Flight Initiation of Nocturnal Passerine Migrants in Relation to Celestial Orientation Conditions at Twilight

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The time of departure of nocturnal passerine migrants was studied by radiotelemetry and tracking radar in South Sweden in spring and autumn. Our objective was to analyse the time of flight initiation in relation to celestial orientation cues during the twilight period at dusk. The telemetry and radar results were compared with data on nocturnal flight departures reported in the literature. There was a considerable variation in time of flight initiation throughout the twilight period. A large fraction of the birds (mostly thrushes) departed mainly during the civil and nautical twilight periods, with a sun elevation between 0° and −12°, while several migrants did not leave until much later in the night. This variation in time of departures speaks against the hypothesis that departure time is connected with a critical skylight situation with respect to the visual accessibility of celestial orientation cues. Characteristic times of departure, as reflected by the associated elevations of the sun below the horizon, seem to differ between different passerine species, latitudes and times of migratory season.

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Nocturnal passerine migrants rely on both celestial and geomagnetic information for orientation (for reviews see, for example, Emlen 1975, Able 1980, Moore 1987, Wiltschko and Wiltschko 1988, 1991). The twilight period at dusk embraces the transition between daylight and darkness, when celestial cues related to the sun (sunset position and horizon glow, skylight polarisation pattern) are clearly visible and when, at the same time, the starry night sky is gradually emerging. Nocturnal passerine migrants probably make use of multiple cues to select a flight direction (e.g. Vleugel 1954, Emlen 1975, 1980, Emlen and Demong 1978), and it has been suggested that orientation information during twilight is of great importance (Emlen 1975, Moore 1987, Helbig 1991). The twilight period may provide a good opportunity for calibration of the birds' magnetic and celestial compasses, based on the sunset direction, skylight polarisation pattern and stars (Able and Able 1990, 1993, 1995, Phillips and Moore 1992). The quiescence period, during which nocturnal passerine migrants remain inactive (e.g. Palmgren 1949), occurs at dusk and may be associated with the process of deciding whether or not to initiate a migration flight and of selecting the proper flight direction (Emlen 1980).

The timing of migratory departure at dusk has also been suggested to be caused by factors not related to orientation cues, such as the variation in the structure of the atmosphere during the daily cycle. Kerlinger and Moore (1989) predicted that, due to the low temperature and reduced turbulent wind conditions at night, to be optimal nocturnal migration by powered flight should be initiated during or shortly after the twilight period and continue for 2–3 hours after sunrise. Many studies have reported that nocturnal passerine migration shows a peak in intensity 1–4 hours after sunset and that the start of migration mainly occurs prior to or within one hour after sunset (for references see Moore 1987).

The length of the twilight period varies with latitude and time of the year, but the sun elevation, measured in degrees above or below the horizon, signifies a given visual celestial aspect independently of latitude, season and time relative to sunset. Thus, if birds rely critically

Table 1. Time of departure in relation to the elevation of the sun of passerine nocturnal migrants caught at Ottenby Bird Observatory and tracked by radiotelemetry in 1993–1995.

Species	Date	Time of departure (Swedish normal time)	Departure time after sunset (min)	Sun elevation at departure	Moon elevation at departure
Song Thrush	29 Apr 95	21.05	96	−10°	−10°
Song Thrush	29 Apr 95	20.26	57	−7°	−7°
Thrush Nightingale	25 Aug 93	20.25	78	−10°	9°
Thrush Nightingale	24 Aug 93	20.41	91	−11°	5°
Song Thrush	22 Oct 93	16.40	4	−1°	17°
Blackbird	25 Oct 93	17.30	61	−8°	22°
Song Thrush	04 Oct 94	17.20	−2	0°	−3°
Song Thrush	10 Oct 94	17.00	−7	1°	14°
Song Thrush	09 Oct 94	21.03	234	−30°	−8°
Thrush Nightingale	23 Aug 93	22.30–06.00	>197	(−19°)	
Song Thrush	13 Oct 93	22.15–06.30	>316	(−38°)	
Song Thrush	07 Oct 94	21.45–07.15	>270	(−33°)	
Song Thrush	05 Oct 94	22.15–06.30	>295	(−35°)	
Song Thrush	11 Oct 94	00.50–04.00	>430	−38°−−19°	−29°−−49°
Robin	28 Oct 93	19.30–21.20	188–298	−25°−−38°	33°–42°

on the availability of multiple twilight cues for their orientation, one should expect them to depart on their migratory flights in a rather narrowly defined situation with respect to the elevation of the sun. To test this we used radiotelemetry and tracking radar to record the time of departure for individual passerines on nocturnal migration in South Sweden. The departure times were then analysed with respect to the elevation of the sun and the associated orientation cue availability in the twilight sky.

Methods

Radiotelemetry

We used small radio-transmitters (0.67 g; BD–2B, Holohil Systems Ltd) glued on the bird's back, to track the movements and departure times of individual birds. The birds were captured on migration at Ottenby Bird Observatory (56°12′N, 16°24′E) on the southernmost point of the Island of Öland (SE Sweden) in the Baltic Sea, during the autumns of 1993 and 1994, and in spring 1995. Immediately after capture a radio-transmitter was mounted on the back of the bird and the bird was kept in captivity for approximately 60 minutes until the glue had dried. We transported the birds by car to release sites 2–3 km north of the capture site. The release sites were located within an area of deciduous woods and shrub which is regularly used for stopover by migrating birds. We used four different species of nocturnal passerine migrants for the radiotelemetry studies in autumn (Thrush Nightingale *Luscinia luscinia*, Song Thrush *Turdus philomelos*, Blackbird *Turdus merula* and Robin *Erithacus rubecula*) and two species in spring (Song Thrush and Redwing *Turdus iliacus*). The Thrush Nightingale is a long-dis-

tance tropical migrant wintering in southeastern Africa (Moreau 1972, Zink 1973). The other species are temperate migrants, with wintering areas in western and southwestern Europe (Pettersson et al. 1986).

We located the birds with radiotransmitters in the stopover areas on several occasions during the day, by using hand-held receivers allowing the signals from a transmitter to be registered at a range of up to 300–500 m in the woods and at distances of approximately 1 km in open country. From well before sunset we constantly tracked the birds' movements until they left on migration flights or for at least 3 hours after sunset. We followed the birds between one and ten days (mean: 4 days), before they left on migration. Out of 15 birds radiotracked we were able to record the actual departure of nine (Table 1). In the other six cases we received information about the broad time interval within which the bird must have left the area. In the morning, we thoroughly searched the area, and on only one occasion did we find a bird which had moved a long distance to a new stopover site. Nearly all birds were stationary and stayed in a restricted area during the complete stopover period. Therefore, we are confident that we were able to relocate the birds when present, and that the birds which we did not find indeed had left the area on a nocturnal migration flight.

Radar tracking

We have also analysed data on departure times of nocturnal passerine migrants recorded by tracking radar during studies conducted at northern Öland (57°22′N, 17°05′E) in spring (31 March–1 May, 1979 and 1980), and at two sites in southern Sweden (60°05′N, 15°55′E and 55°42′N, 14°12′E) during autumn (Sept., Oct., 1982, 1983). The radar studies were

mainly focused on daytime bird migration, but regularly continued till twilight and the first hour(s) of darkness, when departing nocturnal migrants, climbing steeply from low altitude, were sometimes recorded. The departure flights were registered by a short-range tracking radar (X-band, 40 kW peak power, 0.3 μs pulse duration, 1800 Hz pulse repetition frequency, 2.2° pencil beam width). Range, elevation and bearing to the target were read by computer every 10 s or 60 s from the radar, which was operated in automatic tracking mode. The radar is equipped with 9 × and 18 × binoculars, and visual observations were reported to a tape recorder simultaneously with the radar registration. Maximum tracking error is about ±25 m in position, and the maximum useful range was 3–10 km depending on whether single birds or flocks were targets (see Alerstam 1987 for more detailed description of radar tracking procedures).

Included in the present analysis are radar trackings of nocturnal passerine migrants (identified visually or by their echo signature of intermittent flapping flight, and slow airspeed), showing an initial consistent climb, at a rate exceeding 0.5 m/s, during at least 2 minutes of the tracking episode. A total of 35 radar trackings (28 in spring and 7 in autumn) fulfilled these criteria. In ten cases (all in spring) the targets were identified visually as thrushes Turdus spp. (Song Thrush, Redwing, Blackbird), climbing towards the twilight sky in flocks of up to 75 individuals (examples of these tracks are plotted in Fig. 88 in Alerstam 1990).

The radar trackings lasted between 3 and 25 min, and they started when the birds had reached altitudes between 170 and 1180 m above the ground, with climb rates between 0.6 and 2.0 m/s. Some birds climbed throughout the tracking interval, while others levelled out at higher altitudes, or even started to descend.

By dividing the altitude at the start of each radar tracking by the initial uniform rate of climb, the climbing time from the ground to the altitude where the birds were intercepted by the radar could be estimated (these climbing times varied between 3 and 32 min for the different cases). The exact time of flight initiation from the ground was then estimated by subtracting this climbing time from the time when the radar tracking started.

Because the radar observations were terminated in the later part of the twilight period or the early night, these data do not provide a systematic picture of the complete distribution of departure times. Rather, the radar data serve to illustrate the variation that may occur in departure times (and the associated angles of sun elevation) among nocturnal passerine migrants during twilight and the earliest part of the night. In the vast majority of the radar- as well as radiotracking cases the twilight sky was clear or only partly clouded, permitting a view of the glow from the sunset sky as well as of the stars.

Use of literature data

Based on the time of departure for individual birds, we calculated, for the relevant date and geographical position, the elevation of the sun at departure. A calculator for astronomical data for the sun (Trimble GPS) was used for these computations. In addition to our own data, we calculated the sun elevation at the mean times of departure as recorded by radar, ceilometer and radiotelemetry at different sites from data published in the literature (Table 2). In studies where only the observation period was given, we used a date in the middle of the period given to calculate the associated average sun elevation for that site.

Twilight conditions

The twilight period involves the entire complex of optical phenomena that take place in the atmosphere when the sun is near the horizon, and can be considered as the skylight transition interval separating illumination conditions typical for the day and night, respectively. This transition in its entirety takes place at sun elevations between approximately +6° and −18° (Rozenberg 1966; Fig. 1). In formal definitions of twilight, sunset is considered as the initial time, and civil twilight ends at sun elevation −6°, nautical twilight at −12°, and astronomical twilight at −18°. At lower sun elevations than this, "deep" night sets in. At the end of the civil twilight period the first and brightest 2–5 stars become visible to a human observer. As the nautical twilight proceeds (sun elevations between −6° and −12°), the illuminance decreases approximately 10-fold for each 2–3° decrease in sun elevation (Fig. 1). During this period the visibility of stars increases and for each 10-fold decrease in illuminance approximately 15–20 new stars become visible. At the end of the nautical twilight period several hundreds of stars are visible. During the period of nautical twilight the position of the sun, seen as a bright multicoloured horizon glow, may still be visible under clear sky conditions, but at sun depressions of 12° below the horizon only star information remains (Rozenberg 1966, Martin 1990, Dusenbery 1992). It should be kept in mind that optical conditions at twilight varies with weather and cloud conditions. Furthermore, the length of the twilight period varies with time of the year and with geographical latitude.

Light from a clear blue sky is polarised and skylight polarisation forms a regular pattern relative to the position of the sun. A band of maximum polarisation occurs 90° away from the sun and forms a broad ring around the earth orthogonal to the direction of the sun. The transmission axis of polarisation (E-vector) and the band of maximum polarisation are vertically aligned in relation to the sun at sunrise and sunset (Lythgoe 1979,

Table 2. Time of departure in relation to the elevation of the sun for nocturnal passerine migrants studied by different techniques.

Method	Period	Location, Country	Main departure period after SS (min)	Mean time ±SD of departure after SS (min)	Mean elevation of sun at departure	Species	Reference
Radiotelemetry	spring	Illinois, North America	30–120[1]	70 ± 47[1] 129 ± 108 (all)	−12° −19°	3 species of thrushes (*Hylocichla* spp.)	Cochran et al. 1967
Radiotelemetry	spring	Illinois, North America	c. 51–55	c. 53	c. −8°	one Swainson's Thrush	Cochran 1987
Ceilometer	spring	Grand Isle, Louisiana, North America	22–60	40–45	c. −10°	a few identified[2]	Hebrard 1971
Ceilometer/heard	autumn	S Sweden	37–57	46	−6°	thrushes (*Turdus* spp.)	Lindgren and Nilsson 1975
Radar (surv.)	spring	S Sweden		33 ± 16 (ENE) 28 ± 38 (N)	−4° −3°	–	Alerstam 1976
Radar (surv.)	autumn	S Sweden		34 ± 19 (SE) 30 ± 23 (SSW)	−5° −4°	–	Alerstam 1976
Radar (surv.)	spring	Sussex, Hampshire, England	35–41	38 ± 1	−5°	–	Parslow 1968
Radar (surv.)	autumn	Sussex, Hampshire, England	29–49	39 ± 1	−5°	–	Parslow 1968
Radar (surv.)	autumn	Nova Scotia, Canada	20–37	28 ± 5	−4°	–	Richardson 1978
Radar (surv.)	autumn	Cape Cod, Massachusetts, North America	–	ca 45	−8°	–	Drury and Nisbet 1964
Radar (surv.)	spring	S Louisiana, North America	30–40	?	−9°	–	Gauthreaux 1971
Radar (ship)	spring, autumn	Mediterranean	40–50	?	?	–	Casement 1966
Radiotelemetry	spring, autumn	Öland, SE Sweden	−7–96[1]	47 ± 43[1]	−6°	Blackbird, Song Thrush, Thrush Nightingale, Robin	This study
Radar (tracking)	spring, autumn	Öland, SE Sweden S Sweden	−69–70 20–93	19 ± 38 (spring) 48 ± 26 (autumn)	−2° −6°	mainly thrushes (*Turdus* spp.)	This study

[1] Excluding departures > 150 min after sunset.
[2] Male Scarlet Tanager *Piranga olivaea*, male Summer Tanager *P. rubra*, male Indigo Bunting *Passerina cyanea*, male Painted Bunting *P. ciris* and Catbird *Dumetella carolinensis*.

Brines 1980, Brines and Gould 1982, Wehner 1989). The degree of polarisation of the light from the twilight sky first increases and then decreases with decreasing sun elevation. Skylight from the zenith, attains its maximum degree of polarisation at sun elevations −2° to −4° (70–80% polarisation; Rozenberg 1966). Beginning at sun elevation −7° the degree of polarisation falls off quite rapidly with decreasing sun elevation, and between −8° and −12° it is approximately 50%. At sun elevations around −16° the degree of polarisation is only about 15% (Rozenberg 1966).

Results

Among the radiotracked birds we were able to establish precise departure times for two birds in spring and seven in autumn (Table 1). In addition, we received general information about time intervals later in the night (including early morning) when six birds left on nocturnal migration flights. Mean time of departure for the radiotracked individuals departing within 150 min after sunset was 47 ± 43 (sd) min after sunset, and sun elevation was on average −6° at the birds' departure. The remaining seven birds (47% of all cases) did not fly off until much later after sunset at sun elevations well below −19°. The tracking radar data from Sweden demonstrated mean departure times 19 ± 38 min (n = 28) after sunset in spring and 48 ± 26 min (n = 7) in
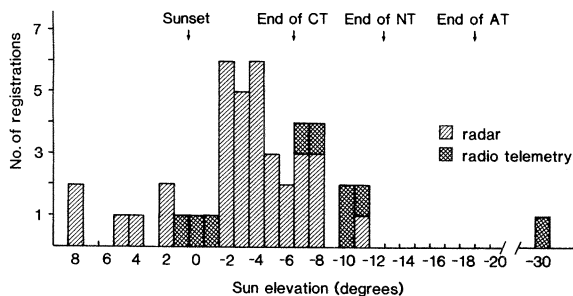
Fig. 2. Number of registrations of birds departing on nocturnal migration flights in South Sweden in relation to elevation of the sun at departure. Hatching refers to flocks or single birds recorded by radar, and cross-hatching to radiotracked birds.

autumn. Mean sun elevation at the birds' take-off was −2° in spring and −6° in autumn, respectively. Departure times as recorded for individual birds by radiotelemetry and tracking radar varied between sun elevations of 8° and −30° (Fig. 2).

Registrations of the daily starting time of nocturnal passerine migration by different techniques (ceilometer observations, radiotelemetry, surveillance and tracking radar), have demonstrated mean departure times from 19 min (radar tracking data on departing thrushes) to 70 min after sunset (radiotracked thrushes; Table 2). The mean sun elevations at departure varied between −2° and −12°. Most studies have focused on the starting time for the main exodus of migrants at dusk, and on the variation of this starting time between days. There are only two studies, a radiotelemetry study by Cochran et al. (1967) and a ceilometer study by Hebrard (1971), that have investigated the temporal distribution of migratory departures in a systematic way throughout a major part of the night, from sunset and onwards.

Cochran et al. (1967) presented information about 18 spontaneous departures (12 under clear skies and 6 under overcast) of *Hylocichla* thrushes equipped with radio transmitters during spring migration in North America. The earliest departure was about 20 min after sunset, and 13 of the departures took place within 150 min after sunset. In the remaining 5 cases (28% of all cases) the birds took off later than this, during the night 3–7 hours after sunset (3 of these late departures occurred under overcast and 2 under clear skies).

Hebrard (1971) used a ceilometer with its light beam directed horizontally above the tree-tops of a woodland in coastal Louisiana, to detect birds departing on spring migration. Observations began shortly before darkness and continued until there was a period of one hour when no birds were seen. The recorded periods of exodus during different nights of the spring season have been recalculated in relation to the sun elevation in Fig. 3. The average time for the first bird seen to depart
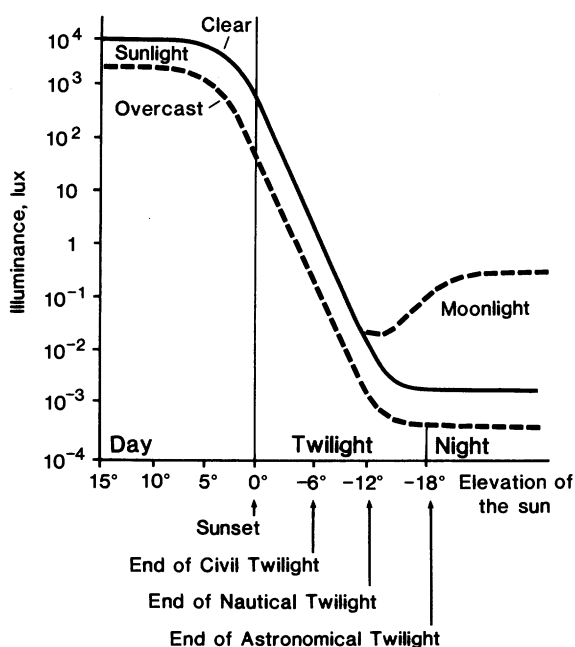

Fig. 1. The change of light intensity during the twilight period, measured as illumination on a horizontal surface at different elevations of the sun. Sunset and ends of civil, nautical and astronomical twilight periods are indicated. Modified after Dusenbery 1992 (cf. also Rozenberg 1966).

during the different nights was 38 min after sunset, corresponding to a sun elevation at −8°. Typically the peak in departure intensity occurred shortly before the end of nautical twilight, at about −10° sun elevation. The duration of the exodus varied from 5–109 min, being positively correlated with the number of birds departing. There is a tendency for birds to depart at gradually higher sun elevations (i.e. in a relatively earlier phase of evening twilight) as the season progresses (Fig. 3).

Discussion

We found considerable variation in time of departure between individuals in our study and also between mean departure times reported in different studies (cf. Fig. 2 and Table 2). Many migrants initiated flights well before the stars became visible (Parslow 1968, Alerstam 1976, Richardson 1978, this study), while especially radiotelemetry studies have revealed that flight departures also take place much later than the end of the civil twilight period (Cochran et al. 1967, this study, cf. Table 2). Cochran et al. (1967) found an indication of greater variation and later departures under overcast skies compared to clear sky conditions, while Gauthreaux (1971) and Hebrard (1971) reported no significant effect of immediate weather factors on departure time. Furthermore, the length of the departure period varied greatly between days. A delayed departure was suggested to be caused by birds arriving late in the

afternoon requiring a longer resting period before departing (Hebrard 1971, but see Morton 1967).

In the present study the majority of departures occurred under clear or only partly overcast conditions. The rather wide scatter in departure times, with departures taking place throughout the entire twilight period as well as during the deep night, lends little support to the idea that departure time is adapted to the availability of a specific combination of celestial orientation cues at twilight. There seems to be no important difference in departure timing, depending on whether the moon is visible or not (Table 1).

The results indicate that there may exist interesting differences between passerine species in typical departure time. In Sweden, thrushes of the genus *Turdus* seem to depart earlier, already during the civil twilight period and sometimes even immediately before sunset (mean departure at sun elevations between −2° and −6°), than other passerine migrants like the Thrush Nightingale and Robin which in our study did not depart before the stars became visible (Table 1). Departures of nocturnal passerine migrants in North America also indicate a distinctly later flight initiation than that of the *Turdus*-thrushes, and in several of the studies the first birds did not take off until the first stars became visible (Cochran et al. 1967, Gauthreaux 1971, Hebrard 1971; cf. Table 2). The risk of a bias in Hebrard's (1971) data, because of a reduced probability of detecting birds in the light beam during the early phases of twilight, can probably be ruled out since the starting times are nicely confirmed by radar observations in the same region (Gauthreaux 1971).

The *Turdus* species often, but not always, depart in flocks, and they seem to show a typical departure time that is intermediate between that of nocturnal non-passerine migrants travelling in flocks, like many shorebirds, terns and diving ducks, and that of smaller passerines migrating individually during the night. The former category regularly initiates night migration already during the hours preceding sunset (Edelstam 1972), while the latter group often do not depart until nautical twilight, as reflected by, e.g., the data for the North American passerines (Cochran et al. 1967, Hebrard 1971).

Hence, the evident difference in departure pattern, with respect to the prevailing sun elevation, between the migrants observed in Sweden (Fig. 2) and in Louisiana (Fig. 3) is probably related to interspecific differences and/or to the latitudinal difference in the daylight cycle. The data in Fig. 3 also indicate that departures may occur in different phases of twilight depending on the time of the season. It should be kept in mind that species migrating to high latitudes must travel, during late spring and early autumn, without directional information from the stars, because the sun remains above or near the horizon throughout the polar summer season.
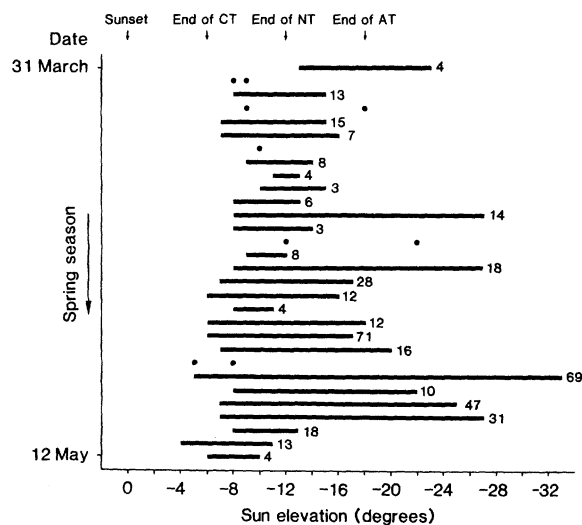

Fig. 3. Departure periods in relation to the sun elevation for different dates as recorded by a horizontal ceilometer in southern Louisiana, North America, in spring. Filled circles refer to individual birds, and lines denote the periods within which departing birds were observed. The figures indicate the number of birds observed for each period. Calculated from departure times given in Hebrard (1971: Table 1).

The variation in take-off time of nocturnal migrants, depending on species, latitude and time of season, represents a fascinating problem, whose potential complexity we are just beginning to discern. This study has provided evidence that nocturnal passerine migrants may depart immediately before sunset, during all phases of the twilight period, as well as in the middle of the night. It seems obvious that the birds must have the capacity to select a proper orientation in all these situations. Visual orientation cues associated with sunset and the star pattern are, without doubt, important for nocturnal passerine migrants (Emlen 1975, Able 1980, Moore 1987, Wiltschko and Wiltschko 1991), but it is uncertain if the requirements for orientation contribute to explaining the timing of the migrants' departures. The birds might be able to perceive, store and calibrate the different orientation cues against each other and thus may be independent of the orientation cues actually available at departure.

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