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ORIGINAL PAPER

Timing of nocturnal passerine migration in Arctic light conditions

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Abstract The nocturnal migration of many passerines starts after sunset and reaches peak intensity during the dark hours of the night. Birds destined for high Arctic breeding grounds encounter a special situation, as they will experience continuous daylight when reaching the high latitudes during the final part of spring migration. How does this affect the pattern of nocturnal migration? We consider three alternative hypotheses; that the period of nocturnal flight activity may become compressed, remain unchanged or become disorganized under Arctic light conditions. We tracked migrating birds by radar north of the Arctic Circle (at Abisko, 68°21′N, 18°49′E, in Swedish Lapland) and show that the pattern during the night, with a migration peak around midnight, persisted even in continuous daylight when the sun remained above the horizon throughout the 24 h of the day. The flight intensity peak under continuous daylight in spring (midnight sun) was very similar to the corresponding peak in autumn, when the migration took place under twilight conditions. The duration of the flight period under continuous daylight in spring lasted 8–10 h and did not seem to be compressed. We hypothesize that the flight period under midnight sun conditions may in fact be more protracted than during short nights, because of release from twilight cues that tend to synchronize initiation and termination of migratory flights. These cues will thus capture and confine the flight period. The results of this provisional study suggest interesting dynamics in timing of nocturnal migratory flights under seasonally and latitudinally changing day length conditions, which will need detailed documentation by future studies of migration intensity at high-latitude sites.

Keywords Bird migration · Passerine migration · Midnight sun · Arctic · Tracking radar · Migration flights

Introduction

Many passerines migrate at night to be able to forage during the day, to avoid predators and to take advantage of the often calmer wind situations with less turbulence (Kerlinger and Moore 1989; Alerstam 2009). Nocturnal migratory flights are often initiated 1–3 h after sunset, during the periods of nautical or astronomical twilight, but flight departures also take place during later parts of the night. Radio telemetry studies of individual migrants at stopover sites have revealed that the timing of migratory departures is more variable and less synchronized than formerly thought and that it varies with species, season, site and the individuals' stopover duration (e.g. Åkesson et al. 1996, 2001; Bulyuk and Tsvey 2006; Bolshakov et al. 2007; Chernetsov 2012; Schmaljohann et al. 2013). Some of these studies show interesting seasonal effects in spring, with departures occurring successively earlier in relation to sunset as the spring season progresses and nights become shorter. Still, the birds wait to depart until the sun is below the horizon also in late spring at midlatitudes of 50–60°N (Bolshakov and Rezvyi 1998; Bolshakov et al. 2007; Chernetsov 2012) so that their potential nocturnal flight period becomes gradually more restricted when nights become shorter (Chernetsov 2012).

What happens when nocturnal migrants proceed to even more northerly latitudes in late spring? When they reach

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north of the Arctic Circle and meet conditions with the midnight sun staying above the horizon?

We have carried out tracking radar studies of bird migration at Abisko, north of the Arctic Circle in Swedish Lapland, during two spring and two autumn seasons. In this study, we analyse the nightly distribution of migratory flight activity of passerines during periods with midnight sun in spring and periods with short nights (civil and nautical twilight conditions) in autumn, to throw light on these questions and to test the following possible hypotheses:

1. Short spring nights at high latitudes may lead to continued compression (see above) of the time window for migratory flights, showing a very short but pronounced migratory peak around local midnight. The migrants may continue to fly only during such a compressed midnight window when reaching north of the Arctic Circle and experiencing conditions where the sun never sets below the horizon.
2. Instead of continued compression, the nocturnal passerine migrants may maintain an activity time window of at least 6 h around midnight (as recorded at midlatitudes in late spring; Chernetsov 2012) also when travelling under conditions of still shorter nights and even midnight sun at higher latitudes in late spring.
3. The migrants may abandon their daily rhythm of flight activity/migratory restlessness (Gwinner 1996) as they travel into Arctic light conditions, leading to a more uniform distribution of flight activity (no pronounced peaks) during the day and night. Such loss of circadian cycles has been reported during both summer (continuous daylight) and winter (continuous darkness) among stationary animals such as reindeer and ptarmigan living far north of the Arctic Circle (van Oort et al. 2005). However, the daily rhythm of migratory restlessness may not necessarily disappear or become freerunning under continuous daylight since the daily variation in Arctic light conditions may still be sufficient to maintain it (Daan and Aschoff 1975; Steiger et al. 2013), and it may also be maintained by coupling to a separate endogenous daytime activity/foraging oscillator (Bartell and Gwinner 2005).

Methods

Abisko research station is a field station located in northern Sweden, 68°21′N, 18°49′E, about 200 km north of the Arctic Circle. From around May 24 until July 20, the sun does not set (Edwards 2010). Passerines breeding in this area thus encounter continuous daylight during a large part of spring migration and only twilight conditions during autumn migration (see sun position over the day at different times of the observation periods in Fig. 1). Migrants passing Abisko must be quite close to their breeding grounds as there are limited amounts of land further north. Migration directions of passerines in the area are generally north in spring and south–south east in autumn, but there is a large scatter of directions, probably due to the closeness to the breeding grounds (Karlsson et al. 2010).

Three different stages of twilight are traditionally recognized: civil twilight (sun 0°–6° below the horizon), nautical twilight (6°–12° below the horizon) and astronomical twilight (12°–18° below the horizon). When the sun is >18° under the horizon, it is night (Rozenberg 1966). Every tracked passerine has been assigned to a light regime category based on the date and time of day which it is tracked.

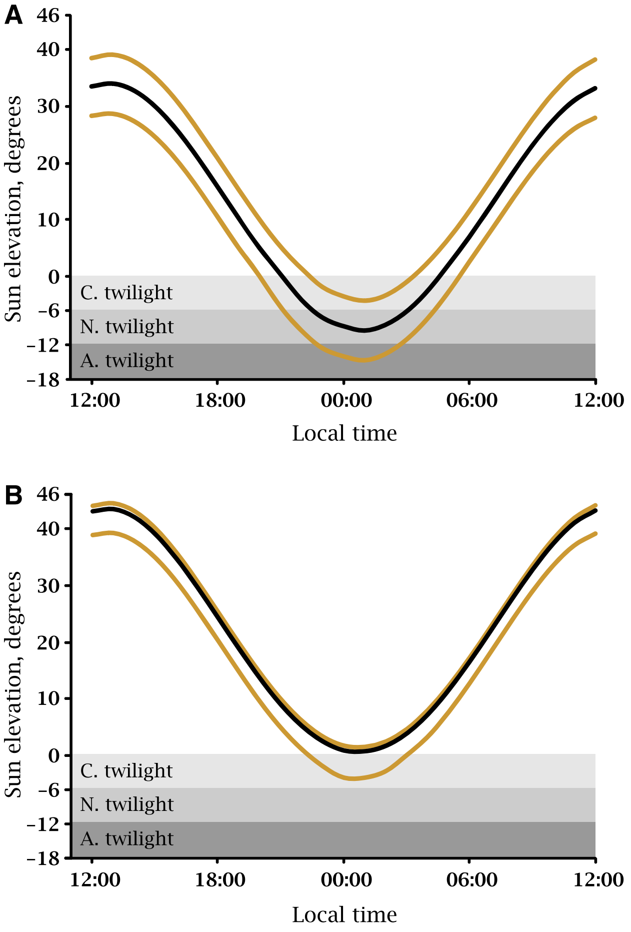

Fig. 1 The sun elevation angle over the horizon from noon to midnight at Abisko, northern Sweden. The first to the last date of sampling during **a** autumn (August 3–September 4) and **b** spring (May 10–June 8) seasons are shown in light colours and median date of sampling (August 20 in autumn and May 30 in spring) in *black* (NOAA solar calculator, 12/8 2013). Civil twilight (C. twilight), nautical twilight (N. twilight) and astronomical twilight (A. twilight) sun elevations are indicated. A sun elevation of below 18° is night

By use of radar, we investigated several aspects of this nocturnal migration under the sun. We tracked birds for two spring and two autumn seasons: 10/5–8/6 and 3/8–13/8 in 2007 and 16/5–7/6 and 3/8–4/9 in 2008. Radar sampling took place during the majority of dates during these study periods, only on nights with rain was there no sampling at all (radar data were obtained during a total number of 40 nights/days in spring and 33 nights/days in autumn). The radar is a mobile tracking radar (200 kW peak power, 0.25 µs pulse duration, 504 Hz pulse repetition frequency, 1.5° beam width, X-band) which was placed at Abisko research station during 2007 and 2008. It was manually operated by scanning the sky and locking on to individual targets identified by the operator from the visual appearance of the echo as birds. The targets were then tracked automatically for around 1–2 min, recording exact 3D position every second. The species of the target cannot be identified on the radar, but bounding flight is clearly distinguishable by the wingbeat signature of the radar echo. Targets where several birds fly close together (flocks) are distinguished from solitary birds by not showing any clear wingbeat signature. We therefore restricted our analysis to birds using bounding flight and flying solitarily, which is characteristic of nocturnal passerine (songbird) migrants. Based on ringing and census data from the area, it is likely that a large part of our material consists of willow warbler (*Phylloscopus trochilus*), pied flycatcher (*Ficedula hypoleuca*), brambling (*Fringilla montifringilla*), redstart (*Phoenicurus phoenicurus*), meadow pipit (*Anthus pratensis*), wheatear (*Oenanthe oenanthe*) and to a lesser extent also other passerines (Strann and Helberg 2004; Strann and Bakken 2004; see also Karlsson et al. 2010). Bramblings and meadow pipits are known to migrate also during the day, when they normally travel in flocks, and flocks have not been included in this study.

It is important to note that our method does not give us a precise density measure of migration, but combining number of hours scanning and number of birds tracked at different times of night gives us a good indication of the general pattern of migration intensity over the night. The radar was mainly operated during night time (2000–0600 hours), but also occasionally during daytime, when weather was favourable and promising for bird migration. Since the number of scanned hours during daytime was low, especially in autumn, our results will mainly focus on the pattern during night hours, with some cautious inferences drawn from the daytime scanning. Number of scanned hours, radar hours, is based on field logs combined with the first and last tracking of every night and has been rounded off to nearest half hour. Included in the sample were mainly periods of one hour, with some 0.5-h periods during initiation or termination of tracking. Times refer to local summer time (GMT + 2 h), where absolute midnight when the sun was at its lowest elevation occurred at 00:42:30 ± 1.5 min during the spring sampling period and at 00:47:30 ± 3.5 min during the autumn sampling period.

Our study has not been designed in an optimal way for documenting and testing the daily distribution of flight intensity, and the inferences from this study should thus be regarded as suggestive rather than absolutely conclusive. We are still confident that our available data are sufficient to reflect important main characteristics of the daily timing of flight activity at Abisko (we point out aspects that need further investigation in the section “Discussion”).

In our analysis, we have used number of radar echoes that were recorded per hour of radar operation as an approximate measure of flight intensity. Since the main part of radar operation was devoted to search for radar echoes from birds, a high flight intensity (high density of birds in the air) would lead to large numbers of tracks recorded per time. This measure would not increase linearly with bird density since, with a tracking time of 1–2 min per target, we would maximally record 30–60 tracks/h at extremely high densities of birds. Since the number of tracks recorded per hour were generally well below this saturation level (Table 1), we have not adjusted for this saturation effect in our calculations (making peak estimates slightly conservative). Observations during each hourly interval were thus treated as separate samples of tracks/h as migration intensity measure. To test whether the distribution of tracks was continuous during the night or not, we compared the migratory flight intensity between clock hours, with clock hour as a categorical variable. We tested this in a mixed linear model with number of tracks per hour as dependent variable and with season and clock hour as fixed factors. Also, included was the interaction between season and clock hour. Night identity was included as a random factor to correct for the dependence of hourly flight intensities within nights. The analysis was performed in IBM SPSS Statistics, v. 21.

Results

We recorded 754 tracks of migrating passerines during 151.5 observation hours (mean rate 5.0 tracks/h) in spring and 738 tracks during 128.5 observation hours (mean rate 5.7 tracks/h) in autumn (Table 1). Number of intensity samples were 167 in spring and 141 in autumn (number of samples slightly exceeded the total number of observation hours because some intensity samples were based on less than one hour of radar coverage, e.g. when radar operation was started, paused or interrupted in the middle of a clock hour interval). In spring, the large majority of tracks (719) were recorded during daylight conditions, and only 35 tracks, from early in the season, were recorded when the sun was just below the horizon, during civil twilight (see

Table 1 (a) Number of passerines tracked by radar in different light conditions at Abisko, northern Sweden. Night did not occur during the study periods, and nautical and astronomical twilight did not occur during the spring study periods (Edwards 2010). (b) Number of passerines tracked during different clock hour intervals (*N* tracks), total time the radar has been operated during different clock hour intervals (sampling time, h), number of occasions the radar has been operated during that clock hour interval (*N* of samples) and the mean number of tracks per hour (Mean track/h) with standard error (SE given for sample sizes >4)

	Observation dates	Daylight	Civil twilight	Nautical twilight	Astronomical twilight	Night	Sum
(a)							
Autumn	3/8–13/8 2007 3/8–4/9 2008	1	268	437	32	NA	738
Spring	10/5–8/6 2007 16/5–7/6 2008	719	35	NA	NA	NA	754

Clock hour	Autumn					Spring				
	N tracks	Sampling time (h)	*N* of samples	Mean track/h	SE	*N* tracks	Sampling time (h)	*N* of samples	Mean track/h	SE
(b)										
20–21	–	0	0	–	–	1	1.5	2	0.5	–
21–22	1	2	3	0.3	–	13	7.5	9	1.4	0.6
22–23	63	21	22	3	0.8	66	26.0	30	2.3	0.5
23–0	144	28.5	31	4.8	0.9	158	31.5	33	4.9	0.9
0–1	189	29.5	30	6.3	1.0	167	25.5	27	6.1	1.3
1–2	205	27	29	7.8	1.2	141	23.0	23	6.1	1.3
2–3	126	16.5	20	7.9	1.2	126	15.5	18	8.7	1.8
3–4	10	1	1	8	–	44	5.5	7	7.0	2.6
4–5	–	0	0	–	–	14	2.0	2	6.0	–
5–6	–	0	0	–	–	8	2.0	2	4.0	–
Daytime	0	3	5	0	–	16	11.5	14	1.1	0.4

Sample times were rounded off to nearest half hour. Times refer to local summer time (GMT + 2 h), where absolute midnight, when the sun is at its lowest elevation, occurred at 00:42:30 ± 1.5 min during the spring sampling period and at 00:47:30 ± 3.5 min during the autumn sampling period

Table 1). Tracks from the autumn were mainly from nautical twilight and civil twilight conditions (Table 1). Night did not occur during the sampling period. The time distributions of tracks indicated a peak of migration intensity during the hours around midnight in both seasons, although the lack of coverage in the late night makes it difficult to say for sure when the intensity decreases in autumn (Fig. 2; Table 1). In both spring and autumn, the number of tracked passerines increased in the late evening and reached a maximum some time after midnight (Table 1; Fig. 2). Our coverage during the late night/early morning is poor, especially in autumn, but in spring, the numbers seemed to gradually decrease and some migrants still remained in the morning (Fig. 2). In spring, we also found a few migrating passerines during daytime (between 0600 and 2000 hours local summer time, GMT + 2), mainly during the morning and before noon, not seen at all during autumn (Table 1). However, the migration intensity during the day was very low, with an average of 1.1 passerines per hour recorded during 11.5 radar hours (several observation periods in favourable weather) during daytime in spring. This intensity was only 13 % of the migration intensity recorded during the migration peak 2–3 h after midnight (Table 1).

The model showed that the number of tracks per hour was significantly related to the time of night ($F_{10,251.5} = 5.2$, $P < 0.001$) but not to season ($F_{1,154.1} = 0.04$, $P = 0.84$.) or the interaction clock hour × season ($F_{7,248.1} = 0.40$, $P = 0.90$). This means that the observed time distributions differed highly significantly from a constant rate of migration throughout the night during both spring and autumn, but our simple model showed no significant difference in either the mean level of intensity or the time distribution of intensity between spring and autumn.

Discussion

Concentration of migration to night hours

Our method does not give a reliable measure of the migration intensity over the entire 24-h period. We have, however, searched for targets at daytime during autumn for

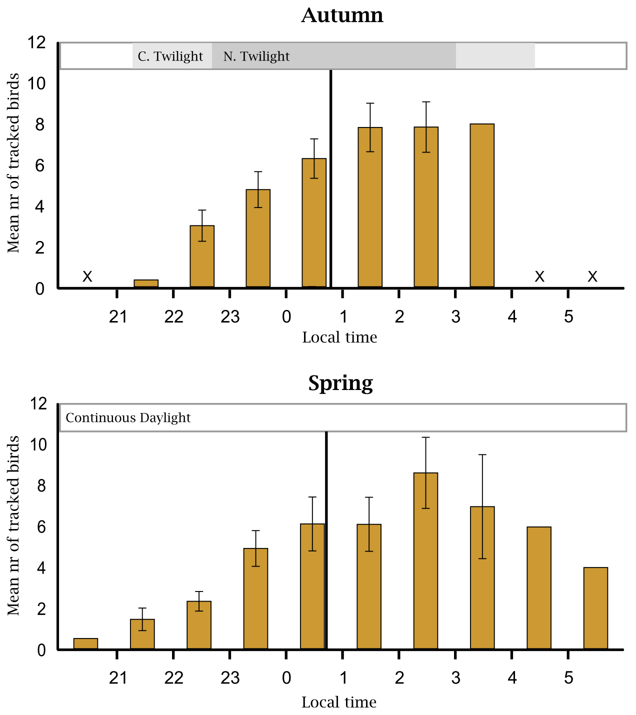

Fig. 2 Mean number of migrating passerines, with ±1 SE in cases were samples >4, tracked per radar operation hour at different clock hours at Abisko, northern Sweden. *X* marks clock hours where there has been no sampling. Time given is local summer time, GMT + 2 h. *Vertical black line* indicates absolute midnight, when the sun is at its lowest elevation, which occurred at 00:42:30 ± 1.5 min during the spring sampling period and at 00:47:30 ± 3.5 min during the autumn sampling period. *Bars* above the graphs show the light conditions on the median date of sampling during the spring and autumn study periods, 2007 and 2008. In spring: 30th May, in Autumn, 20th August. *White*: daylight, *light grey*: civil twilight, *dark grey*: nautical twilight

3 h, divided into five attempts at different times and days without finding a single passerine. In spring, we sampled for 11.5 h during daytime, divided into 14 attempts at different times on six different days, finding only 16 passerines (tracks were recorded during on only two of the observation days). This is very low in comparison with what we see during the night hours (Table 1). We therefore conclude that it is highly unlikely that the migration is evenly distributed during the day and night (as predicted by hypothesis three), but rather that there is a concentration of migration to the night hours (hypothesis one and two; and the mixed GLM analysis demonstrated that the intensity distribution was not uniform during the night). Although our data clearly suggest a generally low level of migration intensity during daytime in spring and autumn, we cannot completely exclude the possibility of peaks during daytime that we have missed because of our short and unsystematic radar sampling attempts during daytime. More extensive and systematic radar monitoring is needed to reveal the detailed characteristics of the distribution of flight intensity during daytime hours under Arctic light conditions.

The pronounced unimodal peaks during night hours in both spring and autumn (Fig. 2) are consistent with observations of willow warblers maintaining their circadian foraging rhythm during breeding periods in Arctic continuous daylight (Brown 1962) as well as their melatonin cycle (Silverin et al. 2009). Speakman et al. (2000) found that insect catches (presumably indicating prey availability for insectivorous migrants) showed a distinct peak during daytime hours, while minimum catches occurred between 2200 and 0600 hours local time at a site not far from Abisko during midsummer. The period of minimum insect catches corresponds to the time periods with high migration intensity in Abisko (Fig. 2), indicating that, at least for insectivorous migrants, the incentive to feed during the day and migrate at night remains even under continuous daylight conditions. This supports the hypothesis that nocturnal migration has evolved to avoid overlap with suitable foraging time among birds with diurnal foraging habits (Brewster 1886; Lank 1989; Alerstam 2009). Our results are also consistent with studies of nocturnal restlessness during migration (zugunruhe). In continuous dim light conditions, redstarts caught during migration still show nocturnal restlessness (Coppack et al. 2008). Also, garden warblers *Sylvia borin* maintain, with some derailment, nocturnal restlessness bouts under continuous dim light conditions (Bartell and Gwinner 2005) as do bramblings (Pohl 2000).

Duration of nocturnal passage of migrants

In both spring and autumn, we find the characteristic pattern of migration increasing a few hours before midnight and peaking a few hours after midnight (Fig. 2). The start and end period of the nights are somewhat uncertain due to low numbers of radar hours during these periods. The duration of the nocturnal migratory passage under continuous daylight in spring was 8–10 h, indicating that it was not further compressed in relation to the period recorded at midlatitudes during late spring (Chernetsov 2012), as stated in hypothesis one. This is surprising and indicates that the successive shortening of the nocturnal flight period does not continue after the birds have migrated north of 50–60°N in spring, or that the flight period reaches a minimum duration when the period of night/twilight is very short, only to expand again when the twilight period gets even shorter and there is a transition to continuous daylight.

During continuous daylight, the sun elevation still changes significantly over the day (Fig. 1) and this also changes the light intensity to some degree (Speakman et al. 2000) as well as the light polarization (Brines and Gould

1982) and the colour of the light (Rozenberg 1966). These cues might be less exact than the distinct twilight transitions. One may speculate that cues associated with the twilight may have helped to capture and synchronize the initiation and termination of migratory flights, thus confining the flight activity to a shorter period than when synchronizing cues are less distinct. Wheatears *Oenanthe oenanthe* setting off on autumn migration from Alaska (65°37′N, when the nights were still rather short, 6–9 h) all departed during the twilight periods when the sun was between 3.5° and 9.5° below the horizon (Schmaljohann et al. 2013). The reason why all birds departed during the first 2 h (29–128 min) after sunset during these relatively short nights may be that it is important for the bird to use most of the (rather few) night hours for flight, allowing a high migration speed for migrants with very distant winter quarters (Schmaljohann et al. 2013).

Another factor influencing the duration of the flights during the night could be that the passerines at Abisko presumably are quite close to their breeding grounds. They might therefore decide to “sprint” the last leg of the journey and fly during longer periods of time each night (Alerstam 2006), considering the importance of arriving in time to the breeding grounds (Kokko 1999).

Light and orientation

It has been suggested that calibration of critical orientation cues during sunset and twilight (e.g. Wiltschko and Wiltschko 1995; Cochran et al. 2004; Muheim et al. 2006) provides another important explanation for the timing of nocturnal flight initiation after sunset (review in Kerlinger and Moore 1989). Still, as demonstrated in this study, the migrants are fit to perform their flights also under Arctic summer conditions when the sun never sets below the horizon. We have previously shown that the directional scatter of the passerine migrants at Abisko is exceptionally large, especially during spring, compared with the typical pattern recorded at lower latitudes (Karlsson et al. 2010). This exaggerated orientation scatter may be associated with the birds shifting from compass to goal orientation when approaching their final destinations as suggested by Karlsson et al. (2010), but one cannot exclude the possibility that it may be due also to increased difficulties for the migrants to maintain high orientation accuracy because of lacking orientation cues associated with sunset, sunrise and night conditions. Even if the sun sets below the horizon when the birds start their autumn migration from Abisko, they fly under twilight conditions that may still prevent the birds from efficiently seeing stellar cues. This would mean that many yearling birds may start their southward migration before star patterns become available as an orientation cue.

Conclusions

These results show that there are interesting dynamic changes in the timing of migratory flights of nocturnal migrants as the birds travel northwards in spring, during nights that become gradually shorter with the seasonal and northerly advancement. Initially, the birds will respond by departing successively earlier in relation to sunset (Bolshakov and Rezvyi 1998; Bolshakov et al. 2007; Chernetsov 2012), but this is not sufficient to compensate for the shortening of the nights, leading to successively shorter nocturnal flight periods (Chernetsov 2012). We put forward the hypothesis that at some point nights will become so short and light that the migrants will become released from the confinement to fly only under twilight conditions, and the flight period will broaden as indicated for the passerine migrants arriving at Abisko in spring under conditions of continuous daylight north of the Arctic Circle. The period when the passerine migrants depart southwards from Abisko on autumn migration does not occur until after the period of midnight sun has ended. At that time, the birds’ nocturnal flight rhythm may be captured and confined to the period when the sun is below the horizon. Hence, the autumn flight periods may be initially short and lasting only a few twilight hours (although the birds will probably depart shortly after sunset to exploit as much as possible of the twilight time for flight; cf. Schmaljohann et al. 2013). Dynamic changes of the circadian rhythm of nocturnal restlessness under rapidly changing light regimes may be facilitated by reduced amplitude in the melatonin rhythm during the birds’ migratory seasons (Gwinner and Helm 2003). The circadian behaviour may also be adaptively modified in different ways under continuous daylight depending on species and ecological conditions (Steiger et al. 2013).

We wish to stress that the detailed characteristics of the temporal flight patterns of nocturnal passerine migrants under Arctic light conditions remain to be documented by systematic measurements. Still, our provisional study, based on extensive radar monitoring and sample sizes of radar tracks, constitutes a first step towards exploring this interesting subject. It will be a challenging and exciting task to investigate further the dynamics of timing of nocturnal migratory flights by recording the daily flight behaviour of individual migrants under shifting day length conditions as they arrive at and depart from breeding sites north of the Arctic Circle. This will provide crucial information for understanding the importance of visual and celestial cues in the regulation of flight timing and orientation of the birds.

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