Ecological factors influence timing of departures in nocturnally migrating songbirds at Falsterbo, Sweden

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Most songbirds depart from stopover sites after sunset and migrate during the night. Several recent studies have reported larger variation in departure time than previously thought; yet, it is still unclear which factors govern departure timing. We investigated the departure timing of four species of nocturnally migrating songbirds using an automated radiotelemetry system at Falsterbo peninsula in southwest Sweden. We made a comprehensive analysis to test a range of factors that have been hypothesized to affect departure timing of nocturnal migrants, such as night duration, season, sun elevation and the birds' intrinsic and environmental conditions. We hypothesized that birds in good condition (large fuel reserves) and under advantageous flight conditions would depart sooner after sunset, in the expected migratory direction. Our analyses showed that the birds departed sooner after sunset during spring than autumn, and different species departed at different times in relation to sunset. In addition, birds departed earlier when nights were shorter, suggesting that night duration is an important factor that may drive much of the observed timing differences between seasons and species. Lean birds delayed their departures compared to fat individuals. When birds experienced favourable wind conditions (tail wind or weak winds) at sunset, they departed earlier. Thus, it appears that the decision to take off for a long-distance flight depends on both body condition and wind conditions. Timing of departure was not correlated with sun elevation, which would have been expected if availability of specific orientation cues (sun, skylight polarization pattern, stars) acted as triggers for departures. These results stress high flexibility and adaptive responses to a complex of ecological factors as the determinants for timing of nocturnal flights in songbirds.

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Most songbirds migrate during the night, enabling them to spend more time foraging during the day, to avoid predators, and to make use of less turbulent winds at nights (Alerstam, 2009; Kerlinger & Moore, 1989). For a long time, it has been widely accepted that migratory songbirds depart on nocturnal flights within a narrow time frame shortly after sunset, with a peak of departures within 1–4 h after sunset (for references see Åkesson, Alerstam, & Hedenström, 1996; Moore, 1987). However, several recent studies have reported migratory departures much later during the night; thus, timing of departure seems to be more variable and occur later than previously thought (Åkesson et al., 1996; Åkesson, Walinder, Karlsson, & Ehnbom, 2001; Bolshakov et al., 2007; Bulyuk & Tsvey, 2006; Chernetsov, 2012; Nilsson, Bäckman, Karlsson, & Alerstam, 2015; Schmaljohann et al., 2013; Sjöberg

et al., 2015). The observed variation in departure times suggests that migratory birds may adjust departure time to optimize the duration of the upcoming flight. Flight duration and ground speed are the main factors determining travel speed (Liechti, 2006; Nilsson, Klaassen, & Alerstam, 2013). Travel speed and total stopover duration in turn add up to the total speed of migration (Alerstam & Lindström, 1990). To explain the variation in total speed of migration it is therefore important to understand the causes of individual variation in the timing of nocturnal departures.

The twilight period is commonly divided into three subcategories based on the sun's elevation angle. Civil twilight starts at sunset and ends at sun elevation $-6°$, nautical twilight ends at sun elevation $-12°$ and astronomical twilight at sun elevation $-18°$. The different twilight periods are related to differences in availability of celestial orientation cues: the position of the setting sun, under clear sky conditions, may be seen as a glow on the horizon even during nautical twilight; the pattern of polarized light from the sun is most prominent during civil twilight; the first and brightest stars become visible during the end of civil twilight, and

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after nautical twilight only information from stars remains (Rozenberg, 1966). Before songbirds depart from a stopover site they integrate directional information for orientation and possibly assess flight conditions (Able, 1982; Able & Able, 1993; Liechti, 2006; reviewed in Moore, 1987; Muheim, Moore, & Phillips, 2006; Muheim, Phillips, & Åkesson, 2006; Schmaljohann et al., 2011; Sjöberg & Muheim, 2016). Several studies on departure timing in nocturnal songbird migrants have focused on departure times in relation to sun elevation and the availability of orientation cues associated with different twilight periods, with the hypothesis that birds depart as a response to the availability of a specific combination of orientation cues. They found that migrating songbirds preferentially depart during or after the nautical twilight period, when both stars and polarized light are available (Åkesson et al., 2001, 1996; Bolshakov & Chernetsov, 2004). In addition, it has been suggested that timing of departures on nocturnal flights is governed by the circadian rhythm of the innate migration programme, modified by intrinsic (e.g. fuel reserves) and environmental factors (e.g. wind conditions; Müller et al., 2016). However, it is still unclear whether departure times differ between different species and seasons, and how departure times are affected by environmental and intrinsic factors. There are some indications that the timing of departures differs between species of nocturnally migrating passerines initiating migration from the same stopover site during autumn migration (Bolshakov & Bulyuk, 2001). Also, European robins, Erithacus rubecula, have been observed to depart from Rybachy on the Courish Spit earlier in relation to sunset during spring migration than during autumn, possibly as a response to the shorter night durations during spring (Bolshakov et al., 2007). A comparison between studies on nocturnal departure timing in relation to sunset in songbirds departing from different stopover sites (hence also different environmental conditions) during autumn and spring migration indicated that night duration affected departure timing, with earlier departures when nights get shorter, with additional effects of body condition (Schmaljohann et al., 2013). Moore and Aborn (1996) suggested that departure time is related to energetic condition, with lean birds departing later than birds with larger amounts of stored fat, since energetic reserves of lean birds only last for a shorter flight. So far, two studies have found such a relationship (Schmaljohann & Naef-Daenzer, 2011; Smolinsky, Diehl, Radzio, Delaney, & Moore, 2013; but see Bolshakov et al., 2007; Bulyuk & Tsvey, 2006). These studies indicated that fatter birds departed earlier after sunset and on longer flights than lean individuals, which departed later and in directions indicating shorter or inland flights. Variation in departure timing between lean and fat individuals could further be related to the suggestion that departure timing relates to different types of movements. Departures after sunset of Swainson's thrushes, Catharus ustulatus, and hermit thrushes, Catharus guttatus, from stopover sites at Lake Erie, Ontario, Canada, were more likely to occur shortly after civil twilight for true migratory flights towards the migratory destinations (Mills, Thurber, Mackenzie, & Taylor, 2011). More local movements, on the other hand, occurred throughout the entire night. Similarly, in a study on route choice in nocturnal migrants after departure from Falsterbo, Sweden, we observed that songbirds departing on a longer flight across the Baltic Sea took off shortly after sunset, while birds departing in other directions took off throughout the entire night (Sjöberg et al., 2015).

The occurrence of clouds and visibility of celestial cues have been considered to affect the timing of departures, both relative to the availability of orientation cues and as a direct effect on flight conditions when visibility decreases (Åkesson et al., 1996). Reed warblers, Acrocephalus scirpaceus, tracked by radiotelemetry at a coastal site in autumn initiated their migratory flights when clouds broke up and celestial cues became visible (Åkesson et al., 2001). However, several other studies have failed to find a relationship between cloudiness and timing of departure (e.g. Bolshakov et al., 2007; Bulyuk, 2012; Bulyuk & Tsvey, 2006).

In this study, we carried out a comprehensive analysis of departure timing from a coastal stopover site by comparing four species of nocturnal songbirds using an automated radiotelemetry system located at Falsterbo peninsula in southwest Sweden. We investigated whether there were differences in timing between the migratory seasons (autumn and spring) and between different species of long- and medium-distance migrants, in order to understand the regulation of departure timing between different species and individuals initiating migration from the same stopover site. Furthermore, we explored whether specific orientation conditions (visibility of celestial cues) as a function of sun elevation explained departure timing. If departures are triggered by specific orientation cues, departures would take place in a narrow time window relative to the sun's elevation, and we would expect the birds to depart later in relation to sunset during spring than autumn migration, because of the relationship between our study species' migratory schedules and the equinoxes (Fig. 1).

We also tested whether and how intrinsic (age, fuel store, departure direction) and environmental factors (night duration and weather conditions at sunset including clouds, wind speed and direction) affected the departure timing of migratory flights in songbirds. We predicted that birds in good condition (larger amount of stored fuel) and birds departing with advantageous flight conditions (weak following winds and clear skies) would depart sooner after sunset and in the expected migratory direction. Night duration is inevitably correlated with progress of season, with longer nights late during autumn migration and shorter nights late during spring migration. If progress of season or night duration drives the variation in departure timing, we would expect either one of the following two patterns. (1) If progress of the season explains the variation, we would expect birds migrating late during either one of the migratory seasons to depart earlier in relation to sunset to speed up their migration by extending the potential flight range for the upcoming flight. (2) If night duration instead is the driving factor, we expect birds during both seasons to depart at an earlier time after sunset with a decrease in night duration, which
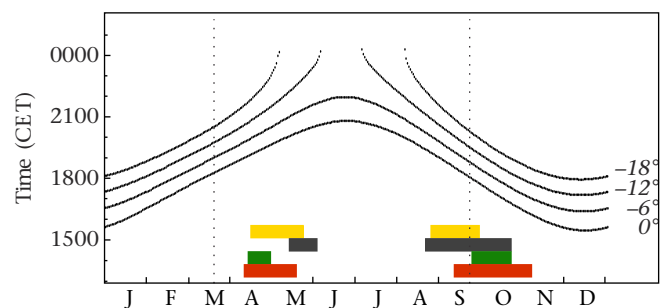
Figure 1. Illustration of annual timing of sunset and twilight periods at Falsterbo peninsula. Black lines represent sun elevation ($0°$ = sunset/start of civil twilight; $−6°$ = start of nautical twilight; $−12°$ = start of astronomical twilight; $−18°$ = start of night) and dotted vertical lines represent spring and autumn equinoxes. In our sample the birds migrated after spring and often at or after the autumn equinox (the sampling periods for the different species are indicated by bars: yellow: willow warbler; dark grey: garden warbler; green: song thrush; red: European robin). The sun sets slower during the hours after sunset on dates after the spring equinox than on dates at or after the autumn equinox; thus, the same elevation angle occurs later after sunset during spring than autumn in our data set. Therefore, if departures were caused by a strict response to a specific sun elevation, we would expect the birds to depart later in relation to sunset during spring than autumn migration.

would mean that they depart sooner after sunset in late than early spring and in early than late autumn.

METHODS

Ringing and Data Collection

The study was performed throughout the migratory seasons of four autumns 2009–2012 and four springs 2010–2013 at Falsterbo Bird Observatory, located on Falsterbo peninsula in southwest Sweden (55°38′N, 12°82′E). We used an automated radiotelemetry receiver system (SRX600; Lotek Wireless, Newmarket, ON, Canada) covering the peninsula (see Appendix; for map see Sjöberg et al., 2015). The receivers collected ID code (individual), date, satellite-corrected time stamp based on GPS, receiving antenna and signal strength (nonlinear scale 30–255) for each detected signal. The ID-coded radiotransmitters (NTQB-2, weight 0.35 g, except during 2010 and 2011 when song thrushes, Turdus philomelos, were equipped with NTQB-3-2, weight 0.67 g; Lotek Wireless) were all stable within their own burst rate (4.9–5.2 s in 2009–2010; 2.9–3.1 s in 2011–2013) enabling filtering of the data by burst rate (see Appendix; Sjöberg et al., 2015). Departures of individuals of four species of nocturnal passerine migrants were included in this study: European robins and song thrushes as medium-distance migrants (Cramp, 1988), and willow warblers, Phylloscopus trochilus, and garden warblers, Sylvia borin, as long-distance migrants (Cramp, 1992). All birds were caught in mist nets as part of the daily ringing scheme at the bird observatory. We selectively tagged birds of different ages and body conditions (i.e. fat stores) to get balanced samples. Fat store was visually estimated on a 0–9 scale (Pettersson & Hasselquist, 1985, modified for Falsterbo Bird Observatory and extended with fat scores 7–9; given in Sjöberg et al., 2015). We did not tag the leanest individuals to avoid adverse effects from the tagging with very few exceptions: one song thrush with fat score = 0, three European robins, three song thrushes and one garden warbler with fat score = 1 (Table A1). Age was determined from plumage characteristics and eye coloration, and grouped into inexperienced (birds on their first migration cycle (calendar year CY 1) in autumn and second-year birds (CY 2) in spring) and experienced individuals (birds that have performed a full migration cycle, adults (CY 2+) in autumn and third-year birds or older (CY 3+) in spring) (Karlsson, Persson, & Walinder, 1985). All birds were handled and tagged within 1 h after capture. The radiotransmitters were glued (contact adhesive, Casco) to the back feathers of the birds after the feathers over a small area were cut to shorten them (Fig. A1).

The Swedish Meteorological and Hydrological Institute (SMHI) collected data every third hour at Falsterbo Bird Observatory. Wind measurements were only taken between 2200 and 0400 CET during spring. The weather reported closest to sunset was used to analyse the effects of weather on timing of departure. Cloud cover was visually estimated by human observers on a 10-degree scale (0/8 = clear sky, 8/8 = total overcast, 9/8 = mist). Wind speed and direction were also used in the analyses; with north/south and east/west wind components calculated from the circular wind direction measurements (N/S component = cos (wind direction); E/W component = sin (wind direction)). The two wind factors (direction and speed) were not combined since previous studies indicated that birds might value speed and direction differently (Covino, Holberton, & Morris, 2014; Schaub, 2004).

Ethical Note

Falsterbo Bird Observatory has been ringing birds during spring and autumn migration since 1947, with a standardized ringing scheme starting in 1980. The ringing scheme in the lighthouse garden consists of daily ringing between 21 March and 10 June during spring and 20 July and 10 November during autumn migration. No ringing is performed in bad weather (rain and/or strong winds). All birds are trapped in mist nets and are ringed, measured and immediately released at the ringing site. Mist nets are up 30 min before dawn, for at least 4 h during spring and 6 h during autumn, and all nets are emptied every 30 min. Mist netting as capture method has a low rate of incidents compared with other methods, e.g. different types of traps (Spotswood et al., 2012); however, incidents do happen and these cases are reported annually by Falsterbo Bird Observatory to the Swedish Ringing Council (Falsterbo Bird Observatory, personal communication). No birds in this study were kept in captivity and the transmitters were mounted directly after ringing by the bird observatory staff. Tracking devices could have a negative effect on survival, energy expenditure and breeding performance of birds (Barron, Brawn, & Weatherhead, 2010; Costantini & Møller, 2013), and the attachment method affects the behaviour of the birds differently (Barron et al., 2010). Since this study focused on a short-term behaviour we chose to mount the transmitter by gluing it to feathers on the birds' back (Fig. A1), instead of using a harness. This method ensures that the transmitter falls off at the latest the next time the bird moults its body feathers, and avoids the bird getting entangled in the harness. It has been shown that glued transmitters have no effect on device-induced behaviours (e.g. preening) and nest success, and they have a lower effect on mortality than transmitters attached with other methods (e.g. different types of harnesses; Barron et al., 2010). The radiotransmitters mounted on the birds never exceeded 5% of the bird's body mass (Table A2). The willow warbler was the only species on which we deployed a tag that weighed more than 3%. We observed that lean willow warblers stayed for more days in the area than individuals with larger fuel stores during autumn migration (Sjöberg, 2015). However, the same was true for European robins, with lower relative transmitter weight. This difference in stopover duration between lean and fat individuals is expected (e.g. Biebach, Friedrich, & Heine, 1986; Goymann, Spina, Ferri, & Fusani, 2010; Moore & Kerlinger, 1987). Furthermore, it has been shown that the shape and position of the device could have severe effects on the birds as the added weight load introduces drag (Bowlin et al., 2010). As recommended by Bowlin et al. (2010), we placed the radiotransmitter closer to the rump of the bird to affect the natural shape of the bird as little as possible.

Statistics and Data Treatment

The time of the last radiosignal (to the nearest 1 s; CET = UTC + 1 h) was used as departure time for each bird. Mean departure times and confidence intervals during the 24 h of the day/night were calculated for each species by vector analysis and tested for significance with circular statistics (Batschelet, 1981). We successfully recorded departures of 255 individual birds during autumn ($N = 141$) and spring migration ($N = 114$) that were included in the circular analyses (for sample sizes within each species, see Table 1). We calculated timing of departure in relation to sunset (h) by using sunset times from rl.se/sol_maane for Falsterbo, Sweden. To allow the use of linear statistical analyses for departure timing relative to sunset we only included departures between 1700 and 0500 CET. To calculate the vanishing bearing for each bird, a circular mean direction (Batschelet, 1981) was

Table 1
Time of departures during autumn and spring in four species of nocturnal passerine migrants at Falsterbo, Sweden, including differences in timing between the migratory seasons

	N (autumn/spring)	Autumn (mean±95% CI[a]/mean±SD[b])	Spring (mean±95% CI[a]/mean±SD[b])	$F/\chi^2/U^{2c}$	Tests between seasons		
					df	P	Test
Departure time (CET; min)[d]							
Willow warblers	40/30	2218±98	2131±80	0.40	25, 32	<0.001	Watson U^2
European robins	44/30	2032±60	2127±55	0.32	27, 38	<0.005	Watson U^2
Garden warblers	18/28	2106±144	2208±56	0.69	14, 25	<0.001	Watson U^2
Song thrushes	39/26	2037±50	2237±81	0.45	23, 35	<0.001	Watson U^2
Time of departure after sunset (h)[e]							
All species		3.52±2.44	2.41±1.65	12.06	1	<0.001	Kruskal–Wallis
Willow warblers	27/22	3.95±2.51	2.02±1.25	6.94	1	0.008	Kruskal–Wallis
European robins	32/26	3.35±2.04	2.71±1.99	1.44	1	0.23	ANOVA
Garden warblers	12/23	3.57±3.17	1.81±0.60	0.25	1	0.61	Kruskal–Wallis
Song thrushes	31/22	3.31±2.52	3.08±2.03	0.12	1	0.73	ANOVA
Sun elevation at departure (°)[f]							
All species		−21.0±9.0	−13.2±5.7	33.68	1	<0.001	Kruskal–Wallis
Willow warblers	19/21	−18.7±8.0	−11.7±4.6	8.16	1	<0.005	Kruskal–Wallis
European robins	30/24	−24.3±9.3	−15.0±4.0	17.31	1	<0.001	Kruskal–Wallis
Garden warblers	8/22	−13.5±7.6	−9.9±1.8	0.34	1	0.56	Kruskal–Wallis
Song thrushes	28/20	−21.3±8.4	−16.1±8.6	4.31	1	0.044	ANOVA

[a] For departure time.
[b] For timing in relation to sunset and sun elevation at departure.
[c] The test statistics vary between statistical methods: F for ANOVA tests, χ^2 for Kruskal–Wallis rank sum tests for heterogeneous variances, U^2 for Watson U^2 tests of circular data.
[d] Based on the full sample, see Methods.
[e] Based on subsample A, see Methods.
[f] Based on subsample B, see Methods.

calculated from all signals from a bird's last 10 min at Falsterbo peninsula, weighing each signal by signal strength (see Appendix; Sjöberg & Nilsson, 2015). We only included observations in the analysis for which we had a reliable vanishing bearing, since the vanishing bearing was included as an independent variable in the generalized linear models (GLMs; see below). Altogether, 102 departures during autumn and 93 during spring migration were included in the analyses of departure timing relative to sunset (subsample A). We analysed the general effect of night duration on departure timing relative to sunset with a linear regression. To explore the effects of night duration within the migratory seasons we performed a GLM with timing in relation to sunset as the dependent factor and night duration, migratory season and the interaction night duration ∗ migratory season as independent variables, with species included as a random factor in the model, both as a main effect and as an interaction with migratory season. We used an astronomical calculator (http://www.sunearthtools.com/dp/tools/pos_sun.php) to calculate the sun's elevation at departure. In the analyses of departures in relation to sun elevation, we only included departures before midnight (85 departures during autumn and 87 during spring migration, subsample B), since departures have been suggested to be triggered by availability of orientation cues related to a certain twilight period after sunset (e.g. Åkesson et al., 2001, 1996; Bolshakov & Chernetsov, 2004). We analysed differences in timing of departures (relative to sunset and sun elevation) between seasons and species with Kruskal–Wallis rank sum tests when the samples had different variances (Levene's test for homogeneity of variance with $P < 0.05$), or with one-way ANOVAs when the samples had homogeneous variances. Since night duration is strongly correlated with migratory season, we performed a GLM for each season to describe the variation in departure timing in relation to sunset by intrinsic and external factors. To find the best approximating model, all models were reduced by backward elimination according to AIC, by using stepwise elimination in Rcmdr in R.2.11.1 software (The R Foundation for Statistical Computing, Vienna, Austria). This function eliminates the factor that causes the largest drop in AIC for the remaining model

until elimination of an additional factor does not cause a decrease in AIC. We used F statistics (ANOVA model, type II) to describe the final model. For simplicity, only the F statistics of the final GLMs are included in the Results (see Appendix Tables A3–A7 for the complete original and final GLMs). The following factors were included in the original models for both seasons separately: species, age, fat, vanishing bearing (grouped into forward migration, i.e. 90°−270° during autumn and 270°−90° during spring, and reverse migration, i.e. 270°−90° during autumn and 90°−270° during spring), cloud cover, wind speed, N/S wind component, E/W wind component, night duration and the interactions: species∗age, species∗fat, species∗vanishing bearing, species∗cloud cover, species∗wind speed, species∗N/S wind component, species∗E/W wind component, species∗night duration, age∗fat and species∗age∗fat. None of the factors were strongly correlated with each other (Pearson $r < 0.5$). To investigate whether the weather improved during nights when birds departed late (after the median time) we performed single sample t tests for the difference in cloud cover (only autumn, see above) and wind speed (autumn and spring) at 1900 and 0100 CET during the night of departure. To examine whether wind direction (as a circular factor) changed between 1900 and 0100 CET during nights when birds departed late, we performed Watson U^2 tests between the two observations. All statistics were performed in Rcmdr package in R.2.11.1 software, except for the GLM on the effects of night duration within each season which was performed using the Lme4 package in R.2.11.1 software, and the circular statistics tests which were performed in Oriana 4.0 (Kovach Computing Services, Anglesey, U.K.).

RESULTS

Timing of Departures Throughout the 24 h of Day/Night

All circular statistics are based on the full sample (see Methods). Mean departure times of all nocturnal songbird species at Falsterbo peninsula occurred during the period between sunset and midnight (Table 1, Fig. 2a–h; all circular distributions $P < 0.05$,

Rayleigh test). Within-species departure times differed between the seasons (Table 1); however, this difference is mostly caused by more synchronized departures (less scatter in departure times) during spring migration. We also found differences between species. During autumn migration, willow warblers departed later than European robins and song thrushes. During spring migration, garden warblers departed later and more synchronized than all three other species, and European robins departed earlier and more synchronized than song thrushes (Table 2).

Departure Timing Relative to Sunset and Night Duration

Analyses of departure time in relation to sunset are based on subsample A (birds departing between 1700 and 0500 CET, with reliable departure direction). The birds departed on average earlier relative to sunset during spring than autumn (Fig. 2i, j; Table 1). However, when analysing the different species separately, only willow warblers departed significantly earlier in relation to sunset during spring than autumn migration (Kruskal−Wallis rank sum test between seasons: $\chi^2_1 = 6.94, P = 0.008$). The species differed in their timing of departure in relation to sunset during spring (Kruskal−Wallis rank sum test between species: $\chi^2_3 = 10.53$, $P = 0.015$), but not during autumn migration (ANOVA between species: $F_3 = 0.40, P = 0.75$). Across species, we found a significant correlation between departure time (both relative to sunset and sun elevation) and night duration (linear regression of departure time after sunset in relation to night duration: $r^2 = 0.085$, $P = 0.0004$), with departures on average taking place sooner after sunset (and at higher sun elevations) when nights were shorter (Figs 2k–l, A2). An interaction between night duration and migratory season was included in the most parsimonious model describing the effects of night duration and migratory season on departure timing (GLM: night duration: $F_1 = 3.13, P = 0.13$; migratory season: $F_1 = 0.17, P = 0.68$; night duration * migratory season: $F_1 = 2.57$, $P = 0.11$; variance estimate of random factor: species = 0.00, residual = 4.27; see Table A3 for the original GLM). However, the correlation between night duration and departure timing showed a positive slope in spring and a weak positive slope in autumn. Thus, the interaction underlines the effect of night duration during spring when the nights get very short (Figs 2k, A2; see environmental factors for further effects of night duration and species on departure timing within the seasons), indicating an effect of night duration rather than progress of season on departure timing (prediction 2 above; a positive slope in spring and a negative slope in autumn would have supported prediction 1).

Sun Elevation at Departure

Species departed at different sun elevations during both autumn (ANOVA between species: $F_3 = 3.99, P = 0.011$) and spring migration (Kruskal−Wallis rank sum test between species: $\chi^2_3 = 23.68$, $P = 0.00003$). All species departed on average at a higher sun elevation during spring (mean ± SD: $-13.2 \pm 5.7°$) than autumn migration $-(21.0 \pm 9.0°)$, with significant differences within each species except for garden warblers (Table 1, Fig. 2l). The analyses of departure time in relation to sun elevation are based on departures after sunset and before midnight (subsample B).

Intrinsic Factors

The GLMs on the effects of intrinsic and environmental factors on departure timing are based on subsample A. During autumn migration, birds with higher fat scores generally departed earlier in relation to sunset than leaner individuals (Table 3, Fig. 3a; for range in fat score at release within each species and season see Table A1).

During spring migration, the effect of fat varied between species (significant interaction; Table 3, Fig. 3b). Willow warblers and European robins with high fat scores departed earlier than leaner individuals. However, the pattern was the reverse in song thrushes. We found no difference in departure time between lean and fat garden warblers. Age was included in the most parsimonious model for spring migration as an interaction with species. Yet, the difference in departure time relative to sunset between young and adult birds were small in all species (mean ± SD: willow warbler: CY 2: 2.14 ± 1.42 h; CY 3+: 1.88 ± 1.09 h; song thrush: CY 2: 3.34 ± 2.45 h; CY 3+: 2.77 ± 1.46 h; European robin: CY 2: 2.62 ± 2.09 h; CY 3+: 2.79 ± 1.99 h; Fig. A3), and it could be questioned whether this correlation is biologically relevant. Vanishing bearing (grouped into forward and reverse migration) was not included in the most parsimonious model during any of the migratory seasons (Fig. A4).

Environmental Factors

Birds exposed to head winds delayed their departures at night during both migratory seasons (Table 3, Fig. 4). Wind speed influenced departure timing in European robins and willow warblers during spring migration, but no such effect was found in garden warblers and song thrushes in the same season (Table 3, Fig. A5). During the autumn nights when some birds departed after the median time relative to sunset (3.05 h after sunset during autumn; 1.93 h after sunset during spring), cloud cover decreased significantly between 1900 and 0100 CET (t test for difference in cloud cover: $t_{50} = -3.61, P = 0.001$). We found no difference in wind conditions between 1900 and 0100 CET during those nights (Watson U^2 tests of difference in wind direction; autumn: $U^2_{51, 51} = 0.09, P > 0.02$; spring: $U^2_{46, 46} = 0.07, P > 0.5$; t tests of difference in wind speed; autumn: $t_{50} = -1.05, P = 0.30$; spring: $t_{45} = 0.08, P = 0.93$).

The length of the night (or progress of season; see above) influenced departure timing in the different species during either migratory season. European robins, willow warblers and garden warblers departed significantly later in relation to sunset when the nights became longer during autumn migration, while song thrushes departed earlier in relation to sunset (Fig. A6a). During spring migration, garden warblers departed earlier during the first part of the migration period, when the nights were longer, than later during the season. In contrast, willow warblers and song thrushes departed later in relation to sunset, when the nights were longer, while there was almost no effect on European robins (Fig. A6b).

DISCUSSION

Disparities Between Species and Seasonal Differences

Like previous observations (Bolshakov & Bulyuk, 2001) we found interspecific differences in departure timing (Fig. 2a–g, Table 2). The long-distance migratory garden warblers and willow warblers departed earlier relative to sunset than medium-distance migratory European robins and song thrushes during spring (Fig. 2k, Table 1). However, the observed differences between species are probably largely a result of differences in night duration when the different species migrate (Fig. 1) and are in addition affected by interspecific differences in how the species respond to intrinsic and environmental factors (Table 3).

Our birds departed from Falsterbo sooner after sunset during spring than during autumn migration (Table 1), which is in line with previous findings that robins depart earlier in relation to sunset during spring than during autumn migration at the Courish
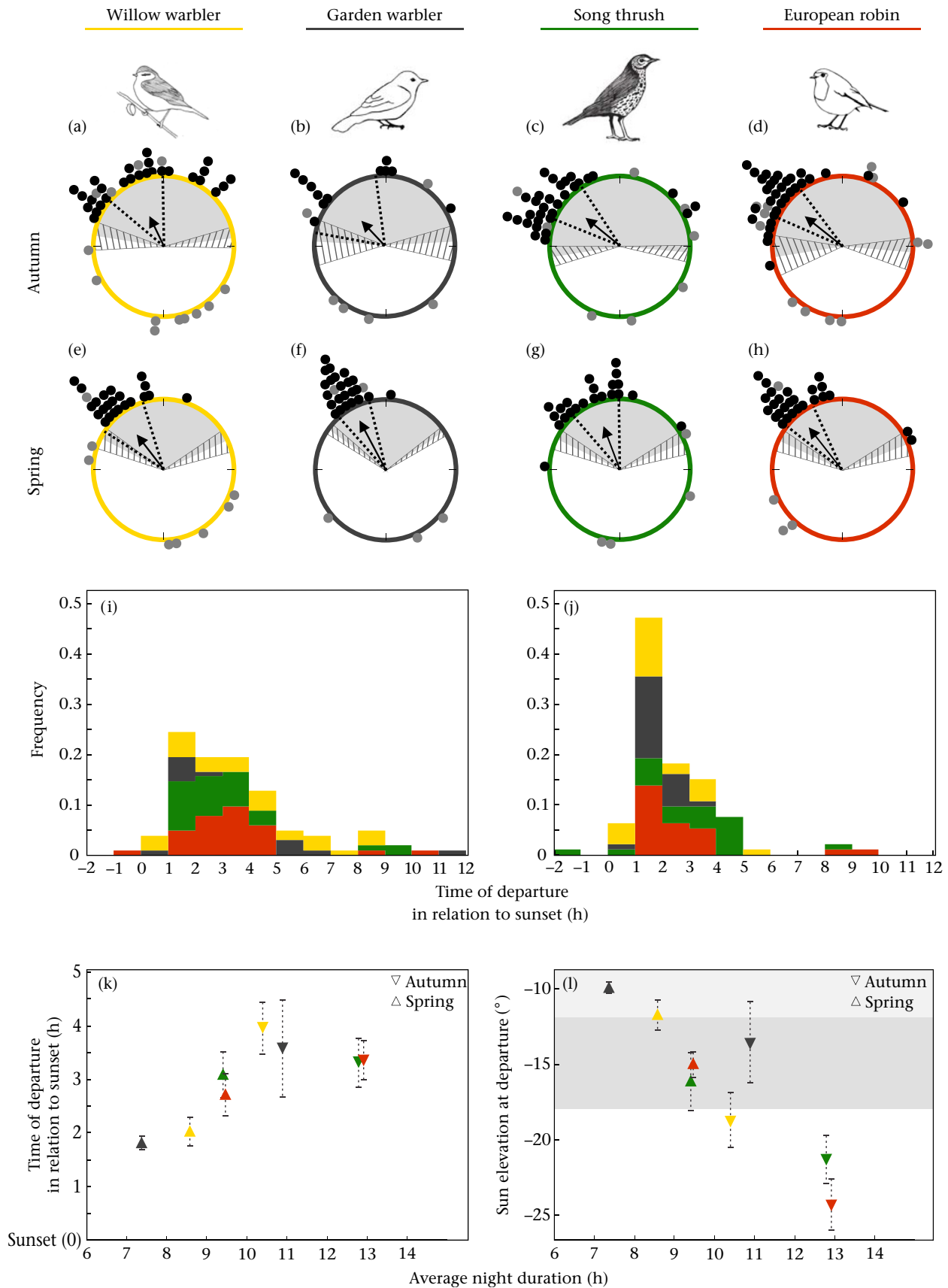
Figure 2. Time of departures of nocturnal passerine migrants (four species as indicated by different colour codes given in Fig. 1) at Falsterbo, Sweden, as recorded by automated radio telemetry. Circular diagrams a–h show departure timing for each species and season during the 24 h of day/night with 0000 CET at the top and 1200 CET at the bottom of each circle. Each symbol outside the circle refers to the departure time of one individual bird (black = records included in analyses of timing in relation to sunset; grey = records excluded

Spit (Bolshakov et al., 2007). Earlier departures during spring may be caused by (1) shorter nights during spring migration that trigger earlier departures to keep flight duration constant (cf. Bauchinger & Klaassen, 2005), or (2) an urge to migrate faster in spring than autumn (cf. Nilsson et al., 2013). The causes are not mutually exclusive, and can, as we suggest, to some degree also explain differences between species migrating early and late during the migratory season.

The relationship between timing of departure relative to sunset (and relative to sun elevation) and night duration suggests that the flight period is adjusted to compensate for shorter nights and, thereby, to avoid the nocturnal flight periods being reduced by the same extent as the nights become shorter (Figs 2k–l, A2). Yet, the pattern is not straightforward, and the general effect of night duration on departure timing was more pronounced during spring than autumn migration (Figs 2k, A2). The different species reacted differently to the length of the night both within and between the seasons (Table 3, Fig. A6). However, the most common pattern, which is delayed departures during longer nights, supports the suggestion that night duration is an important factor affecting the timing of departures (Bolshakov et al., 2007; Schmaljohann et al., 2013). Schmaljohann et al. (2013) based their conclusion that night duration affected departure time on data gathered from several species at different sites, and hence in different stages of their migration and under different environmental conditions (e.g. before barriers of different sizes). Here, we confirmed this pattern in several songbird species departing from the same stopover site. Falsterbo as a stopover site at a relatively high northern latitude may be expected to be visited relatively early during autumn migration and relatively late during spring migration. Hence, the majority of birds migrating during the same season can be expected to be in a similar migratory stage. Possibly, the migrants favour ending their nocturnal flights at dawn, when they can more easily find suitable habitat and foraging sites than during the dark night. This would explain why they waited on average almost 4 h (sun elevation $-15°$ to $-25°$; Fig. 2k–l) before departing on their nocturnal flights during the long autumn nights (see also Åkesson et al., 1996, 2001; Chernetsov, 2012). Thus, our results suggest that the birds may regulate their nocturnal flight period by departing at different times during the night. Information about flight durations and landing times are needed to fully understand the correlation between departure time and night duration.

A relationship between departure timing and length of the night might be an effect of progress of the season rather than night duration per se. Yet, if that was the case we would expect birds that migrate late during the migratory season to depart earlier in relation to sunset (to speed up and reduce their delay in migration) not only during spring, but also during autumn. Instead, the birds, irrespective of species, departed later with increasing night duration during both seasons, even though the effect was larger during spring migration (Fig. A2). At the species level, we observed earlier departures with the progression of both spring and autumn seasons only in song thrushes (Fig. A6). However, the majority of species delayed their departures with longer nights during both seasons, which supports the prediction that birds adjust their departure time as a response to night length. The much larger variation in departure timing during autumn than during spring migration and the more pronounced strategy to delay departures during long nights during autumn migration (Figs 2, A2, A6) further support the hypothesis that the effect is caused by night duration and not by progress of the season. Possibly, the short spring nights in Sweden, especially those close to summer solstice, force the birds to depart early after sunset to fit in a full night of flight after departure, while the long autumn nights leave room for extended flights without departing earlier. The earlier departures after sunset in spring than autumn migration could also be an effect of birds maximizing their migration speed in order to arrive early to the breeding grounds during spring migration (cf. Nilsson et al., 2013). More data with overlapping night durations during the different migratory seasons are required to fully disentangle the effects of night duration and progress of the season.

Relative Importance of Ecological Causes and Sensory Constraints

If orientation cues act as triggers for departure, we would have expected the birds to depart in a fixed range of sun elevations. Our results illustrate the opposite; the birds departed at a wide range of sun elevations during both autumn and spring migration (Fig. 2l). They departed on average at lower sun angles during autumn than during spring migration. In contrast to earlier observations, only a small proportion of the birds departed from Falsterbo during the nautical twilight period, when both stars and the polarized light pattern are visible (Fig. 2l). Instead, most birds departed after the nautical twilight period, allowing them to integrate all possible orientation cues before departure, supporting earlier observations that departures on nocturnal flights do not take place within a fixed range of sun elevations (Åkesson et al., 2001, 1996; Bolshakov et al., 2007; Schmaljohann et al., 2011; cf. Bolshakov et al., 2007). Thus, availability of orientation cues associated with the different twilight periods may limit how early a bird can depart, in order for it to fully integrate the information, but without limiting how late a bird can depart during the night. Departure associated with certain sun elevations would have caused the birds to depart later in relation to sunset during spring than during autumn migration (Fig. 1). However, we observed the opposite pattern, i.e. the birds departed earlier during spring than during autumn migration. If departures were triggered by factors related to the sky compasses, we would also have expected overcast conditions at sunset to delay departures. Indeed, during autumn migration cloud cover decreased during nights in which birds departed late, which supports previous suggestions that birds prefer to fly under clear skies (Åkesson et al., 2001). Altogether, availability of orientation cues seems to play a role in departure timing, mainly by limiting how early birds can depart, but it does not explain the observed variation in departure timing.

Intrinsic Factors

In line with our expectations, we found that lean individuals departed later than individuals with larger fuel stores, and the effect was more pronounced during autumn than during spring (fat reserves were on average larger in spring; Fig. 3, Table A1). Our finding that birds with larger fuel loads tended to depart earlier supports the energetic hypothesis (Moore & Aborn, 1996), which proposes that fat birds depart before leaner individuals, since they potentially have a longer upcoming flight. We have previously observed an

from those analyses, cf. text). Mean vectors (arrows) with length proportional to the mean vector length (cf. Batschelet, 1981) show the mean timing with 95% angular confidence intervals indicated by the dotted lines (cf. Table A1). Shaded sectors refer to the night (between mean times of sunset and sunrise) with the range of variation in sunset and sunrise times indicated by hatched sectors. Histograms i and j show the distribution of departure times in relation to sunset during autumn and spring, respectively. Mean departure time ($\pm$SE) in relation to sunset and season is plotted relative to average night duration for each species (k). Mean sun elevation at departure ($\pm$SE, degrees below horizon) is plotted relative to night duration (l), grey areas indicate nautical twilight (light grey; ends at sun elevation $-12°$) and astronomical twilight (dark grey; ends at sun elevation $-18°$). Data in i–l are restricted to the nocturnal and near-nocturnal period 1700–0500 CET.

Table 2
Differences in departure times throughout the 24 h of day/night between four species of nocturnal passerine migrants at Falsterbo

	N	Willow warblers	European robin	Garden warblers	Song thrushes
Autumn					
Willow warblers	40	–	<0.05	NS	<0.01
European robins	44	0.25	–	NS	NS
Garden warblers	18	0.08	0.08	–	NS
Song thrushes	39	0.28	0.07	0.10	–
Spring					
Willow warblers	30	–	ns	<0.001	NS
European robins	30	0.05	–	<0.001	<0.05
Garden warblers	28	0.43	0.45	–	<0.001
Song thrushes	26	0.15	0.22	0.45	–

Watson U^2 tests were used to compare the times of departure between the different species within each season, U^2 values for these pairwise tests are shown below the diagonal and P values are given above the diagonal.

Table 3
Effects of intrinsic and environmental factors on time of departure (hours after sunset) of nocturnal passerine migrants at Falsterbo peninsula during autumn and spring

	Sum of squares	F	df	P
Autumn				
Species	51.52	3.77	3	0.013
Age	16.87	3.71	1	0.057
Fat	29.22	6.43	1	0.013
Cloud cover	11.83	2.60	1	0.11
Wind speed	11.07	2.43	1	0.12
N/S component	23.34	5.13	1	0.026
E/W component	10.78	2.37	1	0.13
Night duration	11.13	2.45	1	0.12
Species∗fat	26.68	1.96	3	0.13
Species∗night duration	39.88	2.92	3	0.038
Spring				
Species	3.76	0.76	3	0.52
Age	2.77	1.69	1	0.20
Fat	0.25	0.16	1	0.70
Wind speed	13.07	7.95	1	0.006
N/S component	17.30	10.53	1	0.002
Night duration	14.51	8.83	1	0.004
Species∗age	18.23	3.70	3	0.016
Species∗fat	24.04	4.88	3	0.004
Species∗wind speed	16.87	3.42	3	0.022
Species∗night duration	18.86	3.83	3	0.013
Age∗fat	5.22	3.18	1	0.078

Results refer to F statistics of the final GLMs as determined by backward elimination according to AIC criteria. AIC autumn = 169.86, AIC spring = 65.03. The original full and final models, including the parameter estimates, are given in Tables A4–A7.

effect of fuel load on the probability of performing reverse or forward movements on short-term ringing recoveries at Falsterbo peninsula (Nilsson & Sjöberg, 2015). Northern wheatears, *Oenanthe oenanthe*, departing from stopover at Helgoland, Germany, with large fuel loads have been observed to depart earlier and in directions leading to longer flights over open sea compared to lean individuals (Schmaljohann & Naef-Daenzer, 2011). Similarly, lean Swainson's thrushes departed throughout the night in directions leading back inland from Fort Morgan peninsula, Alabama, while fat individuals departed shortly after sunset and in directions leading across the Gulf of Mexico (Smolinsky et al., 2013). We observed vanishing bearings indicating reverse movements during both spring (29 of 93 individuals) and autumn (40 of 102 individuals) migration. Contrary to our predictions that birds departing in the expected migratory direction would depart earlier than birds departing in other directions, our results failed to indicate any correlation between departure timing and vanishing bearing (grouped into forward and reverse migration, not included in the most parsimonious model for either autumn and spring migration; Fig. A4). The lack of correlation between vanishing bearing and departure timing contrasts with the observation that departures of

migratory and local scale movements are initiated at different times (Mills et al., 2011). However, almost all our tagged individuals had sufficient fuel deposits for the relatively short flight across the Baltic Sea, since we did not tag the very leanest individuals (Table A1), which might be why we did not find an effect of vanishing bearing on departure timing. The exclusion of diurnal departures in our analyses (only data from 1700−0500 CET were used in the GLMs) might have further prevented us from finding an effect of vanishing bearing. However, we previously observed that departure timing did not differ between departures on forward and reverse migration from Falsterbo peninsula, even when diurnal departures were included (Nilsson & Sjöberg, 2015). Furthermore, the vanishing bearings recorded by automated radiotelemetry systems may not fully correspond with the birds' travel direction (Deppe et al., 2015; Sjöberg & Nilsson, 2015), especially not when the birds are confronted with a barrier and might hesitate before departure.

Environmental Factors

Consistent with our predictions that birds would depart sooner after sunset in favourable flight conditions, the birds delayed their departure when wind conditions during sunset were not optimal, i.e. when wind speeds were high and winds opposing (Figs 4, A5). Wind conditions did not improve during nights when birds departed late. However, the birds might have postponed their departure awaiting better flight conditions. Delaying departures during unfavourable winds may be adaptive, if conditions improve later during the night. Additionally, flight duration will be shorter, and thereby energy expenditure not as large. Nocturnal songbird migrants tracked by radiotelemetry at a coastal stopover site in southeast Sweden have previously been observed to depart predominantly in tail wind conditions when crossing the sea on autumn migration flights (Åkesson & Hedenström, 2000). The effect of wind conditions on timing of nocturnal flights underlines the impact of weather conditions on bird migration (Åkesson & Hedenström, 2000; Åkesson, Walinder, Karlsson, & Ehnbom, 2002; Alerstam, 1979; Liechti, 2006; Richardson, 1978, 1990; Zehnder, Åkesson, Liechti, & Bruderer, 2002). Furthermore, as previously mentioned, cloud cover decreased after sunset on nights when birds departed late, and was included in the most parsimonious model for autumn migration (Table 3). However, it is not possible to disentangle whether the effect of overcast is an effect of decreased urge to migrate under suboptimal weather conditions rather than decreased availability of orientation cues.

Conclusion

We found a striking difference in departure times in relation to sunset between the migratory seasons, and interesting variation in
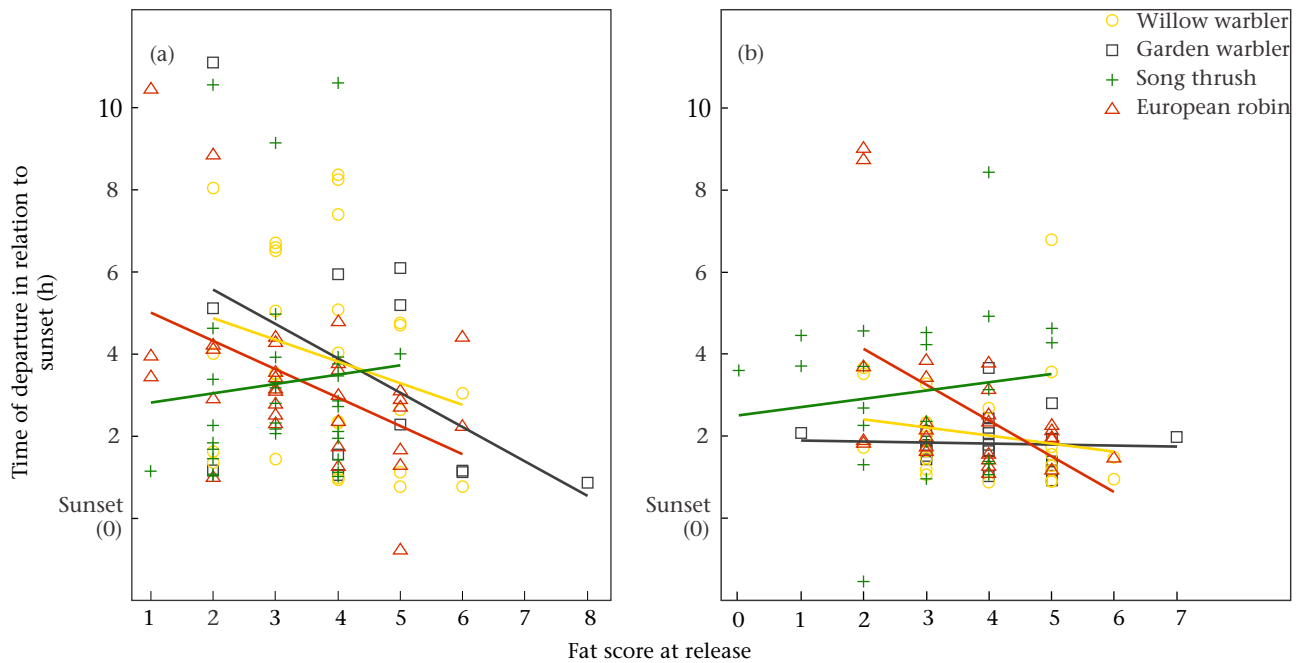
Figure 3. Time of departure (hours after sunset) in relation to fat score for nocturnal passerine migrants at Falsterbo during (a) autumn and (b) spring migration. For distribution of fuel load at departure for each species see Table A1.
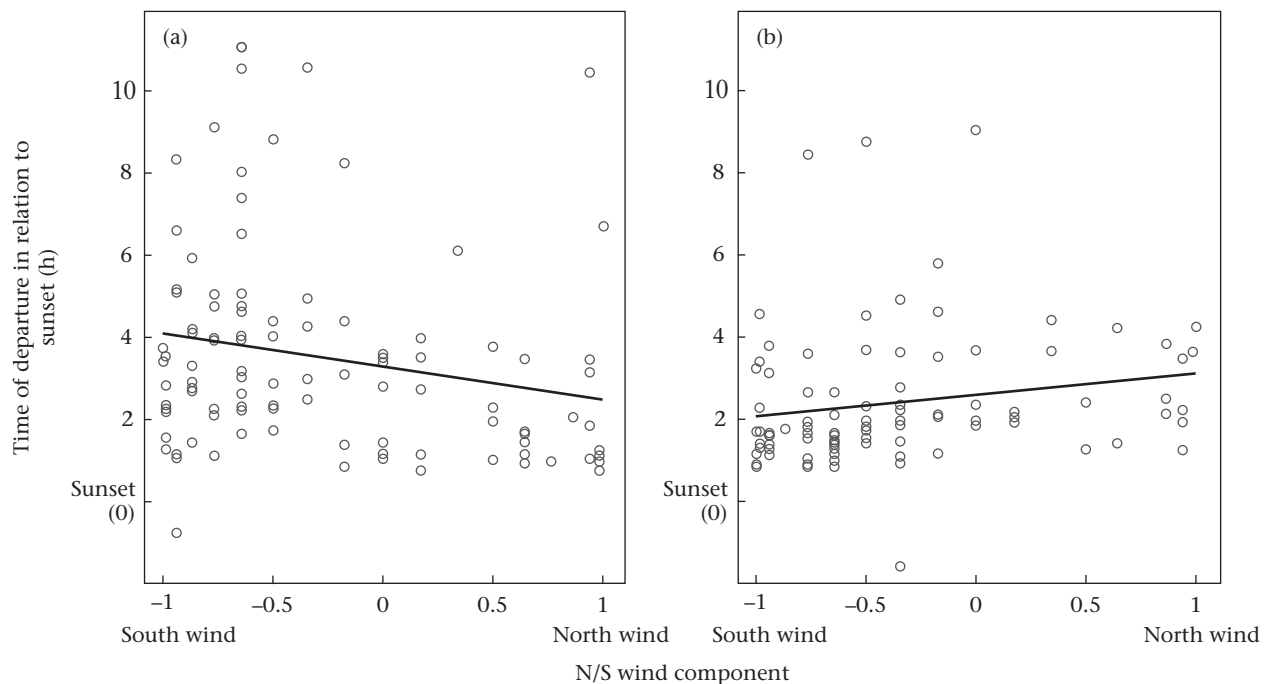
Figure 4. Time of departure (hours after sunset) in relation to N/S wind component (S winds = −1, N winds = 1) for nocturnal passerine migrants at the Falsterbo peninsula during (a) autumn (*N* = 102 individuals of four species) and (b) spring (*N* = 93 individuals of four species).

timing between the different species included in our study. This variation seems to be explained largely, but not fully, by differences in night duration, both between and within the seasons when the different species migrate. Our results clearly illustrate that the timing of departures on nocturnal flights is driven by species-specific ecological factors related to the migratory seasons, modified by intrinsic (mainly fuel reserves) and environmental factors

(mainly wind conditions). Furthermore, availability of celestial orientation cues associated with different twilight periods seems to limit how early a bird can depart, but does not explain the variation in departure timing later during the night. In summary, we found effects of migratory season, species, night duration, fuel load, age and wind conditions and cloud cover at the time of sunset on how migratory songbirds time their departure from a stopover site.

Acknowledgments

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Appendix

The Falsterbo peninsula is ideal for radiotelemetry since the area is relatively small, has a flat topography and is largely surrounded by water. The radiotelemetry system consists of three receiver stations (SRX600; Lotek Wireless) along the northeast—southwest coastline, mounted on top of a lighthouse (25 m above ground), a water tower (43 m above ground) and the roof of a farm building (5 m above ground) approximately 2.9 km apart (for map see Sjöberg et al., 2015). Each receiver is connected to three to five custom-made six-elements Yagi antennas matching the frequency band of the transmitters (151.5 MHz) via an eight-port antenna switchbox (ASP_8, Lotek Wireless). The antennas pointed in the following directions: lighthouse: 20°, 70°, 170°, 220°; farmhouse in 2009: 0°, 150°, 210°; from spring 2010 and onwards: 40°, 140°, 210°, 320°; water tower: 0°, 72°, 144°, 216°, 288°. At each station, the receivers sequentially monitored each antenna, so that every transmitter could be logged at least once per cycle at each antenna (scanning durations per antenna: 5.3 s in 2009 and 2010, 3.2 s in 2011—2013, resulting in total antenna cycle durations of 15.9—26.5 s in 2009 and 2010, 12.8—16 s in 2011—2013).

The receivers were active and continuously collected data throughout the study period. The gain was identical for all antennas to enable calculations of vanishing bearings. However, the gain of the different receivers was adjusted separately, since variations in location and surroundings affected the sensitivity of the receivers at the different stations to different degrees. Usually, gain was set to 70—90 (possible scale 0—99). This resulted in a maximum detection range of at least 3 km on the Falsterbo peninsula (we have detections of the same signal from all three receiver stations). For each detected signal the receivers collected ID code (individual), date, satellite-corrected time stamp based on GPS, antenna and signal strength (nonlinear scale 30—255). The data were filtered to remove false signals before analysis by making use of the transmitters' stable burst rates (4.9—5.2 s in 2009—2010; 2.9—3.1 s in 2011—2013). Specific burst interval was calculated for each transmitter (in ms) by making use of the binary files downloaded from the receivers, which contain the exact time of each signal (Mills et al., 2011; Taylor et al., 2011). For a signal to be included, at least three signals in the transmitter's specific burst interval, with a maximum error of ±10 ms, was required per min. The life span of the transmitters was guaranteed to be at least 18 days; however, we obtained several track records that significantly exceeded this. However, all signals from tags active for more than 24 days were excluded, since we could not tell for sure whether the transmitters were still attached to a living bird or whether the bird had died or dropped the transmitter.

A circular mean vanishing bearing was calculated from the last receiver station a bird was in contact with, using all valid signals from the bird's last 10 min at Falsterbo peninsula (Batschelet, 1981) and weighing each signal by signal strength (cf. Sjöberg & Nilsson, 2015). To be accurate, the calculations were made only if the bird was in contact with several (two or more) antennas during the last 10 min period. If a bird was in contact with several antennas from a receiver station different to the last station it was in contact with, the calculated direction from this receiver station was used as the vanishing bearing. Birds whose departures were recorded at only one antenna, and for which we could not calculate a vanishing bearing, were removed from the analyses on departure timing relative to sunset (subsample A). Previously, we estimated the mean measurement error of vanishing bearings ±SD to 9.5±12.1° (Sjöberg & Nilsson, 2015). To calculate the measurement error for vanishing bearings we attached radiotransmitters to dead birds. We hung the birds under helium balloons (at 50—100 m altitude) at known positions (0.3—3.0 km from the receiver station) and compared calculated directions based on the radiosignals (circular means of 10 min periods) with true directions. These errors may be slightly under- or overestimated, since the directions (loxodrome) were calculated from the receiver station to the position of the person holding the balloon, which did not always coincide with the exact position of the transmitter because of wind drift (up to approximately 10°), which increased the calculated error.

Table A1
Variation in fuel load (fat score) at release within each species within each migratory season

Species	Autumn				Spring			
	N	Mean±SD	Minimum	Maximum	N	Mean±SD	Minimum	Maximum
Willow warbler	27	3.78±1.15	2	6	22	3.95±1.29	2	6
European robin	32	3.43±1.39	1	6	26	3.62±1.13	2	6
Garden warbler	12	4.41±1.83	2	8	23	3.96±1.19	1	7
Song thrush	31	3.06±0.96	1	5	22	2.86±1.32	0	5

Table A2
Variation in transmitter weight in % body weight of the different species

Species	N	Mean±SD (%)	Minimum (%)	Maximum (%)
Willow warbler	70	3.99±0.37	3.15	4.93
European robin	74	2.14±0.14	1.72	2.41
Garden warbler	46	1.90±0.16	1.31	2.22
Song thrush	65	0.73±0.25	0.48	1.12

Table A3
Parameter estimates for the original and final GLM in the analysis of the effects of night duration and migratory season on departure timing

	Estimate[a]	SE	t	P
Original GLM				
Intercept	2.16	1.76	1.22	0.22
Night duration	0.11	0.15	0.78	0.44
Migratory season (autumn)				Intercept
Migratory season (spring)	−4.77	2.61	−1.83	0.069
Species (random factor)	0.00			
Night duration * migratory season	0.46	0.26	1.76	0.080
Species (random factor) * migratory season	0.00			
Final GLM				
Intercept	2.16	1.76	1.22	0.22
Night duration	0.11	0.15	0.78	0.44
Migratory season (autumn)				Intercept
Migratory season (spring)	−4.77	2.61	−1.83	0.069
Species (random factor)	0.00			
Night duration * migratory season	0.46	0.26	1.76	0.080

Species is included as a random factor, both as a main effect and in interaction with migratory season. AIC for the original model = 847.5, AIC for the final model = 845.5.
[a] Variance estimates for random factors.

Table A4
Parameter estimates for the original GLM in the analysis of the effects of intrinsic and environmental factors on timing of departure of nocturnal passerine migrants during autumn migration

	Estimate	SE	t	P
Intercept	9.16	8.31	1.10	0.27
Species (willow warbler)				Intercept
Species (European robin)	−10.58	10.76	−0.98	0.33
Species (garden warbler)	−27.81	26.93	−1.03	0.31
Species (song thrush)	8.55	13.85	0.62	0.54
Age (young birds)	−1.68	3.69	−0.45	0.65
Fat	−0.99	0.80	−1.25	0.22
Vanishing bearing (forward/ backward)	−1.13	1.06	−1.07	0.29
Cloud cover	0.09	0.20	0.45	0.66
N/S wind component	−1.69	0.81	−2.08	0.041
E/W wind components	−0.55	0.66	−0.84	0.41
Wind strength (m/s)	−0.10	0.24	−0.41	0.68
Night duration	−0.13	0.78	−0.17	0.87
Species (willow warbler) * age (young birds)				Intercept
Species (European robin) * age (young birds)	0.58	4.71	0.12	0.90
Species (garden warbler) * age (young birds)	2.92	11.15	0.26	0.79
Species (song thrush) * age (young birds)	4.31	4.68	0.92	0.36
Species (willow warbler) * fat				Intercept
Species (European robin) * fat	0.29	0.89	0.33	0.74
Species (garden warbler) * fat	0.58	4.04	0.15	0.89
Species (song thrush) * fat	1.49	1.05	1.41	0.16
Species (willow warbler) * vanishing bearing (forward/backward)				Intercept
Species (European robin) * vanishing bearing (forward/backward)	0.56	1.39	0.41	0.69
Species (garden warbler) * vanishing bearing (forward/backward)	3.31	4.22	0.79	0.44
Species (song thrush) * vanishing bearing (forward/backward)	2.63	1.68	1.57	0.12
Species (willow warbler) * cloud cover				Intercept
Species (European robin) * cloud cover	0.08	0.29	0.27	0.79
Species (garden warbler) * cloud cover	0.21	0.92	0.23	0.82
Species (song thrush) * cloud cover	−0.02	0.31	−0.08	0.94
Species (willow warbler) * wind strength (m/s)				Intercept
Species (European robin) * wind strength (m/s)	0.29	0.29	1.00	0.32
Species (garden warbler) * wind strength (m/s)	0.33	0.37	0.89	0.38
Species (song thrush) * wind strength (m/s)	0.19	0.30	0.64	0.52
Species (willow warbler) * N/S wind component				Intercept
Species (European robin) * N/S wind component	1.89	1.11	1.71	0.092
Species (garden warbler) * N/S wind component	2.24	2.24	1.00	0.32
Species (song thrush) * N/S wind component	0.43	1.10	0.39	0.70
Species (willow warbler) * E/W wind component				Intercept
Species (European robin) * E/W wind component	0.87	0.94	0.89	0.38
Species (garden warbler) * E/W wind component	−1.71	3.33	−0.52	0.61
Species (song thrush) * E/W wind component	−0.47	1.03	−0.46	0.65
Species (willow warbler) * night duration				Intercept
Species (European robin) * night duration	0.57	0.93	0.62	0.54
Species (garden warbler) * night duration	1.87	1.53	1.22	0.23
Species (song thrush) * night duration	−1.43	1.16	−1.24	0.22
Age (young birds) * fat	0.64	0.92	0.69	0.49
Species (willow warbler) * age (young birds)* fat				Intercept
Species (European robin) * age (young birds) * fat	−0.45	1.21	−0.38	0.71
Species (garden warbler) * age (young birds) * fat	−0.92	3.40	−0.27	0.79
Species (song thrush) * age (young birds) * fat	−0.86	1.30	−0.66	0.51

Table A5
Parameter estimates for the original GLM in the analysis of the effects of intrinsic and environmental factors on timing of departure of nocturnal passerine migrants during spring migration

	Estimate	SE	t	P
Intercept	−7.01	6.42	−1.09	0.28
Species (willow warbler)				Intercept
Species (European robin)	10.13	8.15	1.24	0.22
Species (garden warbler)	8.87	16.10	0.55	0.58
Species (song thrush)	−9.54	11.80	−0.81	0.42
Age (young birds)	−2.62	2.39	−1.10	0.28
Fat	−0.42	0.37	−1.13	0.26
Vanishing bearing (forward/backward)	0.44	0.92	0.48	0.64
Cloud cover	−0.11	0.14	−0.84	0.41
Wind strength (m/s)	0.28	0.20	1.39	0.17
N/S wind component	1.03	0.85	1.22	0.23
E/W wind components	−0.06	0.72	−0.08	0.94
Night duration	1.10	0.72	1.53	0.13
Species (willow warbler) * age (young birds)				Intercept
Species (European robin) * age (young birds)	1.71	3.15	0.37	0.71
Species (garden warbler) * age (young birds)	1.62	3.71	0.44	0.66
Species (song thrush) * age (young birds)	3.56	3.11	1.15	0.26
Species (willow warbler) * fat				Intercept
Species (European robin) * fat	−0.39	0.51	−0.77	0.45
Species (garden warbler) * fat	0.19	0.80	0.24	0.81
Species (song thrush) * fat	0.94	0.59	1.60	0.11
Species (willow warbler) * vanishing bearing (forward/backward)				Intercept
Species (European robin) * vanishing bearing (forward/backward)	−0.19	1.16	−0.17	0.89
Species (garden warbler) * vanishing bearing (forward/backward)	−0.43	1.20	−0.36	0.72
Species (song thrush) * vanishing bearing (forward/backward)	0.79	1.24	0.64	0.53
Species (willow warbler) * cloud cover				Intercept
Species (European robin) * cloud cover	0.16	0.18	0.89	0.38
Species (garden warbler) * cloud cover	0.09	0.19	0.49	0.63
Species (song thrush) * cloud cover	0.31	0.23	1.35	0.18
Species (willow warbler) * wind strength (m/s)				Intercept
Species (European robin) * wind strength (m/s)	0.19	0.24	0.77	0.44
Species (garden warbler) * wind strength (m/s)	−0.61	0.36	−1.67	0.10
Species (song thrush) * wind strength (m/s)	0.08	0.30	0.28	0.78
Species (willow warbler) * N/S wind component				Intercept
Species (European robin) * N/S wind component	−0.29	1.00	−0.29	0.77
Species (garden warbler) * N/S wind component	0.46	1.35	0.34	0.73
Species (song thrush) * N/S wind component	−1.42	1.39	−1.02	0.31
Species (willow warbler) * E/W wind component				Intercept
Species (European robin) * E/W wind component	−0.26	0.90	−0.29	0.76
Species (garden warbler) * E/W wind component	−0.25	0.97	−0.25	0.80
Species (song thrush) * E/W wind component	1.81	1.15	1.58	0.12
Species (willow warbler) * night duration				Intercept
Species (European robin) * night duration	−1.00	0.89	−1.13	0.26
Species (garden warbler) * night duration	−0.74	2.33	−0.32	0.75
Species (song thrush) * night duration	0.34	1.29	0.27	0.79
Age (young birds) * fat	0.84	0.56	1.50	0.14
Species (willow warbler) * age (young birds) * fat				Intercept
Species (European robin) * age (young birds) * fat	−0.62	0.78	−0.80	0.43
Species (garden warbler) * age (young birds) * fat	−0.47	0.91	−0.52	0.61
Species (song thrush) * age (young birds) * fat	−0.39	0.84	−0.46	0.65

Table A6
Parameter estimates for the final GLM in the analysis of the effects of intrinsic and environmental factors on timing of departure of nocturnal passerine migrants during autumn migration

|	Estimate	SE	t	P
Intercept	3.14	7.22	0.44	0.66
Species (willow warbler)				Intercept
Species (European robin)	−8.70	9.32	−0.93	0.35
Species (garden warbler)	−13.23	9.77	−1.36	0.18
Species (song thrush)	14.03	12.05	1.16	0.25
Age (young birds)	0.87	0.45	1.93	0.057
Fat	−0.52	0.37	−1.39	0.17
Cloud cover	0.15	0.09	1.61	0.11
Wind strength	0.13	0.09	1.56	0.12
N/S wind component	−0.83	0.37	−2.27	0.026
E/W wind component	−0.53	0.34	−1.54	0.13
Night duration	0.06	0.68	0.08	0.93
Species (willow warbler) * fat				Intercept
Species (European robin) * fat	−0.25	0.46	−0.54	0.59
Species (garden warbler) * fat	−0.11	0.56	−0.20	0.84
Species (song thrush) * fat	0.94	0.55	1.70	0.094
Species (willow warbler) * night duration				Intercept
Species (European robin) * night duration	0.67	0.81	0.83	0.41
Species (garden warbler) * night duration	1.19	0.84	1.41	0.16
Species (song thrush) * night duration	−1.45	1.02	−1.42	0.16

This model is described with F statistics in Table 3.

Table A7
Parameter estimates for the final GLM in the analysis of the effects of intrinsic and environmental factors on timing of departure of nocturnal passerine migrants during spring migration

|	Estimate	SE	t	P
Intercept	−9.52	5.07	−1.88	0.065
Species (willow warbler)				Intercept
Species (European robin)	12.98	6.30	2.06	0.043
Species (garden warbler)	13.03	10.28	1.27	0.21
Species (song thrush)	−15.59	8.97	−1.74	0.087
Age (young birds)	−0.77	1.15	−0.67	0.51
Fat	−0.36	0.25	−1.42	0.16
Wind strength (m/s)	0.16	0.15	1.05	0.30
N/S wind component	0.91	0.28	3.25	0.002
Night duration	1.40	0.56	2.49	0.015
Species (willow warbler) * age (young birds)				Intercept
Species (European robin) * age (young birds)	−1.53	0.80	−1.92	0.059
Species (garden warbler) * age (young birds)	−0.81	0.81	−1.00	0.32
Species (song thrush)* age (young birds)	1.11	0.90	1.24	0.22
Species (willow warbler) * fat				Intercept
Species (European robin)* fat	−0.50	0.33	−1.51	0.14
Species (garden warbler) * fat	0.02	0.37	0.05	0.96
Species (song thrush) * fat	0.78	0.33	2.35	0.022
Species (willow warbler) * wind strength (m/s)				Intercept
Species (European robin) * wind strength (m/s)	0.32	0.19	1.71	0.092
Species (garden warbler) * wind strength (m/s)	−0.31	0.22	−1.43	0.16
Species (song thrush) * wind strength (m/s)	−0.07	0.21	−0.32	0.75
Species (willow warbler) * night duration				Intercept
Species (European robin) * night duration	−1.29	0.69	−1.86	0.067
Species (garden warbler) * night duration	−1.33	1.37	−0.97	0.33
Species (song thrush) * night duration	1.37	0.93	1.45	0.15
Age (young birds) * fat	0.44	0.25	1.78	0.079

This model is described with F statistics in Table 3.
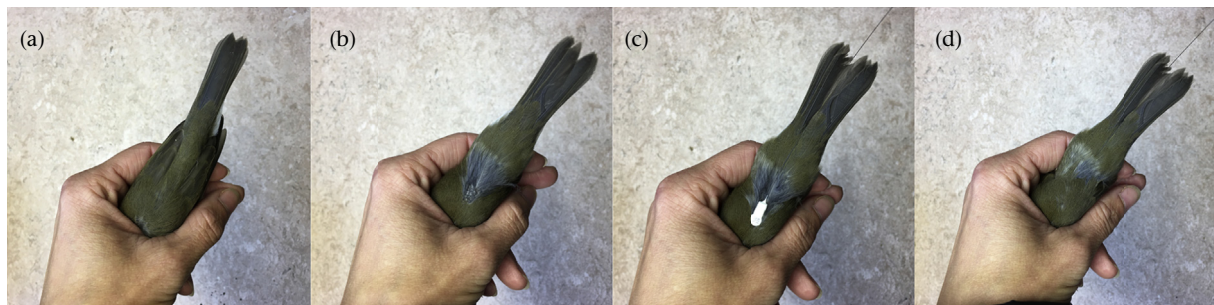
Figure A1. Illustration of attachment of a radiotransmitter showing a bird (a) before attachment, (b) after cutting the feathers on the back, (c) after attachment of the transmitter and (d) after covering the transmitter with feathers.
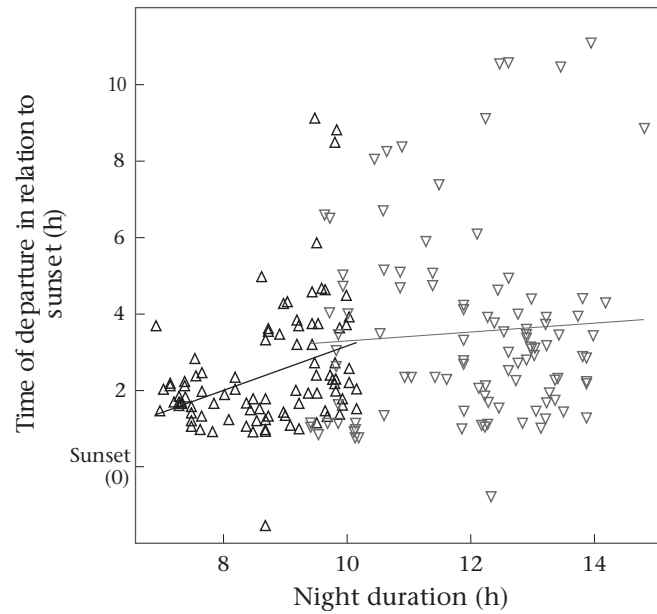
Figure A2. General effect of night duration on departure timing during spring (upward triangles) and autumn (downward triangles) migration.
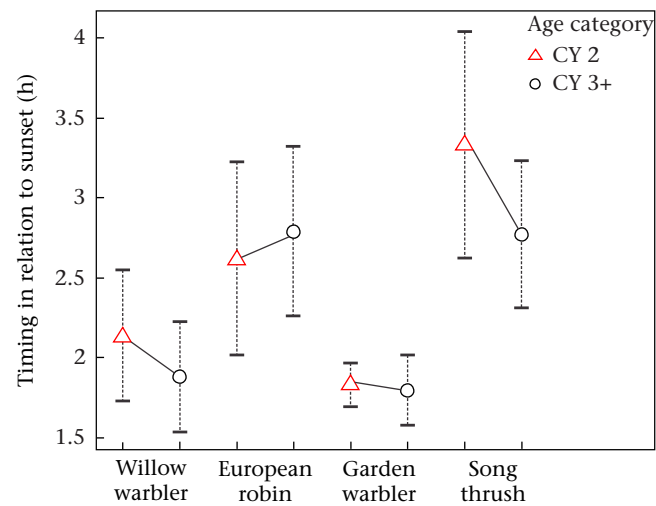
Figure A3. Effects of age on timing of departures during spring migration. Timing in relation to sunset is plotted for the different species and age categories (mean timing ±SE; for interaction effects see Table 3).
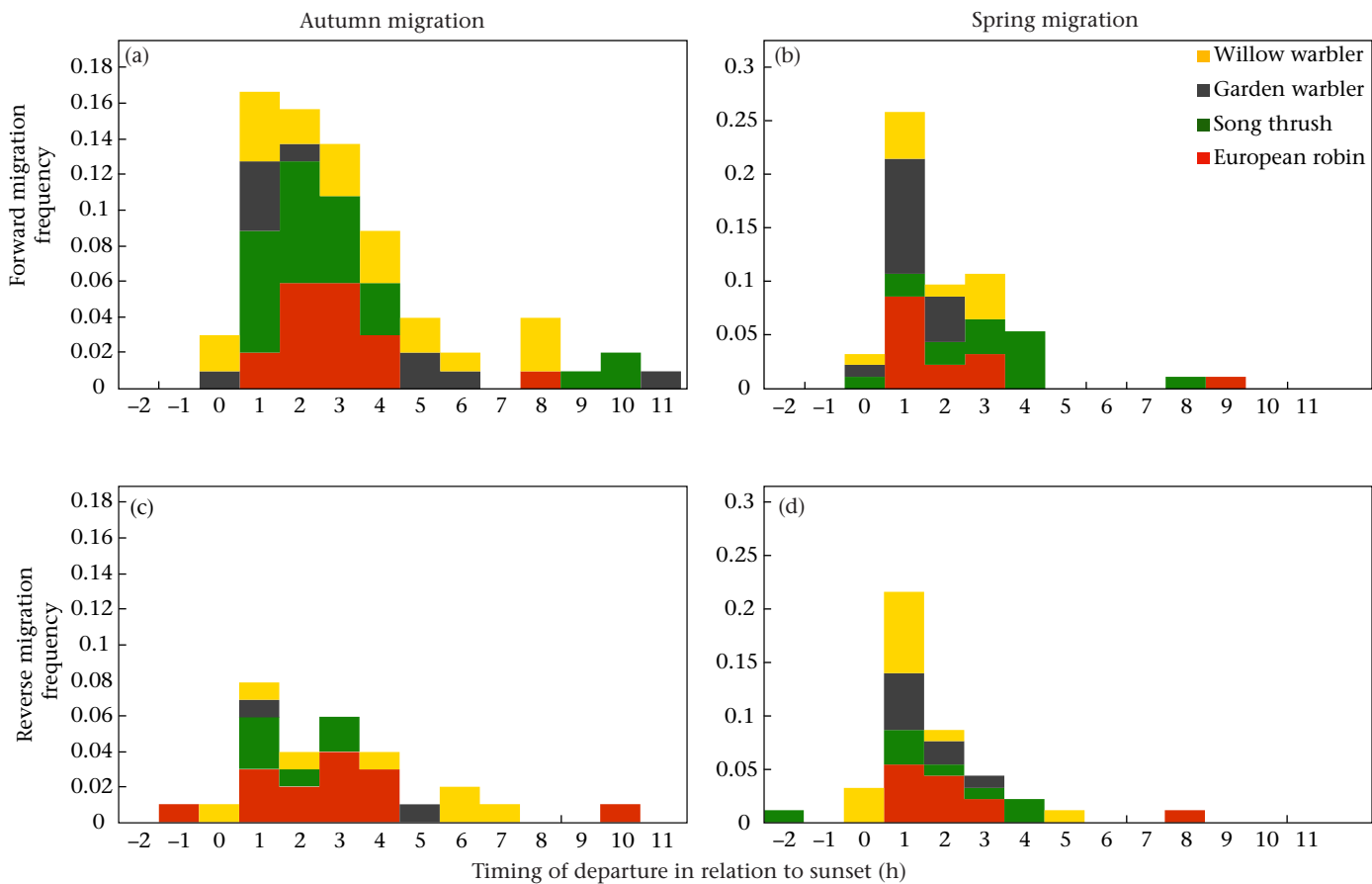
Figure A4. Distribution of departure times in relation to sunset during autumn and spring migration for the different species and individuals performing forward (90°–270° during autumn and 270°–90° during spring migration) and reverse (270°–90° during autumn and 90°–270° during spring migration) migration.
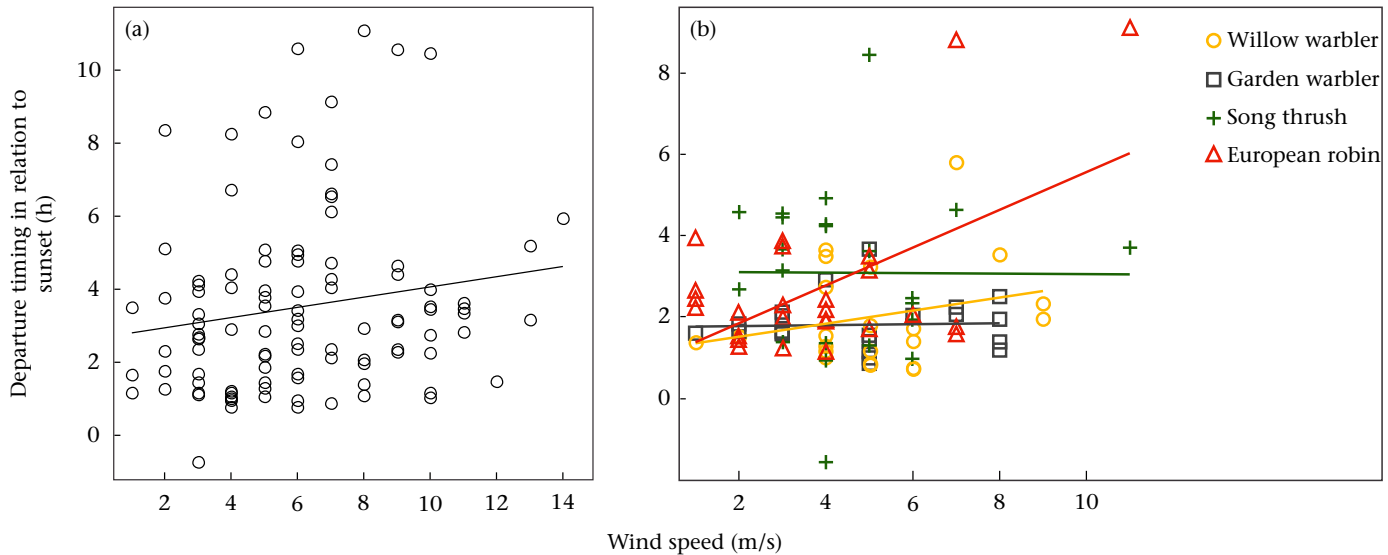
Figure A5. Effects of wind speed on timing of departures. Timing in relation to sunset is plotted in relation to wind speed at sunset during (a) autumn and (b) spring migration. See Table 3 for statistics.
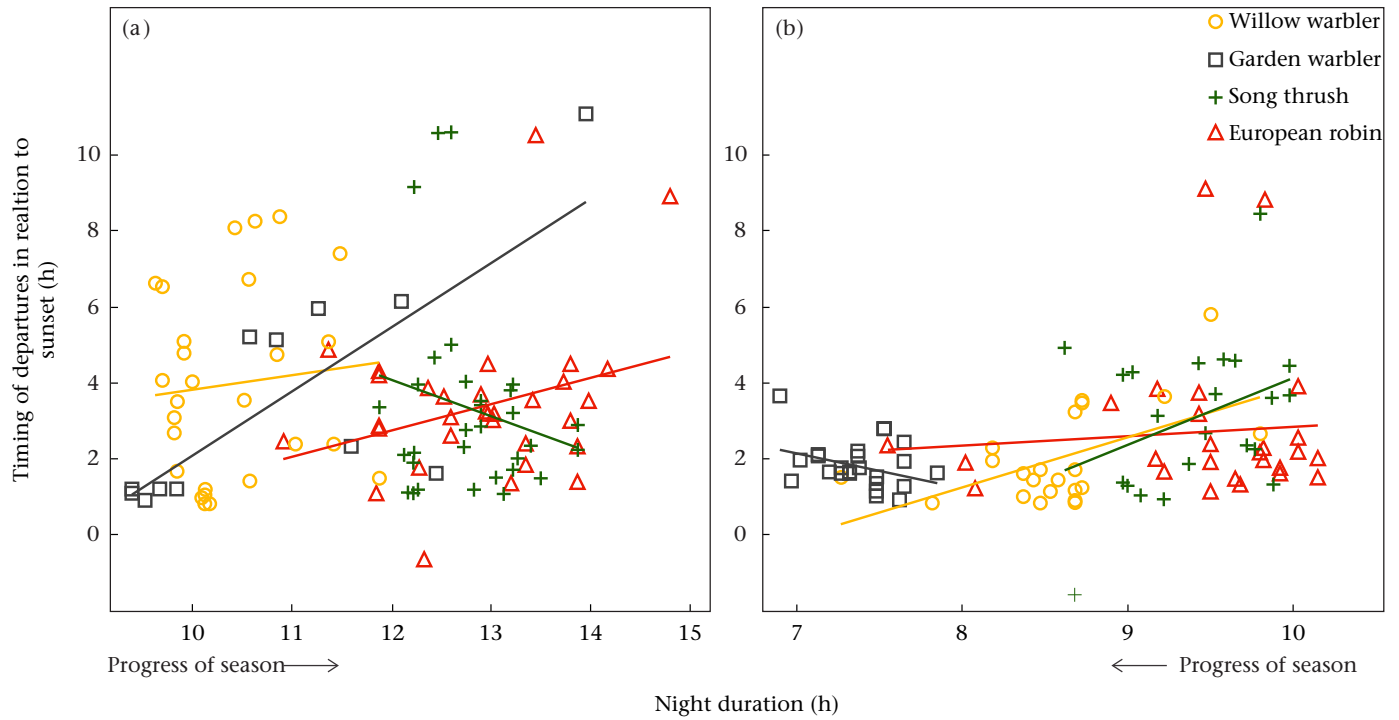
Figure A6. Time of departure after sunset in relation to night duration during (a) autumn and (b) spring migration. See Table 3 for statistics.