To fuel their migratory endurance flights, most birds accumulate large quantities of fat prior to departure. It therefore seems logical that the decision to depart on a migratory flight depends on fuel stores, at least to some extent; very small fuel stores prohibit migratory endurance flight. However, studies linking migrants’ estimated fuel stores (or sometimes actual fat stores) to departure likelihood or to migratory restlessness measured in captive birds (an accurate proxy for migrants’ motivation to depart from stopover) have provided inconsistent results. Fuel stores are not static though, but highly dynamic. Instead of investigating fuel stores at a given time, we therefore focussed on quantifying the dynamic process of fuelling and how it affects migrants’ motivation to depart. We did so by temporarily caging wild northern wheatears Oenanthe oenanthe at a stopover site during autumn migration. Birds were kept under controlled conditions, receiving ad libitum food. Changes in fat mass (measured by quantitative magnetic resonance) and migratory restlessness were closely monitored. We found that the change in fat mass was a good predictor of the change in migratory restlessness. Individuals accumulating little fat did not show much change in their restlessness, while individuals accumulating much fat showed a strong increase in restlessness. Our study therewith provides clear support for the idea that fat stores affect birds’ motivation to migrate, and shows that for migrating birds, increasing fat stores are an important cue to depart from stopover. Fat accumulation affected the change in migratory restlessness in the same manner for relatively lean and relatively fat birds. Additionally, food intake or changes therein did not explain the change in migratory restlessness we observed. We therefore hypothesize that the fat tissue itself signals changes in energetic state, likely through production and release of hormones, affecting birds’ motivation to migrate.

Keywords: avian, departure, fattening, timing, Zugunruhe
Introduction

To fuel their migratory endurance flights, birds mainly (95%) burn fat and to a lesser extent (5%) protein (Jenni and Jenni-Eiermann 1998). The fuel is amassed by a combination of intense feeding and metabolic and hormonal adaptations (Bairlein 1985, 2002, Ramenofsky 1990), and stored in the bird’s body, much of it subcutaneously. Such fuelling occurs prior to migratory departure from the breeding or wintering grounds, and at stopover sites in between flight bouts until the final destination is reached. As fully depleted fuel stores preclude endurance flight, for lean birds fuel stores logically affect the motivation to leave a stopover site and depart on a migratory flight (Loria and Moore 1990, Fusani et al. 2009, Goymann et al. 2010). Many individual migrants, however, do not arrive at stopover with fully depleted fuel stores, and fuelling is not the only reason why migrants land at a stopover site. Migrants may land, for example, to avoid flying during the day (Alerstam 2009) or in inclement weather (Shamoun-Baranes et al. 2017), to reduce the amount of oxidative damage incurred during flying (Eikenaar et al. 2020), or because they need to compensate for sleep loss as a consequence of nocturnal flight (Ferretti et al. 2019). For those migrants carrying enough fuel to support the next flight, the effect that fuel stores may exert on the motivation to depart from stopover may not be as clear cut as it is for lean individuals.

Indeed, although many cross-sectional studies have observed a positive association between the size of the fuel stores and departure likelihood (Cherry 1982, Loria and Moore 1990, Fusani et al. 2009, Goymann et al. 2010, Smith and McWilliams 2014, Dossman et al. 2016, Packmor et al. 2020), quite a few other studies did not find such an association (Ellegren 1991, Salewski and Schaub 2007, Tsvey et al. 2007, Andueza et al. 2013, Beauchamp et al. 2020). As fuel stores are highly changeable over the stopover period (Lindström 1991, Delingat et al. 2009), perhaps a more robust way to investigate the link between migrants’ fuel stores and their motivation to depart is to collect within-individual data. Previous theoretical and empirical work has investigated whether and how the rate of fuelling (fuel deposition rate, FDR) impacts departure behaviour (Alerstam and Lindström 1990, Hedenström 2008, Alerstam 2011, Schmaljohann and Eikenaar 2017, and references therein).

Most of these studies hypothesized and tested for an effect of FDR on departure fuel stores (fuel load) as a cross-sectional variable, although in a few cases departure likelihood was used as the dependent variable instead of departure fuel load (Schaub et al. 2008, Schmaljohann and Eikenaar 2017). Stopovers, however, are dynamic periods during which a migrant’s motivation to depart may change as a consequence of changes in internal and external factors, such as fuel stores and weather conditions, collectively termed departure cues (Jenni and Schaub 2003). To investigate whether fuel stores act as a departure cue for migrating birds, a within-individual study of migrants’ motivation to depart may therefore be a desirable addition to the cross-sectional studies on FDR. If fuel stores indeed affect the motivation to depart on a migratory flight, changes in fuel stores should be accompanied by changes in a bird’s motivation to depart on a migratory flight. As a measure of birds’ motivation to migrate, researchers have routinely used the intensity of (nocturnal) migratory restlessness, also called Zugunruhe (Gwinner et al. 1988, Yong and Moore 1993, Smith and Norment 2005, Lupi et al. 2017, Klimmer et al. 2020). Migratory restlessness occurs when migratory birds are confined to a small space during the migration periods, and consists mainly of wing-fluttering and hopping (Biebach et al. 1985, Berthold et al. 2000). Taking advantage of this behaviour at a spring stopover site, Eikenaar and Schläfke (2013) showed that in northern wheatears Oenanthe oenanthe temporarily caged with ad libitum access to food, within-individual change in fuel stores was positively correlated with the within-individual change in nocturnal migratory restlessness. This strongly indicates that in spring, fuel stores are important for the decision to depart on a migratory flight.

Here, we performed a comparable and complementary study to that of Eikenaar and Schläfke (2013) during autumn migration. Spring and autumn migration are different life-cycle stages, with (passerine) migrants typically being ‘hurried’ to timely reach their breeding territories and making shorter stopovers in spring than in autumn (Schmaljohann 2018). Another difference to the study of Eikenaar and Schläfke (2013) is that, instead of estimating the birds’ fuel stores, we determined the birds’ fuel stores by measuring their fat mass using quantitative magnetic resonance (QMR). QMR is a non-invasive method that can be used to accurately and rapidly (ca 6 min for this study) measure fat mass in live, non-sedated birds (Guglielmo et al. 2011).

Methods

Experimental procedures

The study was conducted on Helgoland (54°11′ N, 07°55′ E), a small island ca 50 km off the German North Sea coast. Northern wheatears (wheatears hereafter) are nocturnal long-distance migrants that very rarely breed on Helgoland (Dierschke et al. 2011). Birds caught on Helgoland mostly originate from Scandinavia, Iceland and Greenland (Delingat et al. 2011). Wheatears are exceptionally suited to free-flying conspecifics (Eikenaar et al. 2019).

From 18 August to 5 September 2020, 33 (27 1st year birds and six adults) migrating wheatears were caught using mealworm-baited spring traps. Upon trapping, birds were ringed, weighed to the nearest 0.1 g and tarsus length was measured to the nearest 0.1 mm. Birds were caught between 8:50 a.m. and 12:30 p.m., and put in individual cages (40 × 40 × 30 cm) within 1 h of trapping. Birds were held in captivity for three nights, after which they were released. Cages
were set up in an indoor room with artificial lighting, which was switched on at local sunrise and switched off at local sunset. At night 30 small LED lamps (LED-band, naturnah VollspektrumLicht, Wrestedt, Germany) distributed over the ceiling produced dim white light conditions of 2.5 mW m$^{-2}$ intensity. Upon caging and every subsequent morning at lights on, each bird received a food tray with 40 g of live mealworms *Tenebrio monitor*, i.e. ad libitum food supply (Fig. 1). Food was removed at lights off and weighed to determine daily food intake. Hourly food intake was calculated by dividing daily food intake by the number of hours the birds had access to the food on that day. For one bird we could not calculate food intake on the first day in captivity, because of food spilling. The temperature in the room was held constant at approx. 22°C, and birds had ad libitum access to water.

The birds were weighed and their fat mass was determined by QMR (below) on the day of caging and again two days later with QMR sessions starting ca 2 h before lights off (Fig. 1). Consequently, the QMR measurements and recording of nocturnal migratory restlessness were temporally close, but not too close for handling stress from QMR measurements affecting migratory restlessness (in long-term captive wheatears, high corticosterone levels as a result of handling stress are back to baseline within 30–60 min, CE, unpubl.). Nocturnal migratory restlessness was recorded automatically with motion-sensitive microphones, attached to the right wall of the cages. Each time a bird moved, this generated an impulse that was transmitted to a recording device. To avoid the recording of occasional non-migratory activity, we set a threshold of three impulses per second before it was recorded as an activity count (Maggini and Bairlein, 2010). Intensity of migratory restlessness was defined as the number of 15 min periods between 1 and 5.5 h after lights off, during which a bird showed at least five activity counts, as this proved to be a good approximation for the motivation of free-flying wheatears to resume migration (Eikenaar et al. 2014). All procedures were approved by the Ministry of Energy, Agriculture, the Environment, Nature and Digitalization, Schleswig-Holstein, Germany (permit number V 242-37068/2016).

**QMR measurements**

We followed the procedures of Kelsey and Bairlein (2019). QMR measurements were conducted using the EchoMRI™ (EchoMRI Body Composition Analyser E26-262-BH, Zinsser Analytic GmbH, Frankfurt am Main, Germany). The EchoMRI was placed in a room with temperature kept at ca 20°C and calibrated every morning with a canola oil standard to ensure the correct functioning of the unit. The settings of the EchoMRI software were customized for analysis of birds > 10 g (‘BIRD’) with ‘three accumulations’, resulting in three consecutive scans, each giving a fat mass. From the three consecutive scans we calculated a mean fat mass. Following Kinner et al. (2020), if the value from one of the scans was more than 0.5 g away from the other two values, it was regarded an outlier and excluded from the calculation of the mean. For three birds each value differed more than 0.5 g from the other two values, which rendered all values outliers. Data of these three birds were excluded from all statistical analyses. Repeatability of the three scans (i.e. excluding QMR measurements with outliers) was 0.98. When scanning, the birds were put into a nylon stocking, with a hole for the bill to stick through (for unobstructed breathing), and placed head-first and ventral side down into a plastic holding tube which was then inserted into the EchoMRI. To restrict the movement of the birds and resulting measurement error, a stopper was placed behind the bird.

At the time of measurements, the birds were not fasted. However, the noise in the QMR data produced by fat from ingested food likely is very small; some birds with a fat mass close to 0 g on the day of caging ate well that day (> 8 g), indicating that the contribution of fat from ingested mealworms to the fat mass as measured in the EchoMRI cannot have been very large. Moreover, all birds ate well while in captivity (mean and SD hourly food intake was $1.21 \pm 0.41$ g and $1.18 \pm 0.27$ g on the first and third day in captivity, respectively) and thus probably had a comparable amount of ingested food in their gastro-intestinal tract during the QMR measurements.

![Figure 1. Schematic overview of the study. QMR: quantitative magnetic resonance. Within-individual changes in fat mass and nocturnal migratory restlessness were calculated by subtracting the values measured on day 1 or night 1 from the values measured on day 3 or night 3.](image-url)
Data analysis

Data were analysed using SPSS 26.0. The relationship between fat mass on the first day in captivity and migratory restlessness in the first night in captivity was assessed with a Spearman correlation. We ran a general linear model (GLM) on the change in migratory restlessness from the first to third night in captivity, with fat mass on the first day in captivity, the change in fat mass from the first to third day in captivity, and their interaction as explanatory variables. Fat mass and change in fat mass were centered prior to analysis to allow interpretation of the main effects (Schielzeth 2010). Fat mass on the first day in captivity and change in fat mass were negatively correlated (Pearson’s $r = -0.42$, $p = 0.022$, $n = 30$), however, this did not result in multicollinearity (all variance inflation factors (VIF) < 1.3). A fat mass of a given amount of grams represents a larger fuel store for a small than for a large bird. To account for this, a second GLM was run, with the only difference to the first GLM that fat mass was divided by tarsus length prior to analysis. Visual inspection of residuals did not indicate deviation from normality.

Results

The mean ± SD and range of body mass, and fat mass of the birds on the first day in captivity was 23.3 ± 2.3 g and 19.2 – 30.7 g, and 1.41 ± 1.01 g and 0 – 4.17 g, respectively. There was a positive trend between the fat mass on the first day in captivity and the amount of migratory restlessness shown in the first night in captivity (Spearman’s $r = 0.32$, $p = 0.085$, $n = 30$, Fig. 2). That this relationship was not significant was mainly attributable to an extreme data point (Cook’s D > 1) from a very fat bird which showed no restlessness at all (excluding this bird: Spearman’s $r = 0.46$, $p = 0.013$, $n = 29$). We, however, have no biological reason to exclude this bird.

Although nearly all birds accumulated fat in the two days in captivity (mean ± SD change in fat mass: 1.43 ± 1.19 g), there was considerable variation in the change in fat mass. Much of this variation could be explained by the total amount of food eaten while in captivity (linear regression: Beta ± SE = 0.10 ± 0.02, $t = 6.14$, $p < 0.001$, $R^2 = 0.58$, $n = 29$). The change in fat mass was predictive for the change in migratory restlessness from the first to third night in captivity (Table 1), with migratory restlessness increasing more when more fat was accumulated (Fig. 3). Fat mass on the first day in captivity or its interaction with the change in fat mass did not explain variation in the change in migratory restlessness (Table 1, Fig. 4). Accounting for differences in body size among the birds (fat mass divided by tarsus length) did not change these results (Table 1). The change in migratory restlessness was neither associated with the total amount of food eaten while in captivity (Pearson correlation: $r = 0.26$, $p = 0.18$, $n = 29$) nor with the change in hourly food intake from the first to third day in captivity (Pearson correlation: $r = -0.27$, $p = 0.15$, $n = 29$).

Discussion

We found that the change in the amount of fat wheatears carried was predictive of the concurrent change in migratory restlessness. Specifically, birds that accumulated little fat typically did not change their restlessness much, whereas birds that accumulated much fat generally showed a strong increase in restlessness (Fig 3). These within-individual results matched the cross-sectional observation of a positive relationship between fat mass on the first day in captivity and migratory restlessness in the first night (Fig. 2). Moreover, birds that were relatively lean on the first day changed their migratory restlessness in response to changes in fat mass in the same way as birds that were relatively fat on the first day (Fig. 4). As (in wheatears) the amount of migratory restlessness shown in the cage is an accurate proxy for actual departure likelihood in the field (Eikenaar et al. 2014), these results indicate that fat accumulation increases wheatears’ motivation to migrate. Our results therewith provide strong support for the idea that (changes in) fat stores act as a stopover point for the idea that (changes in) fat stores act as a stopover

Table 1. The effects of fat mass on the first day in captivity (Fat), the change in fat mass from the first to third day in captivity (Fat change), and their interaction on the change in migratory restlessness from the first to third night in captivity in wild northern wheatears. Two model outcomes are presented, one analyzing raw fat mass data and one in which fat mass was divided by tarsus length to account for body size differences. For both models $n = 30$ and $R^2 = 0.24$.

|                          | $\beta \pm SE$ | $t$ | $p$ | df |
|--------------------------|----------------|-----|-----|----|
| **Raw data model**       |                |     |     |    |
| Fat                      | 1.57 ± 1.29    | 1.22| 0.24| 1  |
| Fat change               | 3.11 ± 1.16    | 2.69| 0.012| 1 |
| Fat × Fat change         | -0.10 ± 1.55   | -0.07| 0.95| 1 |
| **Body size model**      |                |     |     |    |
| Fat                      | 42.19 ± 35.22  | 1.20| 0.24| 1  |
| Fat change               | 86.50 ± 32.04  | 2.70| 0.012| 1 |
| Fat × Fat change         | -130.85 ± 1177.91 | -0.11| 0.91| 1 |

Figure 2. Migratory restlessness in the first night in captivity in wild northern wheatears as a function of their fat mass in the first day in captivity. $n = 30$. The regression line with 95% confidence interval is given.
departure cue for migratory birds. This is not trivial, because stopover duration to a large extent determines the speed of migration (Schmaljohann 2018), which in turn can affect fitness through arrival time at the breeding and wintering grounds (Marra et al. 1998, Smith and Moore 2005). The results from our autumn study match and complement that of a similar study performed on wheatears in spring (Eikenaar and Schläfke 2013). This indicates that changes in fuel (fat) stores affect the decision to depart from a stopover site in both spring and autumn migration seasons, at least in long-distance migrating wheatears.

Instead of the absolute change in fuel stores used in the current study, FDR has been predicted to be of major importance to departure decisions, at least for birds aiming at minimizing the overall migration time (Alerstam and Lindström 1990). This idea gained indirect support from some field studies showing a positive relationship between FDR and departure fuel load (reviewed by Alerstam 2011). Direct and more robust support in the form of a relationship between FDR and departure likelihood is scarcer (Schaub et al. 2008, Schmaljohann and Eikenaar 2017), but also indicates that FDR affects departure decisions. Although the patterns from studies on FDR and our findings cannot be easily compared due to their cross-sectional versus within-individual nature and differences in methodological set-up, both stress the importance of changes in fuel stores for stopover departure decisions.

Our study additionally provides some guidance towards unravelling the physiological mechanism(s) behind the translation of the departure cue ‘fuel stores’ to departure behaviour. The relationship between changes in fat mass and changes in migratory restlessness was independent of the initial fat mass of the birds at the first QMR measurement (no interaction between initial fat mass and the change in fat mass). Fat accumulation thus affected the change in migratory restlessness in the same manner for relatively lean and relatively fat birds. Additionally, food intake or changes therein did not explain the change in migratory restlessness we observed. This strongly suggests that the fat tissue itself signals migrants about changes in energetic state, affecting the motivation to migrate. Fat (adipose) tissue can produce several peptide hormones, such as leptin and adiponectin, that in mammals are known to signal energy sufficiency and adiposity and that are dysregulated when fat mass is strongly altered (Guerre-Millo 2002). The functioning of these hormones in birds, however, is much less clear and care should be taken to extrapolate results from mammalian studies to birds. For example, in mammals, plasma leptin concentrations rise with increasing fat stores to signal the animal to reduce food intake and fat storage (Ahima and Flier 2000). In birds, however, leptin genes have only limited expression in adipose tissue, and leptin may thus not be very important in signalling energy stores in birds (Boswell and Dunn 2015, 2017). Another gap in understanding the physiological mechanism(s) underpinning the relationship between fuel (fat) stores and the motivation to migrate is that, to our best knowledge, no adipose hormone is yet known to stimulate locomotor activity in birds. Adiponectin is perhaps involved in the regulation of the seasonal occurrence of migratory restlessness (Stuber et al. 2013), however, whether it plays a role at the smaller temporal scale, thereby possibly affecting stopover decisions, is unknown. The physiological link(s) between fat tissue and locomotor activity in birds, in our case migratory restlessness, thus for now remain unclear. Combined lipidomic and transcriptomic analyses in experiments comparable to the current study might provide more insight into which adipose hormones (possibly) link fattening and the motivation to migrate.

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Author contributions

Cas Eikenaar: Conceptualization (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead). Thiemo Karwinkel: Investigation (equal); Methodology (supporting); Visualization (lead); Writing – original draft (supporting). Sven Hessler: Investigation (equal); Methodology (supporting); Writing – original draft (supporting).

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Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.8w9gh3md> (Eikenaar et al. 2021).

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