Simulation of migratory flight and stopover affects night levels of melatonin in a nocturnal migrant

Leonida Fusani* and Eberhard Gwinner

Max-Planck Research Centre for Ornithology, Von-der-Tann Strasse 7, 82346 Andechs, Germany

Several species of diurnal birds are nocturnal migrants. The activation of nocturnal activity requires major physiological changes, which are essentially unknown. Previous work has shown that during migratory periods nocturnal migrants have reduced night-time levels of melatonin. Since this hormone is involved in the modulation of day–night rhythms, it is a good candidate regulator of nocturnal migratory activity.

We studied whether melatonin levels change when nocturnally active blackcaps (Sylvia atricapilla) are experimentally transferred from a migratory to a non-migratory state. We simulated a long migratory flight by depriving birds of food for 2 days, and a refuelling stopover by subsequently re-administering food. Such a regimen is known to induce a reduction in migratory restlessness (‘Zugunruhe’) in the night following food reintroduction. The experiments were performed in both autumn and spring using blackcaps taken from their breeding grounds (Sweden) and their wintering areas (Kenya). In autumn, the food regimen induced a suppression of Zugunruhe and an increase in melatonin in the night following food reintroduction. In spring, the effects of the treatment were qualitatively similar but their extent depended on the amount of body-fat reserves. This work shows that the reduction of night-time melatonin during migratory periods is functionally related to nocturnal migration, and that fat reserves influence the response of the migratory programme to food deprivation.

Keywords: bird migration; migratory restlessness; Zugunruhe; melatonin; Passeriformes

1. INTRODUCTION

Bird migration is a complex phenomenon that requires a number of behavioural and physiological adaptations. These adaptations are particularly complex in species that are normally active only during the day but perform migratory flights mainly or exclusively at night. Hence, in these species migration is associated with a major switch in the circadian pattern of activity. Even if kept in cages, nocturnal migrants exhibit intense nocturnal activity (‘Zugunruhe’) during the migratory seasons, in addition to the normal diurnal activity. The physiological mechanisms that underlie such a dramatic behavioural transition are, basically, unknown.

One good candidate factor in the regulation of nocturnal migration is the pineal hormone melatonin. In passerine birds, melatonin is a major component of the circadian system that regulates day–night rhythms (reviewed in Cassone & Menaker 1984; Gwinner et al. 1997). In one of the few studies that have investigated hormonal correlates of nocturnal migration, Gwinner et al. (1993) compared the plasma profiles of melatonin in captive garden warblers (Sylvia borin) between migratory and non-migratory periods. In a constant 12 L:12 D cycle, the 24 h profile of plasma melatonin did not differ in its general pattern between the migratory periods and other times of the year, in that melatonin levels were high at night and low during the day (Gwinner et al. 1993). This is in agreement with the general rule that in birds and other organisms melatonin levels are elevated only during night time, irrespective of whether the species is diurnal or nocturnal (Arendt 1998; Kumar et al. 2000). However, in the garden warblers the nocturnal melatonin peak was significantly lower during the migratory periods than before and after them (Gwinner et al. 1993), suggesting the possibility of a functional relationship between peak melatonin levels and nocturnal activity. This hypothesis was supported by a study conducted on a nocturnal migrant closely related to the garden warbler, the blackcap (Sylvia atricapilla). The migratory behaviour of this species is well known. Birds breeding in northeastern Europe are long-distance migrants that winter in equatorial Africa (Berthold et al. 1990a). The populations of blackcaps on the Atlantic islands of Madeira and Cabo Verde, however, do not migrate (Berthold et al. 1990b). We have shown that blackcaps of migrating populations show seasonal changes in the amplitude of melatonin (Fusani & Gwinner 2001). In these birds, night levels of melatonin were lower during the migratory period, when birds showed nocturnal activity, than before and after this period, when birds did not show nocturnal activity (Fusani & Gwinner 2001). This is in agreement with the results of the earlier study on garden warblers (Gwinner et al. 1993). By contrast, non-migratory birds from Cabo Verde did not show such changes and the nocturnal activity observed in several of these birds was not accompanied by a reduction in melatonin levels (Fusani & Gwinner 2001).

To study further the relationship between Zugunruhe and nocturnal levels of melatonin we used an experimental protocol that allowed us to turn Zugunruhe on and off, the ‘fasting-and-refeeding’ protocol (Biebach 1985; Gwinner et al. 1985, 1988). It is known from previous studies on spotted flycatchers (Muscicapa striata) (Biebach 1985) and garden warblers (Gwinner et al. 1985, 1988) that food reintroduction after a short period of food deprivation temporarily suppresses Zugunruhe. This
experimental protocol presumably mimics the situation of a migrating bird that has been fasting during a long flight and subsequently interrupts migration upon reaching a suitable refuelling site. Preliminary experiments using the ‘fasting-and-refeeding’ protocol suggested that melatonin levels increase after induced suppression of Zugunruhe (Gwinner 1996).

In the present work, we studied the effects of food deprivation and subsequent refeeding on the nocturnal activity and night-time melatonin levels of migratory blackcaps. Our prediction was that night-time melatonin levels would increase after inducing a reduction in Zugunruhe. The experiments were done with blackcaps taken from Sweden before autumn migration and from Kenya before spring migration because birds from long-distance migratory populations show robust long-lasting Zugunruhe in captivity (Berthold et al. 1990a). In addition, we wanted to compare the responses to the ‘fasting-and-refeeding’ protocol between autumn and spring because several studies have shown that aspects of the migratory pattern such as migration speed differ between autumn and spring migrations (Berthold et al. 1990a). Our results provide an experimental demonstration of a functional relationship between melatonin and Zugunruhe.

2. MATERIAL AND METHODS

(a) Experimental animals

Male blackcaps were trapped at Tovetorp Zoological Research Station, Sweden (58°56’ N, 17°08’ E) at the beginning of September 1999, and in the area of Naro Moru, Kenya (00°15’ S, 37°04’ E) at the end of February 2000. The birds were transported to our institute and housed in individual cages equipped with infrared motion sensors connected to a computer to record locomotory activity (see § 2c). The blackcaps from Sweden were exposed to a decreasing day length simulating southward migration until 18 October, when the day length reached 12 h. From this day onwards, the birds were kept in a 12 L : 12 D photoperiod (lights on at 06.00) until the end of the experiments. The birds from Kenya were directly moved to a 12 L : 12 D photoperiod. All birds were housed in the same room at 20 ± 1 °C. The light intensity in the cages was greater than 250 lux during the light phase and less than 0.01 lux during the dark phase. Food and water were given ad libitum and were renewed every day immediately after lights off. Birds were captured with the permissions of the Swedish Environmental Protection Agency and of the Kenya Wildlife Service. All the experimental procedures were carried out in accordance with the guidelines of the relevant German agencies.

(b) Experimental design

Experiments started at the end of October for autumnal migration and in mid-May for spring migration. Birds were randomly assigned to one of three groups: food-deprived group 1 (FD1; autumn, n = 10; spring, n = 9), food-deprived group 2 (FD2; autumn, n = 10; spring, n = 7) and controls (autumn, n = 10; spring, n = 9). Birds were further assigned to experimental blocks of five or six birds (one or two birds from each group). The experiments for each block were performed on consecutive days to simplify the experimental procedures. From the day before the beginning of the food deprivation (day 0) to the end of the experiments (day 11), the body mass (BM) of each bird was recorded daily between 12.00 and 13.00. In spring, we additionally recorded the extent of body-fat deposition on a scale from 0 to 8 (Schwabl et al. 1991). On day 1, just before lights off, the food dish was removed from the cages of FD1 and FD2 birds. To expose all birds to the same amount of disturbance, we opened the cages of the control birds and touched the food containers but did not remove them. The animals in the two food-deprived groups, FD1 and FD2, received no food on days 2 and 3, but fresh water was given as usual. Food deprivation is not stressful for birds with large fat reserves (Schwabl et al. 1991). On day 4, at lights on, fresh food was given to all birds. In the following night, between 23.30 and 00.30, the FD1 and control birds were weighed and bled from the jugular vein using a heparinized needle and a 1 ml syringe under safelight conditions. The experiment was terminated at this time for FD1 and control birds, and the birds were used for another experiment. The birds of the FD2 group were not bled and their weight and activity were recorded daily for the following 7 days (days 5–11). This group served to study the long-term effects of the food-deprivation protocol.

(c) Activity recording and analysis

The cages were equipped with individual infrared motion detectors connected to a personal computer. Locomotory activity was recorded continuously with a 2 min resolution. Activity data were then processed with a purpose-written program (written by Willi Jensen) to filter noise bursts, and to reduce the number of 10 min intervals during which a bird showed locomotory activity each night.

(d) Melatonin assay

Plasma melatonin levels were determined by radioimmunoassay as described previously (Van’t Hof & Gwinner 1999). Briefly, melatonin was extracted from the plasma (100 µl) with chloroform after addition of tritiated melatonin (New England Nuclear, Boston, MA, USA) to estimate the recoveries. The extracted samples were dried under a N2 stream and re-dissolved in 200 µl of tricine buffer. Samples were then washed with petroleum benzine to remove residual fats. An aliquot (80 µl) was transferred to scintillation vials, mixed with scintillation liquid and counted to an accuracy of 2% to calculate the recoveries. A second aliquot (100 µl) was incubated with tritiated melatonin and a specific antibody (Endocrine Sciences, Tarzana, CA, USA). Free melatonin was removed by adding dextran-coated charcoal and centrifugation, the bound fraction was decanted in scintillation vials and counted to an accuracy of 2%. Standard curves were fitted with four-parameters logistic interpolation. The lower detection limit per tube (as determined by the first point outside the 95% confidence interval of the zero standard) was 0.39 pg. The mean (± s.d.) recovery was 86.7 ± 1.9%. The intra-assay variation was less than 5.5% for all assays, and the inter-assay variation was 6.2% (two assays).

(e) Analysis

Data were analysed with SPSS 11.0 (SPSS Inc., Chicago, IL, USA). Comparisons between groups and seasons were done by means of two-way ANOVA, followed by post-hoc tests when appropriate. When the interaction between season and treatment was significant, we performed direct comparisons with multiple t-tests. Two-way repeated-measures ANOVA was used to examine changes within groups during the experiments. When there was a significant effect of the within-subjects factor, we performed direct comparisons and applied the serial Bonferroni’s correction (Rice 1989). Corresponding non-parametric
tests (Kruskal–Wallis ANOVA, Mann–Whitney U-test, Friedmann repeated-measures ANOVA and Wilcoxon signed ranks test) were used when the data did not meet the requirements for parametric tests. All tests were two-tailed and the significance level was set at $\alpha = 0.05$. Where not otherwise specified, data are reported as mean $\pm$ s.e.m.

3. RESULTS

(a) Body mass and fat

There was no difference between autumn and spring birds in the length of the tarsus, an indicator of body size (autumn, $20.87 \pm 0.09$ mm; spring, $20.74 \pm 0.16$ mm; $t = 0.68$, d.f. = 53, n.s.). Birds had a higher BM in spring than in autumn ($25.06 \pm 0.54$ g versus $21.53 \pm 0.33$ g, respectively; $t = 5.76$, d.f. = 53, $p < 0.001$). Therefore, we used the difference in BM relative to that on the day preceding the onset of food deprivation (day 0) for statistical comparisons. Both season (A) and treatment (B) affected BM at days 3 and 4 and at the time of sampling (24.00 on day 4), with no significant interaction between the two factors (day 3: A, $F_{1,34} = 4.9$, $p < 0.05$; B, $F_{1,34} = 193.8$, $p < 0.001$; A $\times$ B, $F_{1,34} = 0.7$, n.s.; day 4: A, $F_{1,34} = 9.9$, $p < 0.001$; B, $F_{1,34} = 86.6$, $p < 0.001$; A $\times$ B, $F_{1,34} = 0.05$, n.s.; day 4, 24.00: A, $F_{1,34} = 17.6$, $p < 0.001$; B, $F_{1,34} = 50.6$, $p < 0.001$; A $\times$ B, $F_{1,34} = 0.8$, n.s., figure 1a). The significant effects of season account for the fact that in spring both food-deprived and untreated birds lost weight during the experiment (figure 1a). Furthermore, recovery of BM after food deprivation in FD2 birds differed between seasons (figure 1b). In autumn, birds had recovered their initial BM at day 7, and increased their BM further to $22.36 \pm 0.46$ g, i.e. 106.5% of their initial BM. By contrast, spring FD2 birds had not recovered their initial BM by the end of the experiments, at day 11, when they had reached $22.78 \pm 0.89$ g, i.e. 93.5% of their initial BM (figure 1b).

The amount of body fat was recorded daily in spring. There was no significant difference in the fat index between FD1 birds and controls at day 3 or day 4 (25th–median–75th; day 3: FD1 $2.75–6.0–6.75$, controls $4.5–5.0–5.75$, Mann–Whitney U-test, $z = 0.84$, n.s.; day 4: FD1 $2.5–6.5–6.5$, controls $4.75–5.5–5.75$, $z = 0.86$, n.s.). This was explained by the fact that the fat index decreased substantially in only a few FD1 birds. Therefore, we performed a Friedmann non-parametric repeated-measures ANOVA separately for each group to compare the change in fat index within groups. The fat index changed significantly during days 0–4 in food-deprived birds (FD1, $n = 9$, $\chi^2 = 17.22$, d.f. = 4, $p < 0.002$) but not in control birds ($n = 9$, $\chi^2 = 9.11$, d.f. = 4, n.s.). A paired comparison with day 0 showed that in FD1 birds the fat index was significantly reduced at day 3 and day 4 (Wilcoxon signed ranks test, $n = 9$: day 3 versus day 0, $z = 2.03$, $p < 0.05$; day 4 versus day 0, $z = 2.23$, $p < 0.05$). Fat birds showed smaller or no changes in the pattern of body-fat accumulation compared with lean birds, as shown by the positive correlation between the decrease in fat index from day 1 to day 4 and the fat index at day 1 ($r_g = 0.69$, $p < 0.005$). This effect is probably methodological and reflects the fact that the body-fat index is not a linear measure.

(b) Nocturnal activity (Zugunruhe)

Zugunruhe was more intense in spring than in autumn. During the 5 days preceding the beginning of the experiments, the average time spent in Zugunruhe was $528.6 \pm 18.1$ min day$^{-1}$ in autumn ($n = 30$) and $594.5 \pm 14.4$ min day$^{-1}$ in spring ($n = 25$) ($t = 2.77$, d.f. = 53, $p < 0.01$).

The effects of the food-deprivation protocol on Zugunruhe are illustrated by the activity recording of the FD2 birds (figure 2). In all autumn birds, Zugunruhe almost completely disappeared in the night following the re-administration of food after 2 days of fasting, and was gradually restored during the following 5–6 days (figure 2). Changes in the mean levels of activity of FD2 birds in autumn and spring are shown in figure 3. The amount of Zugunruhe fluctuated in the first four nights after the beginning of the experiments (days 0–3), which probably reflects disturbance resulting from the manipulation of the birds. However, the fluctuations appeared larger in
Figure 2. Activity record of a representative food-deprived bird (FD2) during the autumn experiment. Each line reports 48 h of recording, and the last 24 h are repeated at the beginning of the following line. The upper black and white bar represents dark and light periods, respectively. The shaded area represents the period of food deprivation. Zugunruhe was interrupted in the night following food reintroduction (day 4, indicated by the arrow) and gradually recovered from day 7.

Figure 3. Amount of Zugunruhe (mean ± s.e.m.) in food-deprived birds (FD2) over the course of the experiment. In autumn, Zugunruhe decreased dramatically in the 5 nights following the reintroduction of food (filled circles). In spring (open circles), only some birds showed a substantial reduction of Zugunruhe in the same period. *p < 0.05, autumn, days 4–8 compared with the 5 days preceding the beginning of the experiments, two-way repeated-measures ANOVA followed by pairwise comparisons. The horizontal bar indicates the period of food deprivation.

autumn than in spring, suggesting a higher sensitivity of autumn birds to external cues (see § 4). The response to the reintroduction of food on day 4 after 2 days of food deprivation differed considerably between seasons. In autumn, the activity of food-deprived birds in the night of day 4 dropped dramatically: activity was reduced to 6.7% of the pre-treatment levels, with very small differences between individuals (figure 3). Activity levels remained low on day 5 and then increased progressively to reach pre-treatment levels on days 9–10, 2 days after the birds had recovered their initial BM. In spring, only 30% of the animals showed a sharp reduction in activity; the remaining 70% did not show any obvious change. The statistical comparison (two-way repeated-measures ANOVA) showed significant effects of season (F_{1,34} = 378.51, p < 0.001), of food regimen (F_{1,34} = 33.23, p < 0.001) and of their interaction (F_{1,34} = 37.44, p < 0.001). Direct comparisons showed that the nocturnal activity was significantly reduced in food-deprived birds in autumn (t = 11.01, d.f. = 18, p < 0.0001) but not in spring (t = 1.25, d.f. = 16, n.s.).

Pairwise comparisons showed that in autumn, but not in spring, activity levels were reduced from day 4 to day 8 compared with the 5 days preceding the beginning of the experiment (figure 3). Similar results were obtained when comparing the activity of FD1 and control birds on day 4 between lights off (18.00) and blood sampling (23.30) (figure 4a). A two-way ANOVA revealed significant effects of season (F_{1,34} = 378.51, p < 0.001), of food regimen (F_{1,34} = 33.23, p < 0.001) and of their interaction (F_{1,34} = 37.44, p < 0.001). Direct comparisons showed that the nocturnal activity was significantly reduced in food-deprived birds in autumn (t = 11.01, d.f. = 18, p < 0.0001) but not in spring (t = 1.25, d.f. = 16, n.s.).

The seasonal difference in the effects of food deprivation and refeeding might be explained by the fact that autumn birds had a lower BM at the beginning of the experiments and reached a lower BM than spring birds at day 4 (17.89 ± 0.36 g versus 20.69 ± 0.72 g, respectively,
of Zugunruhe at day 4 (autumn: \( n = 20, r = -0.491, p < 0.05 \); spring: \( n = 18, r = 0.2, \text{n.s.} \)).

### 4. DISCUSSION

We have shown that, in autumn, blackcaps in migratory condition deprived of food for 2 days dramatically interrupted Zugunruhe after food reintroduction on the third day. In spring, only a small percentage of the birds responded to the food regimen with a significant reduction of nocturnal activity, and the response was highly correlated with the amount of fat reserves. The interruption of Zugunruhe in autumn was accompanied by a significant increase in the night peak of melatonin, and similar but less pronounced effects were seen in spring. Thus, this study demonstrates the existence of a functional relationship between melatonin and Zugunruhe during nocturnal migration.

The clear-cut effects of food deprivation and subsequent refeeding on the Zugunruhe of blackcaps confirms that food is a strong modulator of the internal migratory programme in these passerine birds. Interruption of Zugunruhe after “fasting-and-refeeding” was first observed in spotted flycatchers (Biebach 1985) and garden warblers (Gwinner et al. 1985). In nature, migrating birds with depleted energy reserves may profit from interrupting migration for a few days (stopover) after finding a suitable refuelling area. A dependence of actual stopover time on the amount of body fat has been described for three species of trans-Saharan migratory passerines including a close relative of the blackcap, the lesser whitethroat (Sylvia curruca) (Biebach et al. 1986). These authors found that in sites with no food available all birds departed in the evening of the day of their arrival, whereas in sites with high food availability lean birds stayed longer than 1 day (Biebach et al. 1986). Interestingly, the estimated median stopover time was 4–5.5 days, a duration similar to that of the ‘virtual stopover’, i.e. nights with low nocturnal activity, observed in the present study (figure 3).

No study has previously examined the effects of fasting and refeeding during spring migration. We found differences between seasons in the response to the food regimen, in that the reduction of Zugunruhe after refeeding was observed in all birds in autumn but in only a few birds in spring. There were, however, some differences between autumn and spring birds prior to the beginning of the experiments: spring birds had higher BM and higher levels of Zugunruhe. If the reduction in Zugunruhe depends on the decrease of the BM below a critical threshold, one might expect stronger effects of food deprivation on autumn birds, which, during food deprivation, reached a lower BM than did spring birds. This interpretation is supported by the observation that in spring the reduction of Zugunruhe was correlated with the BM on the day of refeeding. Previous work has shown that in other species the effects of the fasting-and-refeeding protocol are stronger when the birds are brought down to a lean (non-migratory) BM (Biebach 1985; Gwinner et al. 1985). In addition, in nature only lean birds extend their stopover to more than 1 day (Biebach et al. 1986). Nevertheless, our results suggest that factors other than the absolute BM modulate the response to the food regimen. Two spring birds reached a low BM (less than 18 g) and yet did not

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Figure 5. Relationship between BM and Zugunruhe at day 4, i.e. the day on which food was re-introduced after 2 days of deprivation, in food-deprived birds (FD1 and FD2); spring: filled circles, autumn: open circles). In spring, BM and Zugunruhe were positively correlated with each other (\( r_S = 0.719, p < 0.002 \)). However, two birds with low BM (arrows) had high levels of Zugunruhe, suggesting that other factors influence the response to food deprivation.

(c) **Melatonin**

Plasma levels of melatonin were higher in autumn than in spring and higher in FD1 than in control birds (figure 4b). The statistical comparison (two-way ANOVA) showed significant effects of season (\( F_{1,34} = 45.38, p < 0.001 \)) and of food regimen (\( F_{1,34} = 4.51, p < 0.05 \)) on melatonin levels, with no significant interaction (\( F_{1,34} = 2.41, p = 0.131 \)). Melatonin levels were inversely correlated with BM loss at the time of sampling in spring but not in autumn (spring: \( n = 18, r = -0.631, p < 0.005 \); autumn: \( n = 20, r = -0.345, \text{n.s.} \)). In spring, there was no significant correlation between melatonin and body-fat index, at day 3 or day 4 (\( n = 18, r_S = 0.426 \) and \( r_S = 0.195, \text{respectively, n.s.} \)). The body-fat index was not recorded in autumn. In autumn, but not in spring, melatonin levels were inversely correlated with the amount
show changes in their level of Zugunruhe after refueling. However, there was a strong correlation between Zugunruhe and body fat, which suggests that, in spring, birds would interrupt migration only when their fat reserves are reduced below a critical threshold. Taken together, our data suggest that in spring the migration programme is less flexible and does not respond to food deprivation to the same extent as in autumn. Previous studies reported differences between autumn and spring migration in blackcaps. For example, males migrate earlier than females in spring but not in autumn (i.e. Izhaki & Maitav 1998; Terrill & Berthold 1989). One possible explanation for this phenomenon is that males experience greater intrasexual competition for territories and/or mates (Myers 1981; Izhaki & Maitav 1998). According to this hypothesis, males could have a higher threshold for interrupting migration in spring than in autumn because of the importance of early arrival for reproductive success. Spring birds in the present study were probably in a breeding or pre-breeding state, as suggested by a previous study in which blackcaps held under similar photoperiodic conditions had enlarged gonads by May (Berthold et al. 1972).

A reduction in the melatonin amplitude during migratory periods has so far been observed in two species, the garden warbler and the blackcap (Gwinner et al. 1993; Gwinner 1996; Fusani & Gwinner 2001). The novelty of the present study is the demonstration that the correlation between the height of the nocturnal melatonin peak and the amount of Zugunruhe does not simply result from parallel although independent seasonal variations in these two phenomena, but rather reflects a causal relationship. At least during the autumnal migration season a rigid relationship between nocturnal melatonin levels and Zugunruhe was found even in birds exposed to a specific environmental stimulus—the ‘fasting-and-refeeding’ protocol. The reduction of the melatonin amplitude during migration might be a direct consequence of nocturnal activity. Alternatively, it might be the result of exposure to higher nocturnal light intensities in active birds that keep their eyes open than in inactive birds that sleep with closed eyes (Gwinner et al. 1993; see discussion in Gwinner 1996). Alternatively, a reduced melatonin amplitude might be necessary for the manifestation of nocturnal activity. Several facts support the latter hypothesis. In songbirds, the locomotory activity rhythm is strictly associated with the melatonin rhythm (Cassone & Menaker 1984; Kumar et al. 2000), and pinealectomy affects the activity rhythms dramatically (Gwinner et al. 1987; reviewed in Kumar et al. 2000). In addition, in non-migratory blackcaps from Cabo Verde melatonin levels at night do not differ between nocturnally active and inactive birds, making an effect of nocturnal activity on melatonin levels unlikely (Fusani & Gwinner 2001).

In the present study, melatonin was generally lower during spring migration, when birds showed higher levels of Zugunruhe, than during autumnal migration. However, because the seasonal difference in Zugunruhe was relatively small compared with the large difference in melatonin levels, this phenomenon may not be related to the day-to-day variations in Zugunruhe and melatonin discussed here. Drastic seasonal changes in peak melatonin levels have been found in other species of bird (Gwinner & Brandstätter 2001). For migratory birds, it has been proposed that a reduction in the amplitude of melatonin, apart from being involved in the regulation of Zugunruhe, might lead to a general damping of the circadian pacemaking oscillation. This would render migrating birds more susceptible to zeitgeber stimuli and thus allow them to synchronize faster to phase shifts and a rapidly changing photoperiod (Gwinner 1996; Gwinner et al. 1997). According to this hypothesis, seasonal changes in melatonin amplitude would be important physiological adaptations for migration. The smaller melatonin amplitude in spring found in the present study might be adaptive because it might help birds to adjust quickly to the changes in photoperiod, which are much more pronounced during the spring migration than during the autumnal migratory season.

In conclusion, this study strongly suggests that melatonin levels and migratory activity are functionally related, and shows that the reduction of night-time melatonin levels during migratory relative to non-migratory periods is larger during spring migration than in autumn migration. We are currently studying the sites and modalities of action of melatonin in the brain to understand how melatonin can affect the expression of nocturnal activity. In addition, future studies will investigate how food availability and the nutritional state can affect melatonin and migratory activity.

The authors are grateful to Thord Fransson of the Swedish Museum of Natural History, Sven Jakobsson of the Tovetorp Zoological Research Station, Stockholm University, and the Swedish Environmental Protection Agency for making it possible to conduct fieldwork in Sweden and for making available their facilities to them. They thank Leon Bennun of the National Museums of Kenya, and Ali Jama and Paula Kahumbu of the Kenya Wildlife Service for their assistance in organizing the work in Kenya. Fred Barasa, Susanna Hall, Giovanni Terranova and Gabriela Wagner contributed to the fieldwork and to the transportation of the blackcaps to Andechs. They thank Ingrid Schwabl for her precious help in the organization of the fieldwork, and Willi Jensen for his invaluable help with the recording and the analysis of the behavioural data. Herbert Biebach and Michaela Hau made helpful comments on previous versions of the manuscript. Finally, the authors thank Ute Abraham, Ulf Bauchinger, Virginia Canoine, Claudia Mettke-Hoffman, Alexander Scheuerlein and many others for their support in several aspects of the project.

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Melatonin and nocturnal migration

L. Fusani and E. Gwinner


As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.