Reed warbler orientation: initiation of nocturnal migratory flights in relation to visibility of celestial cues at dusk

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We used radiotelemetry to investigate the time of migratory flight initiation relative to available celestial orientation cues and departure direction of a nocturnal passerine migrant, the reed warbler, *Acrocephalus scirpaceus*, during autumn migration. The study was carried out at Falsterbo, a coastal site in southwest Sweden. The warblers initiated migration from times well after local sunset and well into the night, corresponding to sun elevations between $-4°$ and $-35°$, coinciding with the occurrence of stars at night. They departed in the expected migratory direction towards south of southwest with a few initiating migration in reverse directions towards northeast to east. Flight directions under overcast conditions (7–8/8) were more scattered than under clear sky conditions (0–4/8). There were fewer clouds on departure nights than on nights when the birds did not initiate migration. For birds staying longer than one night at stopover the horizontal visibility was higher and precipitation was less likely on departure nights than on the previous night. The results show that the visibility of celestial cues, and stars in particular, are important for the decision to initiate migration in reed warblers. However, cloud cover, horizontal visibility and precipitation might be correlated with other weather variables (i.e. wind or air pressure) that are also likely to be important for the decision to migrate.

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Nocturnal migration is common among passerine migrants (Alerstam 1990; Martin 1990), which then have access to a number of cues for orientation based on the geomagnetic field, the stars, the position of the sun at sunset and the related pattern of skylight polarization (for reviews see for example, Emlen 1975; Able 1980; Moore 1987a; Baker 1984; Wiltschko & Wiltschko 1991, 1995). The migrants probably make use of multiple cues to select a flight direction (e.g. Vleugel 1954; Emlen 1975, 1980; Emlen & Demong 1978). Maximum simultaneous access of celestial and geomagnetic cues are available during the transition period between day and night at twilight and this period should therefore be important for selecting a migratory course (e.g. Emlen 1975; Moore 1980, 1987a; Able 1982, 1989; Helbig & Wiltschko 1989; Helbig 1991; Sandberg 1991; Åkesson & Bäckman 1999). It may provide a good opportunity for the birds to calibrate their magnetic and celestial compasses before departure, based on the sunset direction, the skylight polarization pattern and the stars at night (Able & Able 1990, 1993, 1995; Phillips & Moore 1992).

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The main flight departure period of passerine nocturnal migration occurs during the evening twilight period and shortly thereafter, with the peak intensity reported to occur 1–4 h after local sunset (for references see Moore 1987a; Åkesson et al. 1996a). However, radiotelemetry and visual observations have shown that individual nocturnal migrants may depart much later than that, well into the night (Cochran et al. 1967; Åkesson et al. 1996a; Bolshakov & Bulyuk 1999). Nocturnal migratory flight initiation relative to the availability of sunset cues (i.e. sun elevation) also varies between species, latitudes and times of year (Åkesson et al. 1996a). The length of the twilight period varies with latitude and time of year; however, the sun elevation, measured in degrees above or below the horizon, corresponds to a given visual celestial aspect independently of latitude, season and time relative to sunset (cf. Åkesson et al. 1996a).

The difference in preferred time of migratory departure (cf. Åkesson et al. 1996a) might be explained by the availability of different celestial orientation cues preferred by the birds on migration. Studies of the natural flight departure pattern at dusk may indicate if this is important to birds and, if so, what specific cue is used. Different departure patterns might be expected: (1) if a specific set of celestial orientation cues were not important the birds would depart any time; (2) if the sun were sufficient to

determine the migratory direction, the birds would leave when the sun's light is still visible and the stars are not yet bright (sun elevations above − 4°); (3) if a multiple set of celestial cues, that is, the sun's position, pattern of sky-light polarization and stars, were needed for orientation then the preferred time to depart would be when both the sun's light and the stars are visible (sun elevations between − 4° and − 12°); and (4) if the stars were the most important orientation cue then the birds would choose the time when the stars are maximally visible and the sun's light has completely disappeared (sun elevations lower than − 12°).

There are, however, other factors that might influence the timing of migration that are not directly related to the availability of orientation cues. Weather conditions are particularly important for the decision to initiate migration (for reviews see Richardson 1978, 1990, 1991). Other factors that may account for nocturnal migration are, for example, the diurnal variation in the structure of the atmosphere, which influences wind conditions, mainly leading to reduced turbulence at night (Kerlinger & Moore 1989); improved atmospheric conditions for the detection of sound signals from the ground or from migrating conspecifics (Evans 1985); and the reduced likelihood of predation (Evans 1985). Birds can also maximize foraging time in daylight by migrating at night, and thereby maximize the speed of migration (cf. Alerstam & Lindström 1990). All these alternative explanations supporting nocturnal migration would result in expected migratory flight departures shortly after sunset. We investigated whether individual nocturnal passerine migrants depart on nocturnal migration during a limited period shortly after sunset or if they, for example, wait until stars become available for orientation.

We investigated the natural migratory flight initiation of autumn-migrating reed warblers, Acrocephalus scirpaceus, at Falsterbo in southwest Sweden. We used radio-telemetry to track the birds' movements at a coastal stopover site prior to departure and to record the time and direction of migration at night. The selected times of departure were then analysed with respect to the elevation of the sun at departure and the associated availability of orientation cues in the twilight sky. As the position of the moon affects the orientation of nocturnal passerine migrants (Moore 1980, 1987b; Marchietti & Baldachini 1997), we also investigated whether the moon had any influence on the birds' selection of migratory directions at departure. In addition, we investigated whether any of the weather conditions related to visibility of celestial orientation cues, that is, cloud cover, horizontal visibility and precipitation, had any effect on the decision to migrate.

METHODS

Experimental Birds and Radiotelemetry

The reed warbler is a nocturnal passerine migrant wintering in tropical West Africa (Moreau 1972; Zink 1973; Roos 1984). Each autumn on average 2000 reed warblers are captured at Falsterbo Bird Observatory. According to

the ringing recoveries they migrate in directions approximately between south and southwest (cf. Roos 1984; Åkesson et al. 1996b), with some performing temporary reverse migration opposite to the expected migratory direction (Åkesson et al. 1996b).

The reed warblers were captured with mist nets in a coastal reedbed area, Flommen (12 ha), located at the southwesternmost part of the Falsterbo peninsula in southwest Sweden (55°23′N, 12°50′E; Falsterbo Bird Observatory). The birds were captured in the early morning hours within the autumn migration period (mid-August to end of September) in 1995–1998 (for exact dates see Appendix). At capture the birds were ringed and aged according to Karlsson et al. (1988) and Svensson (1992). All but two experiental birds were in their first calendar year. The amount of visible subcutaneous fat was estimated according to a 10-point scale for visual fat classification (cf. Pettersson & Hasselquist 1985, extended with 3 points at Falsterbo Bird Observatory). To increase the probability of immediate migratory departure we selected only large birds with fat levels 5 or higher for radiotelemetry. The mass of the birds at capture was recorded to the nearest 0.1 g with a 50-g Pesola spring-balance.

We used small radiotransmitters (0.67 g; BD-2B, Holohil Systems Ltd, Woodlawn, Ontario, Canada) glued with permanent adhesive on the bird's back to track the movements and the time of migratory flight departure for individual reed warblers. Before gluing, we cut the feathers to within 5 mm of their base to a small (10 × 15 mm) area on the back of the bird. The transmitter and glue were applied to these feather stubs, and surrounding feathers covered the transmitter while attached. The transmitter would be shed at the latest at the next moult in the winter quarters. The mean mass of the radiotransmitters was 4.6% (range 3.9–5.4%) of the birds' own mass. Permission to use radiotelemetry to track passerine migrants was given by the regional Ethical Committee for Animal Experiments in Lund/Malmö, the Ministry of Agriculture and the Swedish Environmental Protection Agency.

The birds were released in the area of capture immediately after the radiotransmitters were mounted (after less than 1 h in captivity). We located the birds on several occasions during the day in the reedbed area, by using hand-held receivers allowing the signals from a transmitter to be located anywhere in the reeds. Nearly all birds were stationary during stopover and moved within a restricted area of the reedbed. Therefore it was easy to relocate the birds in the reedbed if present. From well before sunset we continuously tracked the birds' movements until they departed or at least 4 h (1995) or 8 h (1996–1998) after local sunset. By applying this method we recorded the exact times of departure for 29 individuals and for 27 of these birds also the direction of departure. To estimate the direction of departure, we slowly moved the antenna receiving the signal horizontally in circles such that the direction from which the strongest signal was received could be identified. A hand-held compass with a luminous display was then used to record the departure direction. The birds were tracked up

to ca. 40 min after departing ($\bar{X} \pm SD=16.8 \pm 10.6$ min, $N=27$), which corresponds to a flight distance up to 20–25 km, calculated for a flight speed of 10 m/s following a straight course in the particular wind condition at departure. For an additional six individuals we could record only the approximate time of leaving the stopover area. We noted the time and date of departure of seven reed warblers in 1995, eight in 1996, 17 in 1997 and three in 1998 (Appendix). In addition to these, three birds presumably lost their radiotransmitters before migration (i.e. the transmitters were short-circuited and changed signal abruptly, sending constantly from the same position in the reeds for the rest of the battery lifetime but during a shorter period than other transmitters) and therefore could not be tracked until migratory departure.

Position of Sun and Moon at Departure

We used a calculator for astronomical data for the sun and the moon (Trimble GPS) to calculate their positions at the times of departure. Different parts of the complete dusk period are defined according to the sun's elevation below the horizon. The Civil Twilight Period starts at sunset (sun elevation 0°) and ends when the upper edge of the sun is − 6° below the horizon (Rozenberg 1966). The Nautical and Astronomical Twilight periods end at sun elevations of − 12° and − 18°, respectively. On the basis of the elevation of the sun above (or below) the horizon one can estimate the availability of celestial cues for orientation (cf. Rozenberg 1966; see also Åkesson et al. 1996a), although this is, of course, highly dependent on cloud cover and visibility, which might vary considerably between days.

Incoming light from the sky is polarized and skylight polarization forms a regular pattern relative to the position of the sun. A band of maximum polarization aligned 90° away from the sun forms a broad ring around the Earth, orthogonally oriented to the direction of the sun. The transmission axis of polarization (E-vector) and the band of maximum polarization are vertically aligned in relation to the sun at sunrise and sunset (Lythgoe 1979; Brines 1980; Brines & Gould 1982; Figure 1 in Wehner 1989). The incoming light at zenith attains its maximum degree of polarization at sun elevations between − 2° and − 4° (70–80% polarization in clear sky conditions; Rozenberg 1966). The sun could be used for orientation both during the day and during the twilight period. The position of the sun during the Nautical Twilight sky as detected by a bright multicoloured horizon glow is visible to the birds until the end of the Nautical Twilight Period (sun elevation − 12°), whereafter the night sky is evenly coloured across the horizon and only stars are visible for orientation. The first stars become visible to a human observer from the end of the Civil Twilight Period, and at the end of the Nautical Twilight Period several hundred are visible. Based on these estimations we compared the time of flight departure of individual birds with the availability of the different celestial cues at twilight.

Data Reduction and Statistics

We calculated the mean orientation at departure according to standard circular statistical procedures given in Batschelet (1981). For the circular distribution, mean angle of orientation (α) is indicated by the arrow and the length of the arrow is a measure of the scatter of the circular distribution (r ranges between 0 and 1, being inversely related to the angular scatter). We applied the Rayleigh test to analyse if the circular distribution differed significantly from a random distribution (Batschelet 1981). The Watson U^2 test was used to test the difference in mean orientation between groups of birds departing under clear and overcast skies (Batschelet 1981).

We used circular correlation to analyse whether the mean orientation was correlated with the direction of the azimuth position of the moon at departure (Batschelet 1981). We excluded birds departing under total or partly overcast skies (7–8/8) as well as departures for which the moon was below 0° elevation.

To analyse the effect of weather variables related to visibility (i.e. cloud cover, horizontal visibility and precipitation) on departure we used information collected every third hour (Swedish Normal Time, Coordinated Universal Time +1 h: 1900, 2200, 0100 and 0400 hours) at the weather station at Falsterbo (located ca. 1 km south of the study area). We used information on the cloud cover (0/8: no clouds; 8/8: completely overcast), the estimated horizontal visibility (km) and the occurrence of precipitation from the weather observation closest in time (< ± 1 h 30 min) to flight departure for each bird. We compared the weather conditions at departure with those on the night prior to departure (at 2200 hours) and, for the departure night, the weather before and after the time of departure. For these analyses only birds that had stayed in the stopover area more than 1 day were included, since they could initiate migration on more than 1 night. Finally, the overall cloud cover and visibility during nights when one or several birds departed were compared with those conditions during nights (2200 hours) when no birds departed but stayed in the stopover areas. Differences between groups were compared with one-tailed Wilcoxon signed-ranks tests, Mann–Whitney U tests, McNemar chi-square tests (Statsoft Inc. 1998) or chi-square and median tests (Siegel & Castellan 1988).

RESULTS

We tracked reed warblers with radiotransmitters at stopover until they departed between 0 (i.e. the birds departed the same day as they were released with radiotransmitters) and 6 days after release (Appendix). The overall mean departure direction for birds departing under clear as well as overcast skies was 195°, which is slightly south of southwest (Rayleigh test: $r=0.57$, $N=27$, $P<0.001$; Fig. 1). However, a few departed in reverse directions opposite to the expected migratory direction. When released, the overall mean fat class of the birds ± SD was 7.3 ± 0.8 (range 5–9, $N=35$) and the mean mass ± SD was 14.5 ± 1.2 g (range 12.3–17.0 g, $N=35$). To increase the probability that the birds departed immediately on

(a)

(b)

$N = 21$
$\alpha = 194°$
$r = 0.76$
$P < 0.001$

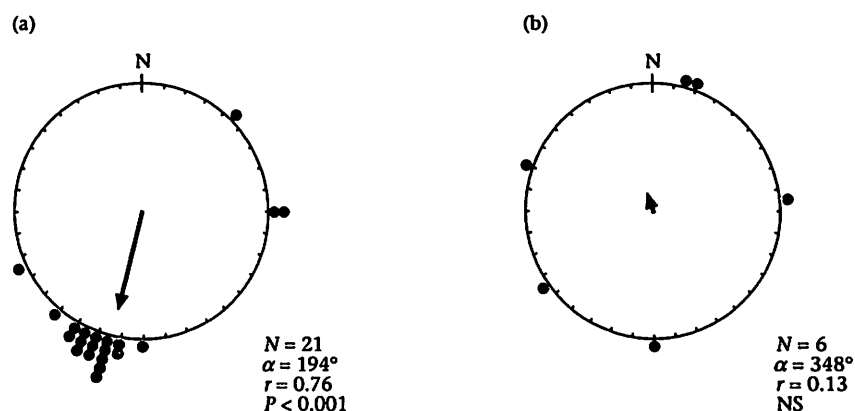$N = 6$
$\alpha = 348°$
$r = 0.13$
NS

Figure 1. Direction of flight departure of migrating reed warblers tracked by radiotelemetry at Falsterbo in autumn under (a) clear skies (0–6/8) and (b) overcast and partly overcast conditions (7–8/8). Mean angles of orientation (α) are indicated by the arrows and the length of the arrow is a measure of the scatter of the circular distribution (r ranges between 0 and 1, being inversely related to the angular scatter). •: Direction of departure of individually tracked birds. The significance level is given according to the Rayleigh test (Batschelet 1981).

migration, we applied the radiotransmitters to large individuals with high body mass and fat score. We found no correlation between fat score at release and the number of days the birds stayed in the stopover area (Spearman rank correlation: $r_s=0.10$, $N=35$, NS). There was no significant difference in number of days spent at the stopover area between birds departing under overcast conditions (7–8/8; median 0.5, $N=8$) and those departing under clear sky conditions (0/8, $N=21$; known departures, Kruskal–Wallis test: $H_1=0.33$, NS). During the stopover period the birds did not engage in local movements away from the reedbed, but appeared to stay nearby. Thus, they seemed to be prepared to depart on migration when released, that is, they had reached the departure time window for migration (cf. Weber et al. 1998), and could be expected to depart on the first night favourable for migration that they experience.

Flight Initiation in relation to Sun Altitude

The reed warblers initiated migration from well after sunset and into the night. Median time of departure after local sunset (for all birds) was 128 min (range 32–634 min, $N=29$; Appendix and Fig. 2). We found no significant difference in median time of departure between clear skies (128 min, $N=21$) and overcast conditions (122 min, $N=8$; median test: $\chi_1^2=0.24$, NS). There was no difference in median time of departure between birds initiating migration the same day as they were released (median 121.5 min, $N=16$) and birds departing the second day at stopover or later (130 min, $N=13$; median test: $\chi_1^2=0.78$, NS). The median sun elevation at departure for birds initiating migration during the first half of the night (i.e. before the sun had reached its lowest elevation for the night) was $-15.0°$ (range $-4°--32°$, $N=24$; Fig. 3). Five birds departed much later than that (408 min after local sunset, corresponding to a median sun elevation of $-31.0°$). In addition to these five birds, another six departed from the area 230–600 min after local sunset, and were not tracked at departure (four left

under overcast conditions and two under clear skies; Appendix). Significantly more birds departed after the Nautical Twilight Period (sun elevations below $-12°$), at a time when mainly compass information from stars remained for celestial orientation (chi-square test: $\chi_1^2=5.0$, $P=0.025$) compared to the Nautical Twilight Period and before, when visual information from the sun and the skylight polarization pattern were simultaneously available (cf. Åkesson et al. 1996a). No birds departed earlier than a sun elevation of $-4°$, which roughly corresponds to the time when the first stars become available for orientation.

Departure in relation to Celestial Cue Visibility

The mean orientation of birds was significantly more scattered under overcast skies (cloud cover: 7–8/8) than under clear skies (0–4/8; Watson U^2-test: $U^2=0.27$, $P<0.01$; Batschelet 1981; Fig. 1).

There was significantly less cloud cover on departure nights (median 2/8, $N=29$) than on nights with no departures (7/8, $N=23$; Mann–Whitney test: $Z=2.04$, $P=0.035$). However, there was no difference in horizontal
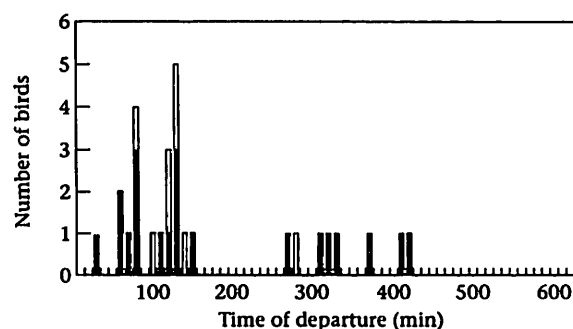

Figure 2. Numbers of reed warblers initiating nocturnal migratory flights at Falsterbo in autumn in relation to time after local sunset (0 min). □: Birds departing under overcast conditions (cloud cover: 7–8/8); ■: departures under clear skies.
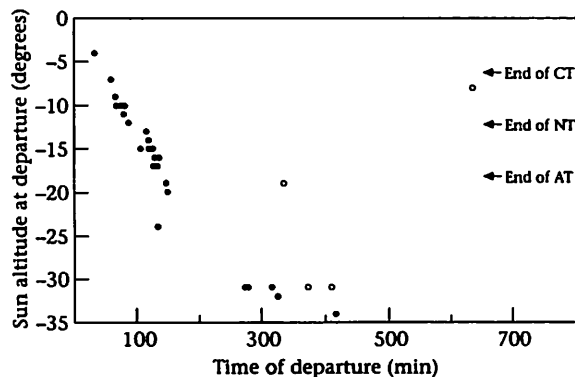
Figure 3. Sun elevation and time of departure of radiotracked reed warblers initiating nocturnal migratory flights at Falsterbo in autumn. Arrows indicate the sun elevation at the end of Civil (CT), Nautical (NT) and Astronomical (AT) Twilight. At sunset the sun elevation is 0°. For further information on availability of celestial cues at twilight see text. o: Sun elevations for birds that departed after the sun had passed the lowest elevation of the night, at times when the sun elevation was increasing.

visibility between the groups (departure: median 25.0 km, $N=29$; stopover: 20.0 km, $N=23$; $Z=-1.75$, NS). Furthermore, for birds that had stayed for more than 1 day, the cloud cover at departure (median 1/8, $N=18$) was significantly lower than on the previous night (2200 hours; 7/8, $N=18$; Wilcoxon signed-ranks test: $Z=1.99$, $P<0.05$). The estimated horizontal visibility was significantly higher on departure nights (median 27.5, $N=29$) than on nights prior to migration (14.0, $N=23$; Wilcoxon signed-ranks test: $Z=2.44$, $P=0.014$). There was also significantly less precipitation on departure nights than on the previous night (McNemar chi-square test: χ_1^2 (A/D)=5.5, $P<0.02$; χ_1^2 (B/C)=8.64, $P<0.01$).

On the night of departure (known departures) the degree of cloud cover was significantly less at departure (median 2 ± 0.5, $N=29$) than 3 h prior to departure (2; Wilcoxon signed-ranks test: $Z=2.03$, $P<0.05$). However, the differences in horizontal visibility between the two time periods were not significant (3 h before departure: median 35.0 km; departure: 30.0 km, $N=29$ for both; Wilcoxon signed-ranks test: $Z=0.02$, NS). The degree of cloud cover and horizontal visibility did not improve between the time of departure and 3 h after departure (cloud cover: median 1/8; horizontal visibility: 30 km, $N=29$ for both; Wilcoxon signed-ranks test: $Z=0.71$ and $Z=1.23$, respectively, $N=29$, NS for both cases).

For reed warblers departing when the moon was visible above the horizon (cloud cover 0–4/8) we found no correlation between the moon azimuth and the direction of departure (circular correlation: $r=0.24$, $N=9$, NS; Batschelet 1981).

DISCUSSION

Flight Initiation and Celestial Cues

The reed warblers initiated nocturnal migratory flights well after sunset, from the end of the Nautical Twilight

Period and well into the night. The time of departures varied considerably from 30 min to more than 10 h after local sunset, and the first departures corresponded well with the time when stars become visible at night. Why do individual reed warblers initiate migratory flights much later than the end of the Civil Twilight Period? Alternative explanations for starting at night involve, for example, avoidance of predation, improved conditions for sound detection important for orientation (e.g. Evans 1985), time-minimized migration by diurnal feeding and migration at night (Alerstam & Lindström 1990) or avoidance of turbulent wind conditions (Kerlinger & Moore 1989). In our study, more than half of the reed warblers (57%) initiated migration between 30 and 150 min after sunset, while the rest (43%) departed at least 3–4 h after sunset, leaving comparatively little time for flight at night. This is supported by Ellegren (1993) who, based on a ringing recovery analysis, reported that the nocturnal flight period for nocturnal passerine migrants lasted less than half the dark period available. Therefore, we find it unlikely that the characteristics of the air structure at night alone (cf. Kerlinger & Moore 1989), or any of the other factors given above, could explain the timing of departure for those birds initiating migration later than 3 h after sunset.

Radiotelemetry and visual observations show considerable variation in departure times between individuals. Peak departure times occurred after the end of the Civil Twilight Period, that is, later than observed in radar studies (Cochran et al. 1967; Hebrard 1971; Åkesson et al. 1996a; Bolshakov & Bulyuk 1999). In contrast to this pattern, a Swainson's thrush, *Catharus ustulata*, that was tracked by radiotelemetry for 7 consecutive nights on migration departed within a relatively limited period (mean 11 min) after civil end of twilight each night (Cochran 1987), indicating that individual migrants might be precise and conservative in selecting the departure time. Since, we could track the departure of each bird only once in this study we do not know if some individuals prefer to depart at a constant time relative to sunset each night. However, our data indicate that reed warblers seem to wait for the most favourable orientation and/or flight conditions before departure independently of the remaining time available for nocturnal migration. Why do we observe this pattern of late departure times in reed warblers? In contrast to our study, the radiotracked Swainson's thrush in North America migrated mainly over land during the spring migration period (Cochran 1987). One explanation might be that birds departing on oversea flights might select favourable weather and wind conditions at departure more than when migrating over land (e.g. Åkesson & Hedenström 2000; S. Åkesson, G. Walinder, L. Karlsson & S. Ehnbom, unpublished data; but see also Fransson 1998), resulting in relatively late departure times. Another explanation may be that spring migrants are in more of a hurry compared to birds migrating in autumn (see below).

Orientation and Celestial Cues

We observed reduced cloud cover at departure both prior to migration on the same night and on nights when

Table 1. Numbers and percentages (in parentheses) of bird species initiating migration during different parts of the twilight period after dusk

| Migratory category | Species | Departure time period | | | | References |
		CT	NT	AT	Later‡	
Long distance	Reed warbler, *Acrocephalus scirpaceus*	1 (5.6)	8 (44.4)	9 (50.0)	10	This study
Long distance	Thrush nightingale, *Luscinia luscinia*	0 (0.0)	2 (100.0)	0 (0.0)	1	Åkesson et al. 1996a
Long distance	Tanagers, *Piranga* sp., Buntings, *Passerina* sp. etc.*	0 (0.0)	7 (25.9)	20 (74.1)	46	Hebrard 1971
Medium distance	Robin, *Erithacus rubecula*	0 (0.0)	32 (38.6)	51 (61.4)	51	Bolshakov & Bulyuk 1999
Short- to medium distance	*Turdus* thrushes†	19 (54.0)	16 (46.0)	0 (0.0)	1	Åkesson et al. 1996a
Medium distance	*Catharus* thrushes	2 (13.3)	11 (73.3)	2 (13.3)	8	Cochran et al. 1967, Cochran 1987

CT: Civil Twilight; NT: Nautical Twilight; AT: Astronomical Twilight; Later: departures after the end of the Astronomical Twilight period. The different species were classified into different categories of migrants, depending on estimated migratory distance. Included are only individual migrants for which the flight departure times are known.
*Departure data given for 20 April and 4 May 1968.
†Birds departing earlier than the local sunset are not included (*N*=7).
‡Birds not included in CT, NT and AT.

birds did not migrate but stayed in the stopover areas compared with nights of departure. Furthermore, the horizontal visibility was higher at departure than on the previous night for birds having a choice to migrate on either of two nights. Migratory flight directions were more scattered under overcast than clear sky conditions, supporting the importance of visual cues for flight departure and, presumably, also for correct migratory orientation. Thus, reed warblers seem to prefer to initiate migration when the cloud cover is decreasing, the horizontal visibility is improving and when there is no precipitation, that is, in weather conditions when they had access to celestial orientation cues at departure. No influence of the moon, when visible, was observed on the birds' orientation at departure.

If migratory flight initiation at night is related to the visibility of a specific set of celestial orientation cues (cf. Åkesson et al. 1996a), then migrants should depart under clear sky conditions at times when those cues are available, while birds departing under total overcast conditions should initiate migration at any time of the night. Indeed, some reed warblers in this study departed under nearly or completely overcast conditions, but the median departure time for those birds did not differ significantly from birds initiating migration under clear sky conditions. Hence, we found no support for Cochran et al.'s (1967) finding that passerines departing under overcast did so at more variable times and later at night than with clear skies.

Influence of Weather on Departure

On a larger scale, migratory intensity is highly influenced by passage of synoptic weather patterns and in particular by the wind (Richardson 1978, 1990, 1991; Alerstam 1979). Despite this general pattern, two studies have reported no or small effects of weather factors on the timing of migration for nocturnal passerine migrants (Gauthreaux 1971; Hebrard 1971), perhaps because they were done during spring migration when migrants are likely to be under time pressure to reach the migration goal (time-minimized migration, cf. Alerstam & Lindström 1990). Fransson (1998) reported little influence of weather on departures from a coastal stopover site in autumn. Taken together, these results are surprising, since optimal migration theory predicts that birds should be sensitive to wind conditions (Liechti & Bruderer 1998; Weber et al. 1998). Thereby they will increase the flight distance covered by a given amount of fuel. In some other nocturnal passerine migrants, the birds seem to depart on migration in tailwind conditions (Åkesson & Hedenström 2000). The effect of wind on the migratory orientation of our radiotracked reed warblers supports these findings (S. Åkesson, G. Walinder, L. Karlsson & S. Ehnbom, unpublished data).

Species Differences in Departure Times?

The time of migratory flight initiation seems to vary between individual passerine migrants as well as between species, and perhaps also between latitudes and different times of year (Åkesson et al. 1996a, and references therein, Table 1). This finding was further supported by our large data set for a single passerine long-distance migrant. Taken together, flight departure data from identified passerine migrants show that short- and medium-distance migrants seem to initiate migration relatively earlier than long-distance migrants during the twilight period after dusk (i.e. long-distance migrants versus *Turdus* thrushes; Table 1). This indicates that there might be differences in preferred departure times between species, which might be explained by the migratory distance. Why do we see this pattern of delayed departures in long-distance migrants? It is possible that the late preferred flight departure time is species-specific and related to the migratory strategy and the availability of a specific set of orientation cues, namely stars at night (cf. Helbig 1990; Able 1993; Åkesson 1994; Åkesson et al. 1996a). Our data strongly support the importance of overall visibility (i.e. decreasing cloud cover, increasing horizontal visibility) for migratory flight departure, indicating the importance of celestial orientation cues during migratory flights (cf. Alerstam & Pettersson 1991; Alerstam & Gudmundsson 1999). The possibility that different bird species are adapted to migrate at different times of the night needs to be investigated further.

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Appendix

Table A1. Flight direction and time of departure (Swedish Normal Time: Coordinated Universal Time+1 h) in relation to the elevations and azimuths of the sun and cloud cover (0–8/8) at departure for nocturnally migrating reed warblers caught at Falsterbo Bird Observatory and tracked by radiotelemetry in autumn 1995–1998

No.	Date	Time of sunset (hours)	Time of departure (hours)	Direction (°)	Cloud cover	Sun elevation (°)	Sun azimuth (°)
BH75919	17 Aug 1996	1938	0111	210	1	−19	16
BH75944	18 Aug 1996	1936	2128	210	1	−13	319
BH76515	27 Aug 1996	1914	2110	180	7	−14	314
BH76676	1 Sept 1996	1901	2059	205	1	−15	311
BK87320	3 Sept 1997	1857	2107	195	1	−16	313
BK00554	5 Sept 1996	1851	1948	195	3	−7	294
BH67074	10 Sept 1995	1840	2245–0530	—	8	−27–0	338–80
BH67088	11 Sept 1995	1838	2017	290	8	−15	300
BK00649	11 Sept 1996	1836	2330–0700	—	1	−29–11	350–99
BH67409	12 Sept 1995	1835	2043	220	2	−17	307
BK87481	12 Sept 1997	1834	2030	85	7	−15	303
BH67489	15 Sept 1995	1827	2220–0530	—	1	−28−−1	330–82
BK00911	15 Sept 1996	1825	1940	205	2	−10	292
BK00943	15 Sept 1996	1825	1940	—	2	−10	292
BK87485	15 Sept 1997	1826	2340	15	7	−31	353
BK87496	15 Sept 1997	1825	2033	—	1	−16	304
BK87487	17 Sept 1997	1821	2132	90	1	−24	317
BN11554	17 Sept 1998	1821	1930	200	2	−10	290
BK87504	18 Sept 1997	1818	0029	90	1	−31	8
BN11503	18 Sept 1998	1819	0104	20	7	−31	346
BN11539	18 Sept 1998	1819	2255	190	1	−31	18
BH67817	19 Sept 1995	1817	2041	235	8	−19	306
BH67803	20 Sept 1995	1814	2400–0600	—	7	−32–1	0–89
BH67801	20 Sept 1995	1814	2345–0600	—	7	−33–1	355–89
BK87517	19 Sept 1997	1816	2340	45	1	−32	354
BK87522	19 Sept 1997	1816	1920	195	1	−9	287
BK87521	20 Sept 1997	1816	0450	190	1	−8	74
BK87529	20 Sept 1997	1813	1845	195	2	−4	280
BK87543	20 Sept 1997	1813	1930	200	2	−11	289
BK87534	20 Sept 1997	1813	1938	205	2	−12	290
BK87570	24 Sept 1997	1803	2010	180	1	−17	297
BK87568	24 Sept 1997	1803	2235	245	1	−31	334
BK87594	26 Sept 1997	1757	0200–0600	—	7	−35–13	358–81
BK87607	27 Sept 1997	1755	2021	195	1	−20	299
BK87577	27 Sept 1997	1755	0050	200	4	−34	16

For six birds departing late at night and not tracked at departure, the time limits between which the birds have disappeared from the area are given. For those time limits the elevation and azimuth of the sun are given.