



Does the length of the night affect the timing of nocturnal departures in a migratory songbird?

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Many animals perform their migratory movements within discrete time periods of the day/night cycle. Among migratory songbirds the majority of species generally restrict their migratory flights to the night. This makes their nocturnal departure timing a key factor determining the potential duration of migratory flights, which in turn affects their travel speed. Previous correlative studies revealed that part of the variation in nocturnal departure timing of migratory songbirds is explained by the respective length of the night, with birds departing earlier when nights are short. As the length of the night is inextricably linked to the time within the season, it has been impossible to ascertain which of the two factors drives variation in nocturnal departure timing. To virtually decouple both factors, that is, length of the night and time within the season, we conducted a series of short-term experiments using migratory songbirds caught at stopover. These birds were exposed to nights of either natural or shortened length. We found that birds exposed to shortened nights showed slightly earlier nocturnal departures than those exposed to the natural length of the night. This coincided with a seasonal pattern in the start of nocturnal migratory behaviour (migratory restlessness during the experimental period and actual departures following release) among birds, irrespective of the experimental treatment. Based on these results we suggest that birds' nocturnal departure timing pursues an innate seasonal schedule of migratory activity, which is adjusted to the current length of the night. Such a mechanistic framework provides the potential for cross-calibrating birds' innate seasonal schedule of migratory activity with the current spatiotemporal progress during migration.

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A vast number of animals across various taxa perform seasonal migrations (e.g. Chapman et al., 2014), which facilitate the exploitation of periodically available resources during reproductive phases and/or the evasion of adverse conditions outside of these. During their migrations many of these animals follow a stop-and-go strategy with alternating cycles of migratory movements and stopover periods (e.g. Alerstam, 1990; Kennedy, 1951; McCord & Davis, 2012; Rice & Balazs, 2008; Sawyer & Kauffman, 2011; Åkesson & Hedenström, 2007). Migratory movements are often concentrated during discrete time periods of the day/night cycle (e.g. Alerstam, 2009; Cartamil & Lowe, 2004; Dujon, Schofield, Lester, Esteban, & Hays, 2017; Ibbotson et al., 2006; Perryman, Donahue, Laake, & Martin, 1999; Semlitsch & Pechmann, 1985). Many songbirds, representing the focal taxon

of the present study, restrict their migratory flights to the night (Alerstam, 1990, 2009; Berthold, 2001). Nocturnal migration reduces birds' energetic costs of transport (Kerlinger & Moore, 1989), water loss (Schmaljohann, Bruderer, & Liechti, 2008) and predation risk (Walter, 1979) compared to diurnal migration. Further, it optimizes birds' time budget for diurnal foraging and nocturnal migratory flights (Alerstam, 2009). The resulting temporally defined diel schedule for migratory flights makes nocturnal departure timing a key factor determining their potential duration and thus the respective distance covered per night. Total migration distance divided by the cumulative duration of migratory flights defines a bird's travel speed. Travel speed, together with the duration of premigratory fuelling and total stopover duration (Schmaljohann & Both, 2017), defines total speed of migration (Nilsson, Klaassen, & Alerstam, 2013). To maximize total speed of migration, nocturnal migrants were assumed to generally time their migratory departures shortly after sunset (Müller et al., 2016). In fact, there is evidence that, under constant laboratory

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conditions and in the absence of any environmental reference to time, migratory songbirds initiate their migratory activity consistently within a narrow time window during the early night (Coppack & Bairlein, 2011; Coppack, Becker, & Becker, 2008). This suggests defined circadian flight schedules based on the innate migration program. Under free-flying conditions, however, nocturnal departure timing of migratory songbirds is not restricted to the early night, but shows considerable temporal variation (Müller et al., 2016). This variation is probably explained by individually different innate migration programs, providing the basic schedule for their migratory activity (e.g. Berthold & Querner, 1981; Coppack & Bairlein, 2011; Gwinner, 1996), and by a set of individually different intrinsic and extrinsic factors which birds integrate for their nocturnal departure decisions (Müller et al., 2016). The result of this integration process is the specific phenotypic response of an individual, that is, its realized nocturnal departure timing in this case. Previous studies generally revealed that with increasing fuel stores (intrinsic factor) and improving wind conditions (extrinsic factor) birds advanced their nocturnal departure timing from stopover (Eikenaar, Müller, Kämpfer, & Schmaljohann, 2016; Schmaljohann & Naef-Daenzer, 2011; Sjöberg, Alerstam, Åkesson, & Muheim, 2017; Sjöberg et al., 2015; Smolinsky, Diehl, Radzio, Delaney, & Moore, 2013); but see (Bolshakov et al., 2007; Bulyuk, 2012; Bulyuk & Tsvey, 2006). Further, nocturnal departure timing was found to be generally earlier in spring than in autumn (Bolshakov et al., 2007; Sjöberg et al., 2017) and/or changed within migratory seasons (Eikenaar et al., 2016; Schmaljohann et al., 2013; Sjöberg et al., 2017). In either case, it was correlated with the current local photoperiod. Birds were found to depart earlier at night or with less temporal variation when nights were shorter, both between and within migratory seasons. This pattern has been interpreted as a behavioural adaptation to maximize the potential duration of nocturnal migratory flight and thus maximize travel speed (e.g. Eikenaar et al., 2016; Schmaljohann et al., 2013; Sjöberg et al., 2017). Yet, this interpretation remains ambiguous, because different species were found to respond differently to a change in the length of the night (Schmaljohann et al., 2013; Sjöberg et al., 2017). Additionally, the effect of the length of the night on nocturnal departure timing was found to be stronger in spring than in autumn within several species (Sjöberg et al., 2017). We further need to consider that the length of the night is a function of the bird's current location and the time within the season, so that both are inextricably linked in correlative studies. Thus, it is impossible to ascertain whether variation in nocturnal departure timing is driven by the length of the night or the time within the season, based on correlative results. It remains therefore a major challenge to assess whether birds (1) adjust their nocturnal departure timing to the currently experienced length of the night, (2) generally pursue an innate seasonal rhythm of migratory activity to time their departures independently of the currently experienced length of the night, or (3) base their nocturnal departure timing on an innate seasonal rhythm of migratory activity adjusted to the currently experienced length of the night (Müller et al., 2016).

We performed a series of short-term experiments, which aimed at the virtual decoupling of the length of the night from the time within the season, to investigate the respective effects on nocturnal departure timing. For these experiments we caught migrating songbirds, northern wheatears, *Oenanthe oenanthe* (wheatears hereafter), at a stopover site (island of Helgoland, southeastern North Sea) throughout their spring migratory season. The birds were randomly divided into two groups. During each experiment (three consecutive day/night cycles) one group was exposed to shorter than natural nights by simulating earlier sunrises (experimental group), while the other group experienced

the natural length of the night (control group). All other experimental conditions were kept constant. We measured birds' nocturnal migratory restlessness and determined the respective amount and start time, which we used as proxies for their departure probability and nocturnal departure timing, respectively (Eikenaar, Klinner, Szostek, & Bairlein, 2014; Schmaljohann, Kämpfer, Fritzsche, Kima, & Eikenaar, 2015). After release, we radiotracked birds' behaviour under free-flying conditions and determined actual departure probability and nocturnal departure timing.

If birds adjust their nocturnal departure timing to the currently experienced length of the night (1), we expected an earlier start of nocturnal migratory restlessness and earlier nocturnal departure in individuals exposed to shortened nights (experimental birds) than in those kept under the natural photoperiod (control birds). If birds generally pursue a seasonal rhythm to time their departures independently of the currently experienced length of the night (2), we expected an advance in both the start of nocturnal migratory restlessness and nocturnal departure over the course of the season among all individuals, but no effect of the experimental treatment. Finally, if birds' nocturnal departure timing is based on an innate seasonal rhythm of migratory activity adjusted to the currently experienced length of the night (3), we expected an effect of the experimental treatment (see 1) coinciding with an advance over the course of the season (see 2) in both the start of nocturnal migratory restlessness and nocturnal departure.

METHODS

Study Site and Study Species

The study was conducted on Helgoland (54°11'N, 07°53'E), a small island in the North Sea approximately 50 km off the German coastline. In spring (April–May) 2016, wheatears were caught during stopover. All birds were ringed, aged and sexed according to Svensson (1992). We measured wing length (maximum chord) to the nearest 0.5 mm (Svensson, 1992) and body mass to the nearest 0.1 g. Wheatears of two subspecies (*O. o. oenanthe* and *O. o. leucorhoa*) pass Helgoland during their migratory periods (Corman, Bairlein, & Schmaljohann, 2014). Wing length was used to assign birds to a subspecies according to Svensson (1992).

Experimental Set-up

Following capture, birds were transferred to individual cages (40 × 30 cm and 40 cm high) set up in two indoor rooms with artificial lighting. Rooms were equipped with 10 cages each. Room temperature and relative humidity were kept constant at approximately 20 °C and 54%, respectively. Birds had ad libitum access to food (mealworms) and water. Food was provided between local natural sunrise and 1 h before local natural sunset in both rooms.

During the experiments, birds experienced one of two different light:dark (L:D) schedules (Fig. 1a). One L:D schedule followed the current local photoperiod (lights on at sunrise and off at sunset; control conditions: CON). The other L:D schedule featured a shortened dark phase (lights on 2 h before sunrise and off at sunset; experimental conditions: EXP; Fig. 1a). The resulting difference of 2 h in these L:D schedules is within the range of change in the natural photoperiod during the wheatear spring migration on Helgoland. Each experiment lasted for three consecutive nights. Subsequently, birds were released in a cohort of up to 20 individuals (approximately 10 per treatment) about 1–1.5 h before local sunset. Birds that left the study site during the night after

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