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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.

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

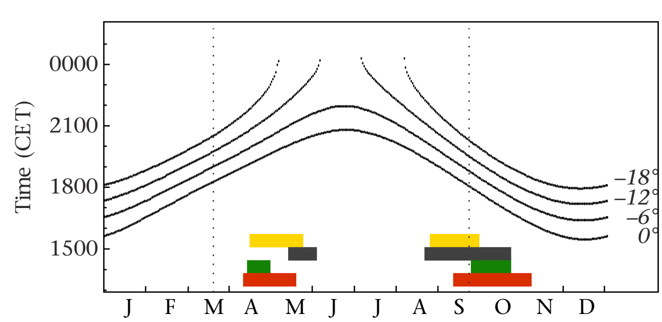

Figure 1. Illustration of annual timing of sunset and twilight periods at Falsterbo peninsula. Black lines represent sun elevation (0° = sunset/start of civil twilight; −6° = start of nautical twilight; −12° = start of astronomical twilight; −18° = start of night) and dotted vertical lines represent 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.