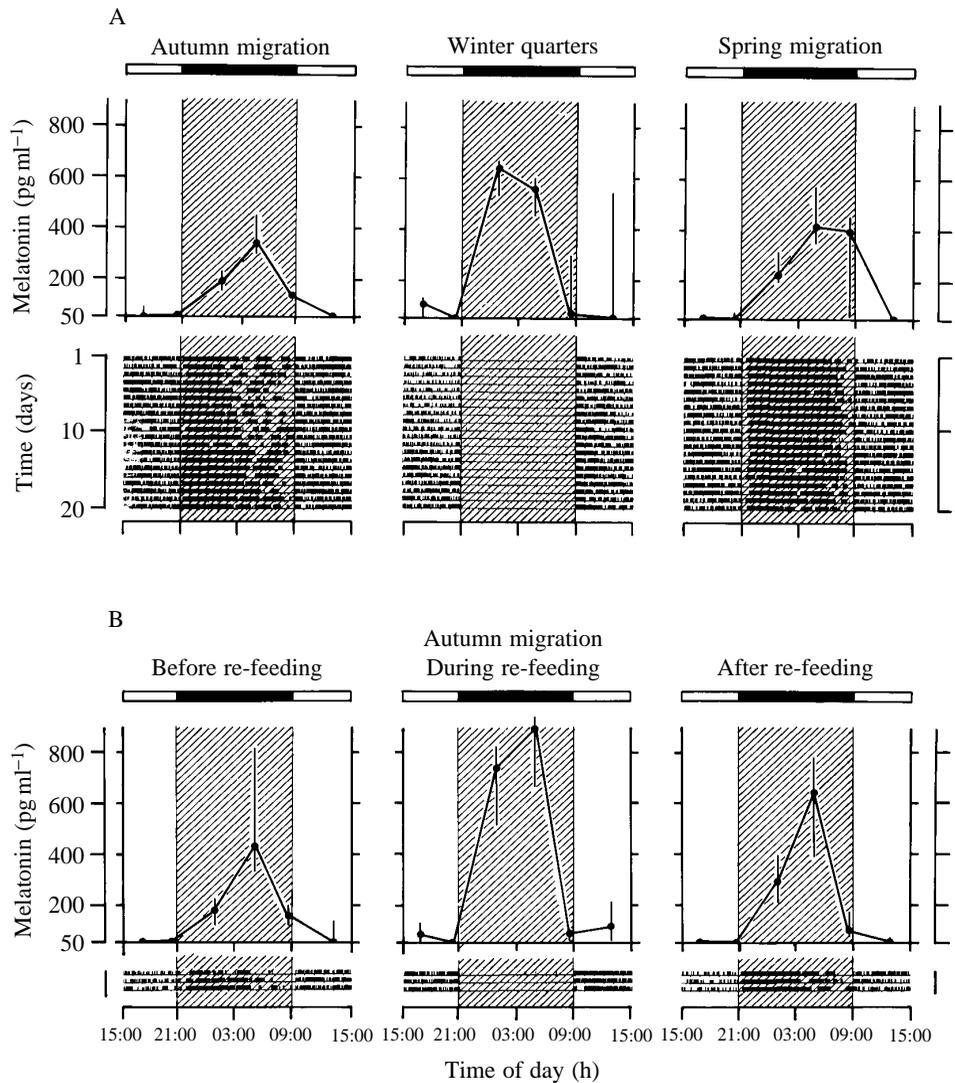
A

B

Fig. 6. 24 h changes of plasma melatonin concentrations (upper panel in A and B) and locomotor activity (lower panel in A and B) of garden warblers kept in a constant 12 h:12 h L:D of about 300 lx:0.01 lx; light on from 09:00 to 21:00 h). For melatonin, medians with quartiles for 5–8 individuals are given. Activity recordings are from individual representative birds. (A) The patterns in mid-winter, when activity was restricted to daytime, and in autumn and spring, when the birds showed intense nocturnal activity. (B) The patterns during the autumn migratory season, when Zugunruhe was interrupted during a phase of re-feeding following starvation, as well as before and after this treatment (A after Gwinner *et al.* 1993; B from E. Gwinner, I. Schwabl-Benzinger and H. Schwabl, unpublished results).

before the reproductive system of the birds has matured, the warblers begin their homeward migration before they can breed. Occasionally, however, experimental garden warblers do become 'trapped' if kept in simulated southern hemisphere photoperiods; in this case, they go through a full gonadal cycle during the northern hemisphere winter (Gwinner, 1988). 'Accidents' of this kind may have resulted in the 'colonization' of southern hemisphere areas by some northern hemisphere long-distance migrating birds.

The garden warblers exemplify one strategy for adjusting migration and reproduction to the complex photoperiodic patterns to which long-distance migrants are exposed: photoperiod modifies the time course of seasonal activities in such a way that an optimal adjustment to season and latitude is guaranteed. Other species are less flexible. The circannual system of pied flycatchers, for example, functions properly only under the very narrow range of photoperiods to which these birds are normally exposed. If they experience inappropriately long photoperiods in winter, the circannual clock becomes arrested (Gwinner, 1989*a*,*b*). This difference in the reactions of the pied flycatcher and the garden warbler

possibly reflects the fact that the wintering range of the pied flycatcher is more restricted than that of the garden warbler.

Physiological basis of circannual and circadian mechanisms

Twice a year, signals provided by the circannual clock mechanism cause alterations in the circadian system leading to the development of nocturnal activity. The nature of these signals is still obscure, reflecting our general ignorance of the physiological mechanisms underlying circannual rhythms (Gwinner, 1986). However, recent evidence suggests that the changes in the daily pattern of locomotor activity resulting in the development of Zugunruhe are associated with concomitant changes in the diurnal pattern of melatonin secretion (Gwinner *et al.* 1993). Fig. 6A shows that the nocturnal rise in plasma melatonin levels is smaller in garden warblers exhibiting nocturnal activity during the spring migratory season than it is in the same birds in mid-winter, when activity is restricted to daytime. An increase in the amplitude of the melatonin rhythm is also seen in birds whose

autumn migratory restlessness was interrupted while the birds were regaining body mass following a phase of body mass reduction (Fig. 6B). Hence, irrespective of whether the warblers terminate Zugunruhe spontaneously or as a result of experimental manipulations, the transition is accompanied by an increase in the nocturnal melatonin peak.

These results can be interpreted in at least two ways. (1) Lower nocturnal melatonin levels during phases of Zugunruhe may be the consequence of the birds' nocturnal activity. It is possible that activity itself reduces melatonin levels. Alternatively, the reduction may result from an increase in the nocturnal light intensity perceived by the birds. The latter explanation is possible because, in the experimental situation, birds were exposed to a weak night-light of about 0.01 lx. Birds exhibiting nocturnal activity move about with their eyes open and their head exposed to the light source and, hence, probably perceive more light than birds that sleep with closed eyes with their head hidden in the plumage. Light is known to inhibit nocturnal melatonin secretion (Binkley, 1988), although it is not clear whether intensities as low as the ones used in this study are sufficient to induce this effect. (2) A reduction in the nocturnal melatonin levels may be the mechanism that triggers Zugunruhe. The periodic secretion of melatonin is known to be a significant component of the avian circadian pacemaking system, particularly among passerine birds (Cassone, 1990; Gwinner et al. 1994). Its elimination by pinealectomy or administration of high levels of exogenous melatonin results in the disturbance or abolition of circadian locomotor activity rhythms. There is evidence that the periodic output of melatonin is required for the internal synchronization of different components of the circadian system. It is conceivable, therefore, that a reduction in the amplitude of the daily melatonin cycle results in changes in the circadian system leading to nocturnal activity.

On the basis of the available data, it is not possible to decide between hypotheses 1 and 2. However, clear predictions can be made on the basis of these two hypotheses, and powerful experimental tests of these predictions are conceivable.

Irrespective of whether the reduced melatonin secretion is the cause or the consequence of nocturnal migratory restlessness, this finding invites speculations about its possible consequences. Recent experiments with house sparrows (Passer domesticus) have shown that high levels of exogenous melatonin (induced by delivering melatonin through subcutaneously implanted silastic capsules) render sparrows more sensitive to a light Zeitgeber (Hau and Gwinner, 1994). As a consequence of this increased sensitivity, resynchronization times (i.e. the times required for the circadian system of a bird to adjust to the phase-shifted Zeitgeber) become shorter (Hau and Gwinner, 1995). One of the interpretations of this phenomenon is that high constant levels of exogenous melatonin eliminate the endogenous melatonin rhythm and thereby render the circadian pacemaking system more passive (i.e. turn it into an oscillator with a lower degree of self-sustainment). The consequence of these changes in the properties of the circadian system should be that resynchronization times decrease. The reduction of the amplitude of the melatonin cycle seen in birds exhibiting nocturnal activity should likewise reduce the self-sustainment of the pacemaker and, therefore, also reduce resynchronization times (Aschoff et al. 1975). Such an effect could be of significance for birds carrying out fast long-distance flights across meridians. Their circadian system should adjust more quickly to the phase-shifted light/dark cycle and this, in turn, may be advantageous, e.g. for foraging behaviour or sun-compass orientation. A reduction in the degree of self-sustainment of the circadian system would also be advantageous for long-distance migrants travelling mainly along a north–south axis as it may allow a faster adjustment of the activity pattern to latitudinal changes in photoperiod. Experiments along these lines are promising and may lead to new insights concerning the way that endogenous clocks are involved in avian navigation function.

Final remarks

During the past 30 years, considerable progress has been made in the understanding of the principles governing the temporal pattern of avian migrations. Endogenous circannual clocks determine the onset and the end of migrations as well as changes in migratory direction. Temporal variations in migratory speed also seem to be partly programmed in a circannual clock. Some evidence suggests that even the migratory distance covered during the autumn migratory season is to some extent a consequence of endogenous circannual programming, although recent experimental data indicate that other mechanisms may also be involved. While circannual clocks control seasonal variations in migratory behaviour, circadian clocks provide the basis for adjustments of daily patterns, as is particularly obvious in species that are normally day-active, but migrate at night.

The role played by circannual and circadian rhythms has so far almost exclusively been studied on a formal level and little attention has been paid to investigations of the underlying physiological mechanisms. Research on the possible physiological basis of circannual rhythms has not yet even suggested where the main mechanisms might be localized. Indeed, it is not even clear whether there are distinct localizable circannual clocks or whether the oscillation results from the interaction of a variety of neuronal, neuroendocrine and endocrine functions. The situation is different in the field of research concerning daily rhythms, where it is known that, in songbirds, the pineal organ and the suprachiasmatic nuclei in the hypothalamus represent major components of the circadian pacemaker. These two structures contain autonomous circadian oscillators that interact according to principles that are at least partly understood. So far, essentially all investigations on the role played by this pacemaking system have concentrated on the analysis of relatively simple circadian patterns. The time seems to be ripe, however, for an extension of the concepts derived from these studies to more complex patterns, such as those of nocturnally migrating birds. In the

past, questions about the circadian mechanisms underlying the seasonal shifts of circadian activity patterns in migratory birds have been addressed only occasionally and infrequently (Palmgren, 1944; McMillan, 1972; Gwinner, 1975; Gwinner *et al.* 1993). In view of the considerable significance of the circadian system in the control of avian migrations – not only in determining the time of day of migration but also in sun-compass orientation – a new focus on these problems is due and is, in the light of the recent progress in our understanding of circadian mechanisms, quite promising.

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