

# TIME OF COMMENCEMENT OF NOCTURNAL RESTLESSNESS IN LONG- AND MIDDLE-DISTANCE PASSERINE MIGRANTS DURING SPRING SEASON

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## ABSTRACT

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Direct visual observations and radio-telemetric studies show that time of nocturnal departures in individual birds is not limited by dusk, but varies broadly. We suggest that beginning of „Zugunruhe” in freshly caged free-living birds corresponds to behaviour in the field. To test this, we studied nocturnal restlessness in long- and middle-distance migrants (19 species,  $N = 258$ , mainly *Sylviidae* family). Birds were trapped 2 to 1 h before sunset and put into individual cages under open sky. The initiation of „Zugunruhe” was recorded by infra-red night vision binoculars or by automatic hopping registration. Nocturnal activity was observed in 30.2% of tested birds. The proportion of active birds was significantly higher among the fat birds, than among the lean ones. Commencement of „Zugunruhe” in individual birds varied up to 420 min after sunset (median – 167 min). The onset of „Zugunruhe” in the fat migrants (median – 110 min) was significantly earlier in relation to sunset than in the lean birds (median – 190 min). Possible causes of variation in the timing of beginning nocturnal activity in the field are discussed.

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## INTRODUCTION

Migratory flight in passerine nocturnal migrants consists of three main behaviours: take-off, transit flight, and landing. Numerous radar studies in the 1960-1970s showed that nocturnal migration of passerines started soon after sunset (Drury and Nisbet 1964, Casement 1966, Parslow 1968, Gauthreaux 1971, Lindgren and Nilsson 1975, Alerstam 1976, Richardson 1978). As migration intensity on radar screens was reaching a peak soon, it was assumed that the main take-off period was restricted to a short twilight period. It was suggested to have an adaptive significance

and to be caused by (1) optimal conditions for celestial orientation (Emlen 1975, Moore 1987, Helbig 1991); (2) good opportunity for calibration of the magnetic and celestial compasses, based on the sunset direction, skylight polarisation pattern and stars (Able and Able 1990, 1993, 1995; Phillips and Moore 1992); and (3) most suitable weather situation during this part of day for nocturnal migrants using flapping flight (Kerlinger and Moore 1989).

However, direct visual observations of take-off activity during twilight and in the darkness (Hebrard 1971; Bolshakov and Rezvyi 1975, 1982, 1998; Bolshakov 1992, Bolshakov and Bulyuk 1999), telemetric studies (Cochran *et al.* 1967; Cochran 1987; Åkesson *et al.* 1996; Moore and Aborn 1996), and tracking radar data (Åkesson *et al.* 1996) do not support this view. In a number of passerine nocturnal migrants departure period is not fixed – birds commence their nocturnal flights during different parts of twilight and dark periods. It was suggested that the variation in take-off time in nocturnal migrants may depend on species, latitude, time of season (Åkesson *et al.* 1996), and/or energy stores of birds that start the migratory flight (Moore and Aborn 1996). Departure time may be controlled to some extent by individual circadian rhythms, change in light-dark pattern along the season, position of the bird in relation to the goal of migration, and the speed of transit migration (Bolshakov and Rezvyi 1998, Bolshakov and Bulyuk 1999).

It has long been known that many passerines, when taken from the wild and caged, show nocturnal restlessness and season-appropriate orientation. Migratory restlessness („Zugunruhe”) appears to be essentially a cage-adapted migratory activity expressed as a reduced flight behaviour, *i.e.* migration in a sitting position (Berthold 1996). „Zugunruhe” starts at the same moment when free-living conspecifics take off and start migratory flight. When freshly trapped birds are put in registration cages and their activity recorded, it is possible to study the timing of take-off activity experimentally and to compare the results with field data. This approach formed the basis of this study.

## MATERIAL AND METHODS

Nocturnal restlessness was studied in passerine nocturnal migrants trapped at daytime stopovers on the Courish Spit of the Baltic Sea during their spring migration. Birds were mist-netted daily 2-1 h before sunset between 10 April and 9 June, in the period 1996-1998. We tested 19 species of passerine nocturnal migrants ( $N = 258$ ), the bulk being long-distance Palearctic-African migrants. Only two species – Blackcap (*Sylvia atricapilla*) and Chifchaff (*Phylloscopus collybita*) are middle-distance migrants, with winter quarters both in southern Europe and northern Africa (Moreau 1972). In seven species – Redstart (*Phoenicurus phoenicurus*), Sedge Warbler (*Acrocephalus schoenobaenus*), Reed Warbler (*A. scirpaceus*), Willow Warbler (*Phylloscopus trochilus*), Whitethroat (*Sylvia communis*), Blackcap and Pied Flycatcher (*Ficedula hypoleuca*) the number of tested individuals was  $\geq 20$  (Table 1). Standard procedure included ageing, weighing, measuring wing chord and

fat scoring after Kaiser (1993). Afterwards, birds were put in separate cages for the whole night (up to 12 birds per night) under the open sky, so that they could see the sunset and starry sky. Solid partitions between the cages did not allow a bird to see its neighbours. In 1996-1997 birds' behaviour was recorded visually by infra-red binoculars from the distance of 10 m ( $N = 117$ ). In 1998 nocturnal activity was studied in cages with automatic recording system ( $N = 141$ ). Hopping was recorded by slanting plates that recorded all forms of locomotor activity (Sandberg *et al.* 1988). Visually birds' activity was recorded over 10 min in the middle of every hour of the night between 90 min after sunset and 90 min before sunrise. In automatic cages the number of hops in every hour in relation to sunset was counted during the same period of the night. Birds were released before sunrise.

Table 1  
Proportion of birds with nocturnal activity

	Number/(percentage) of active birds	Number of tested birds
<i>Lanius collurio</i>	1 (-)	1
<i>Luscinia luscinia</i>	1 (25)	4
<i>Luscinia svecica</i>	2 (50)	4
<i>Phoenicurus phoenicurus</i>	6 (19.4)	31
<i>Saxicola rubetra</i>	0 (-)	1
<i>Locustella naevia</i>	1 (-)	1
<i>Acrocephalus schoenobaenus</i>	14 (41.2)	34
<i>Acrocephalus palustris</i>	1	3
<i>Acrocephalus scirpaceus</i>	9 (39.1)	23
<i>Hippolais icterina</i>	1 (-)	4
<i>Sylvia atricapilla</i>	4 (25)	20
<i>Sylvia borin</i>	4 (33)	12
<i>Sylvia communis</i>	1 (3.1)	32
<i>Sylvia curruca</i>	0 (-)	9
<i>Phylloscopus collybita</i>	4 (31)	13
<i>Phylloscopus trochilus</i>	8 (34.8)	23
<i>Phylloscopus sibilatrix</i>	7 (58)	12
<i>Muscicapa striata</i>	2 (18)	11
<i>Ficedula hypoleuca</i>	11 (55)	20
Total	30.2%	258

In this paper we discuss only two parameters of nocturnal activity: (1) presence of restlessness in the study night, and (2) the hour in relation to sunset when rest-

lessness commenced. To study possible effects of fat stores we analysed our results separately for the lean (fat scores 0-3) and the fat (fat score  $\geq 4$ ) individuals.

When activity was recorded visually, those birds were treated as active, which showed constant restlessness during at least two hours. Birds were considered to be inactive if they did not show any activity at night or showed weak irregular activity. In experiments with automatic design, birds were treated as active when the mean number of hops per hour during the dark period (from 120 min after sunset to 120 min before sunrise) reached at least 10. We concluded that nocturnal activity commenced in the 2<sup>nd</sup> hour after sunset if a bird displayed constant high activity in this and the following hour of night; in the 3<sup>rd</sup> hour – if after the lack of activity between 90-120 min after sunset the bird started hopping in either half of the third hour; in the 4<sup>th</sup> hour – if after no activity in the 2<sup>nd</sup> and 3<sup>rd</sup> hour a bird started hopping in the 4<sup>th</sup> hour, *etc.*

## RESULTS

### Proportion of active birds

Overall, nocturnal activity was recorded in only 30.2% of tested long- and middle-distance migrants. In seven species with the number of tested birds 20, proportion of birds that displayed „Zugunruhe” varied between 3.1% in the Whitethroat and 55% in the Pied Flycatcher (Table 1). Pooling all species, the proportion of active birds was considerably rising with higher fat scores (Fig. 1). The proportion of active individuals was significantly lower ( $\chi^2 = 4.53, p < 0.05$ ) among birds with fat scores 0-3 (21.1%,  $N = 184$ ) than in birds with fat scores  $\geq 4$  (40.5%,  $N = 74$ ).

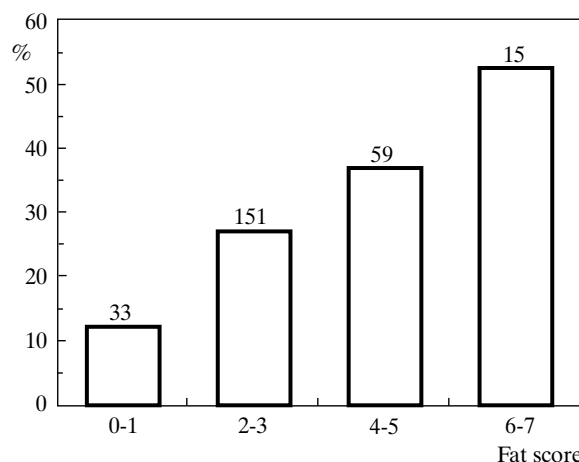


Fig. 1. Percentage of active birds with defferent fat scores. Numbers above the bars indicate sample sizes.

### Body mass and fat score in active and inactive birds

Among species with the number of tested individuals  $\geq 20$ , the mean body mass of the active birds was significantly higher than that of the inactive conspecifics only in the Sedge Warbler. In other species, the active birds were heavier, differences, however, were not significant (Table 2). The active birds carried significantly more (Kolmogorov-Smirnov test:  $\lambda = 1.48$ ,  $p < 0.05$ ) fat than the inactive ones (medians – 3.7 and 3.1, respectively; Fig. 2).

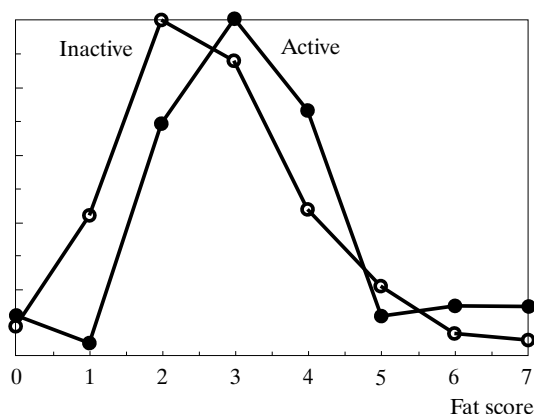


Fig. 2. Distribution of fat scores for active and inactive birds.

Table 2  
Mean body mass,  $M \pm SD$  ( $N$ ), of active and inactive birds

	Active	Inactive	Significance
<i>Phoenicurus phoenicurus</i>	16.7 $\pm$ 1.05 (6)	15.9 $\pm$ 1.42 (25)	ns
<i>Acrocephalus schoenobaenus</i>	14.0 $\pm$ 1.29 (14)	13.1 $\pm$ 0.95 (20)	<b><math>p &lt; 0.05</math></b>
<i>Acrocephalus scirpaceus</i>	12.8 $\pm$ 0.79 (9)	12.5 $\pm$ 0.66 (14)	ns
<i>Sylvia atricapilla</i>	19.0 $\pm$ 2.08 (5)	18.5 $\pm$ 2.15 (15)	ns
<i>Phylloscopus trochilus</i>	9.6 $\pm$ 0.66 (8)	9.5 $\pm$ 0.59 (15)	ns
<i>Ficedula hypoleuca</i>	13.2 $\pm$ 0.98 (11)	12.9 $\pm$ 1.21 (9)	ns

### Time of commencement of nocturnal activity

Time of beginning „Zugunruhe” in individual birds varied broadly – from 2 (start of recording) to 7 h after sunset (median – 167 min). In species with the number of tested individuals  $\geq 20$ , the period of beginning nocturnal activity was 3-4 h (Table 3). Pooling all species, the lean individuals started restlessness 80 min later than the fat conspecifics, in relation to sunset (medians – 190 min and 110 min, respectively; Fig. 3). Frequency distributions were significantly different in the fat and the lean birds (Kolmogorov-Smirnov test:  $\lambda = 1.80$ ,  $p < 0.01$ ).

Table 3  
Time of beginning nocturnal activity in relation to the sunset (numbers of cases)

	Hours after sunset								Time between sunset and sunrise (h)
	2	3	4	5	6	7	8	9	
<i>Lanius collurio</i>			1						7.4
<i>Luscinia luscinia</i>			1						8.1
<i>L. svecica</i>			1		1				7.7
<i>Phoenicurus phoenicurus</i>	3		1	2					9.2-7.0
<i>Locustella naevia</i>	1								7.5
<i>Acrocephalus palustris</i>			1						7.3
<i>A. schoenobaenus</i>	9	3		2					8.2-6.8
<i>A. scirpaceus</i>	3	3	2	1					7.6-6.8
<i>Hippolais icterina</i>	1								7.8
<i>Sylvia atricapilla</i>	1	1	1	2					8.8-6.9
<i>S. borin</i>	2	1		1					8.6-7.0
<i>S. communis</i>		1							7.4
<i>Phylloscopus collybita</i>		2		1		1			9.4-8.3
<i>P. trochilus</i>	2		1	4	1				9.2-8.6
<i>P. sibilatrix</i>	2	1	2	2					9.2-8.8
<i>Muscicapa striata</i>				1	1				8.6-8.2
<i>Ficedula hypoleuca</i>	4	2	3	2					9.3-7.2
Total	28	14	14	18	3	1	0	0	

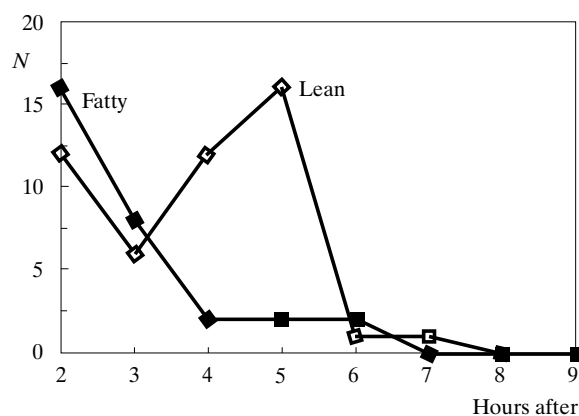


Fig. 3. Time of activity's onset in fatty (fat scores 4-7) and lean (fat scores 0-3) birds.

## DISCUSSION

In our experiments, birds were taken from the nature at the very end of day, practically after terminating foraging. They were put into open individual cages, which allowed them to see the sunset and starry sky to perceive natural weather factors, e.g. air temperature, pressure, and humidity. Their behaviour was strongly restricted only in choosing roosting place.

Pooling all species, only small proportion of tested birds – 30.2% – showed a pronounced nocturnal restlessness (Table 1). The lack of „Zugunruhe” in many birds could have been caused by: (1) handling stress, (2) low endogenous motivation for flight in transit birds, (3) presence in the sample of birds that have completed migration, (4) unfavourable weather conditions in some nights, and (5) lack of access to celestial cues under overcast. In this contribution, these factors are not discussed. It is however noteworthy that many birds were, no doubt, captured after completing migratory flight with depleted fuel stores. Motivation for resuming flight is known to increase along with rebuilding fat stores (for review see Dolnik 1975). This was also evident in our experiments with freshly captured birds (Fig. 1, 2; Table 2). However, in Wood Warbler and Pied Flycatcher, despite the high percentage of individuals with fat scores  $\leq 3$  (92% and 85%, respectively), the highest proportions of active birds were recorded (Table 1). In these and some other species, the expression of migratory activity was influenced by habitat quality and the probability of rebuilding fat stores (Biebach 1985; Gwinner *et al.* 1985, 1988; Terrill 1988). The high percentage of active individuals among the lean birds could also be related to the high proportion of birds that have nearly finished migration (see below).

Individual birds started nocturnal restlessness in the interval between 90 and 420 min after sunset (Table 3). As (due to methodological reasons) activity was not recorded until 90 min after sunset, at least some birds could actually have started activity before 1.5 hours after sunset. In the nature, first nocturnal migrants usually depart 22-40 min after sunset (Casement 1966, Cochran *et al.* 1967, Parslow 1968, Gauthreaux 1971, Hebrard 1971), or even earlier (Bolshakov 1992, Åkesson *et al.* 1996, Moore and Aborn 1996, Bolshakov and Rezvyi 1998).

In all species with the number of tested individuals  $\geq 20$ , timing of beginning nocturnal activity varied broadly, from the second to the seventh hour after sunset. In other tested species „Zugunruhe” also commenced at different time (Table 3). Thus, our data suggest that many long- and middle-distance migrants in spring may depart not only at twilight, but later at night as well. With night duration of 9.2-6.8 h (Table 3), birds may take off during the major part of night. At present, considerable variation in the timing of take-off during spring migration was recorded in several species of *Hylocichla* thrushes (Cochran *et al.* 1967), Fieldfare – *Turdus pilaris* (Bolshakov 1992), Song Thrush – *T. philomelos* (Åkesson *et al.* 1996), Summer Tanager – *Piranga rubra* (Moore and Aborne 1996) and Robin – *Erithacus rubecula* (Bolshakov and Rezvyi 1998, Bolshakov and Buljuk 1999). These data are at variance with the concept of synchronised take-off, restricted to dusk (Kerlinger and Moore 1989, Alerstam 1990). The very wide scatter in departure time provides little support for the concept that the departure time is adapted to the availability of specific combination of celestial orientation cues at twilight (Åkesson *et al.* 1996). It is not improbable that birds, which take off in the darkness after twilight, integrate and transfer directional information during the transition between daylight and darkness to landmarks or stars (Moore and Aborn 1996).

Already found very broad variation in take-off time in the nature and in the onset of „Zugunruhe” in freshly trapped migrants in this study suggests that the pattern is controlled by individual endogenous circannual and circadian programmes (clocks) that are in a complex fashion related to seasonal changes in LD dynamics (Bolshakov and Rezvyi 1998, Bolshakov and Bulyuk 1999). Circadian system is known to have considerable significance in control of avian migration (Dolnik 1975; Gwinner 1975, 1996; Berthold 1993, 1996). One of the factors influencing departure time in spring may be also the distance from the goal of migration. Large variation in the timing of departure may be caused primarily by the behaviour of birds approaching the goal of migration (Bolshakov and Bulyuk 1999).

We showed that lean birds started nocturnal migratory restlessness significantly later than fatter individuals (Fig. 3). Many lean birds that showed restlessness in cages could be finishing migration and approaching their goal, whereas fat birds were mostly still on migration. The analysis of condition of transit and local Reed Warblers in spring on the Courish Spit showed that local birds carried significantly less fat and were lighter than transit individuals (Chernetsov 1999). At least in this species, the late onset of nocturnal activity in a fraction of lean birds could have been caused by the fact that they were approaching the goal of their migratory journey. On the other hand, some lean birds may be transit individuals that did not find suitable conditions for restoring depleted fat reserves at the stopover site. Food deprivation studies with captive migrants (Gwinner *et al.* 1985, 1988) suggest that such birds can also make short nocturnal flights in search for good foraging sites. It is not improbable that in the nature, such birds depart later in relation to sunset. It allows to finish the nocturnal flight at dawn, facilitating stopover site selection without special daytime movements.

Due to methodological reasons, proportions of birds showing activity at the beginning of the night and later obtained by us (Fig. 3) may not correspond to the actual number of early and late departures in the nature. Proportions of transit and local birds in our samples remain unknown. In the nature, proportions of early and late take-offs evidently varies in relation to percentage of transit migrants and birds approaching their final destination.

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