



## Fuel accumulation advances nocturnal departure: a migratory restlessness study on northern wheatears at stopover



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Migrating animals typically make stopovers to rest and replenish the fuel used during previous travel bouts. In birds, fat or fast refuelling individuals are generally more likely to depart from stopover than lean or slow refuelling birds. The departure decision, however, involves more than the day-to-day departure likelihood. Also, the time of night (or day) at which migrants depart is relevant, as this largely determines the duration of the flight bout and thereby affects the speed of migration. Because stopovers serve to replenish fuel stores, longitudinal data are most informative regarding the relationship between fuel stores and nocturnal departure time, but no such data exist. To fill parts of this gap, we caught and temporarily caged migrating northern wheatears, *Oenanthe oenanthe*, at a spring stopover site. We related the birds' evening fuel stores to their start of nocturnal migratory restlessness. In northern wheatears, this is a reliable proxy for their actual departure time under free-flying conditions. We observed a strong negative within-individual effect of fuel stores on the start of migratory restlessness. With an increase in fuel stores birds advanced their start of restlessness. This clearly shows that evening fuel stores are important for migrants' timing of departure at night. Hence, next to the regulation by innate rhythms, the timing of nocturnal departures during spring migration also depends on cues from fuel stores.

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Animal migration generally consists of alternations of migratory movements with stopover periods. During stopover animals rest and/or replenish fuel used during previous migratory stages. In birds, the rate of fuel replenishment at stopover is lower than the rate of fuel expenditure in flight (Alerstam & Lindström, 1990). The time required to complete migration is therefore mainly determined by the duration of stopovers and to a lesser extent by the total time spent flying (Schmaljohann, Fox, & Bairlein, 2012; Wikelski et al., 2003). Consequently, factors shaping a migrant's decision to leave a stopover site and resume migration have a paramount effect on the total duration of migration (Nilsson, Klaassen, & Alerstam, 2013). Total duration of migration may affect, through the actual arrival time at the breeding and/or wintering grounds, migrants' fitness (Currie, Thompson, & Burke, 2000; Marra, Hobson, & Holmes, 1998; Marra & Holmes, 2001; Smith & Moore, 2005). Owing to the importance of stopover duration for migrants' fitness, factors shaping stopover departure decisions are well studied. For example, it has repeatedly been

shown that both the size and the accumulation rate of fuel (fat) stores are critical to this decision, with fat or rapidly refuelling birds being more likely to depart than lean or slowly refuelling birds (e.g. Bairlein, 1985; Eikenaar & Schläpke, 2013; Goymann, Spina, Ferri, & Fusani, 2010; Schaub, Jenni, & Bairlein, 2008; Schmaljohann et al., 2013). Thus, by affecting departure likelihood, fuel stores and refuelling shape the speed of migration.

A parameter that has received relatively little attention, but that none the less could also have a pronounced influence on the speed of migration, is the time of departure during the day. As most migratory bird species travel exclusively at night (Bruderer, 1997; Dorka, 1966), the time after sunset at which a bird departs from stopover largely determines the duration of that night's flight bout. Traditionally, migrants were assumed to generally set off shortly after sunset (reviewed in Moore, 1987). Later radiotelemetry studies, however, revealed considerable variation in nocturnal departure time between individuals of the same species (Åkesson, Alerstam, & Hedenström, 1996; Bolshakov & Chernetsov, 2004; Moore & Aborn, 1996; Schmaljohann & Naef-Daenzer, 2011; Smolinsky, Diehl, Radzio, Delaney, & Moore, 2013). Some of these studies found that, similar to departure likelihood, part of this variation is explained by current fuel stores; fat individuals departed early in the night, whereas in lean individuals nocturnal

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departure time was highly variable (Schmaljohann & Naef-Daenzer, 2011; Smolinsky et al., 2013). By departing early, fat migrants are able to make longer flight bouts than lean migrants (Moore & Aborn, 1996; Schmaljohann & Naef-Daenzer, 2011). Other studies, however, did not find an effect of fuel stores on nocturnal departure time (Bolshakov & Chernetsov, 2004; Schmaljohann et al., 2011, 2013). The main purposes of stopover are to rest and/or to replenish fuel stores. Hence, to investigate the relationship between fuel stores and departure time, it may be more informative to relate changes in fuel stores, rather than current fuel stores, to departure time. This was the aim of the current study.

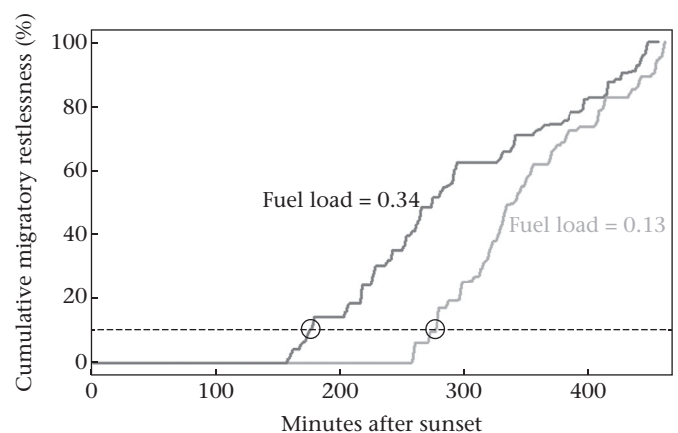
Obtaining accurate measurements of changes in fuel stores in free-flying individual migrants is notoriously difficult (Delingat, Dierschke, Schmaljohann, & Bairlein, 2009). Therefore, we caught migrating northern wheatears, *Oenanthe oenanthe* (wheatear hereafter) at stopover, and subsequently caged them for 3 days allowing us to repeatedly measure their evening fuel stores and their subsequent start of nocturnal migratory restlessness. Wheatears are well suited for our aims; when caged most individuals immediately start feeding with refuelling rates comparable to those measured in the field (Corman, Bairlein, & Schmaljohann, 2014; Eikenaar & Schläfke, 2013). More importantly, the start of nocturnal migratory restlessness is a good proxy for nocturnal departure time in free-flying wheatears, as the start of restlessness in the cage predicts actual departure time in the field the night following restlessness measurements (Schmaljohann, Kämpfer, Fritsch, Kima, & Eikenaar, 2015). With our approach we can thus investigate how fuel stores affect an individual's motivation to depart at a certain time of night. We expected that the size of a migrant's fuel stores would predict the start of migratory restlessness during the night, in that the larger an individual's fuel stores are, the earlier it starts to show restlessness.

## METHODS

The study was conducted on Helgoland (54°11' N, 07°55' E), a small island ca. 50 km off the German North Sea coastline. Wheatears are nocturnal long-distance migrants that pass Helgoland during spring and autumn migration, but rarely breed on the island (Dierschke, Dierschke, Hüppop, Hüppop, & Jachmann, 2011). In 2014 and 2015 throughout April and May, the peak of wheatear spring migration on Helgoland (Dierschke et al., 2011), the birds were caught using mealworm-baited spring traps. Traps were monitored continuously and upon trapping, birds were ringed, wing length (maximum chord) was measured to the nearest 0.5 mm, and body mass to the nearest 0.1 g. Birds were sexed based on plumage (Svensson, 1992). Wing length was used to differentiate the subspecies *O. o. oenanthe* and *O. o. leucorhoa* (Svensson, 1992). The *leucorhoa* wheatears making stopovers on Helgoland breed in Iceland, Greenland and northeastern Canada, whereas the *oenanthe* wheatears passing Helgoland are mainly Scandinavian breeding birds (Delingat, Hobson, Dierschke, Schmaljohann, & Bairlein, 2011). Individuals that could not be assigned to subspecies were not considered in this study. About 1 h after trapping, birds were put in individual cages (40 × 40 cm and 30 cm high) set up in a single indoor room with artificial lighting. In total 219 adult wheatears (105 males and 114 females) were caged for 3 consecutive nights, after which they were released in the morning. Throughout the study the lights in the room were switched on at local sunrise and switched off at local sunset. The temperature in the room was held constant at ca. 20 °C, and birds had ad libitum access to water. Each morning, immediately after lights were switched on, each bird was weighed to the nearest 0.1 g, after which it received ad libitum food (40 g of mealworms). In the evening, 1 h before lights off all birds were weighed, and food trays

were removed. Evening fuel stores were calculated as: evening fuel load = (evening body mass [g] – lean body mass [g])/lean body mass [g]. Lean body mass was calculated from a linear regression based on 220 'lean' wheatears caught on Helgoland in previous years: lean body mass [g] = 0.29 g/mm × wing length [mm] – 6.85 g (linear regression:  $N = 220$ ,  $F_{1,218} = 95.07$ , adjusted  $R^2 = 0.30$ ,  $P < 0.0001$ , after Schmaljohann & Naef-Daenzer, 2011). Fuel load thus represents the estimated amount of fuel a bird carries relative to its lean body mass. We stress here that our estimation of fuel load is only a simplified description of the actual amount of energy, i.e. fat and protein, a bird potentially has for its migratory flight. More robust estimates could be obtained by using a quantitative magnetic resonance body composition analyser, e.g. Guglielmo, McGuire, Gerson, and Seewagen (2011).

Migratory restlessness was recorded automatically with motion-sensitive microphones, which were attached to the right wall of each cage. Each time a bird moved, this generated an impulse that was transmitted to a recording device. To exclude nonmigratory activity, a bird had to generate at least 3 impulses/s before it was recorded as an activity count (following Maggini & Bairlein, 2010). A second machine produced a CSV file in which the activity counts were summarized over 1 min periods. The start of migratory restlessness was defined as the time (min) after lights off when the 10th quantile of the cumulative migratory restlessness over the entire night was reached (Fig. 1). This measure has been shown to be a good proxy for actual departure time (Schmaljohann, Kämpfer, et al., 2015). The frequency distributions of the start of restlessness in the two subspecies are depicted in Fig. 2. A potential issue for our study was that on some nights (usually the first) a bird showed no restlessness at all prohibiting the calculation of the 10th quantile ( $N = 8$ ), or showed restlessness only late at night ( $N = 50$ ). As field studies on radiotagged wheatears ( $N = 63$ ) have shown that wheatears do not depart from Helgoland later than 360 min after sunset (Schmaljohann et al., 2011; Schmaljohann, Kämpfer, et al., 2015; Schmaljohann & Naef-Daenzer, 2011), we expect that these late starts of restlessness are not indicative of departure-related behaviour in the cage. Therefore, when a bird showed no restlessness or started restlessness more than 360 min after lights off, we excluded this night from the data set.



**Figure 1.** An example of the cumulative migratory restlessness of an individual wheatear on 2 different nights. Start of migratory restlessness was defined as the time (minutes after sunset) when the 10th quantile of the cumulative restlessness (dashed line) was reached. The evening fuel loads of the bird on the 2 different nights are given in the shade of grey corresponding to that of the cumulative line. With an evening fuel load of 0.34 this bird started its migratory restlessness 102 min earlier than when it had a fuel load of 0.13.

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