

Revealing the control of migratory fueling: An integrated approach combining laboratory and field studies in northern wheatears *Oenanthe oenanthe*

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Abstract Migratory birds rely on fueling prior to migratory flights. Fueling in migrants is controlled by intrinsic as well as extrinsic factors. From captive studies we have started understanding the internal mechanisms controlling bird migration. Field studies have demonstrated the effects of external factors, such as food availability, weather, competitors, parasites or diseases, on the stopover behavior of migrants. However, an integrated approach is still missing to study coherently how the innate migration program interacts with the varying environmental cues and to estimate the contribution of the innate migration program and the environment to realized migration. The northern wheatear *Oenanthe oenanthe* offers a unique opportunity for integrated studies. It breeds across almost the whole Holarctic with just a “gap” between eastern Canada and Alaska. All breeding populations overwinter in sub-Saharan Africa which makes the northern wheatear one of the most long-distant migratory songbirds with extraordinary long non-stop flights across oceans. It is a nocturnal migrant which travels without parental or social aid/guidance. Thus, young birds rely entirely on endogenous mechanisms of timing, route selection and fueling on their first outbound migration. By establishing indoor housing under controlled conditions the endogenous control mechanisms of northern wheatear migration could be revealed. At the same time, environmental factors controlling fueling could be investigated in the field. On migration wheatears occur in a variety of habitats with sparse vegetation where their stopover behavior could be quantitatively studied in the light of “optimal migration” theory by the use of remote balances, radio-tagging and even experimentally manipulated food availability. The present paper summarizes our approach to understand the control of migration in northern wheatears by combining field and laboratory studies at various spatial and temporal scales, and linking various sub-disciplines [*Current Zoology* 59 (3): 381–392, 2013].

Keywords *Oenanthe oenanthe*, Fueling, Stopover, Optimal migration, Predation risk, Endogenous control, Innate program, Nocturnal restlessness, Corticosterone

1 Introduction

Since the pioneering work by Eberhard Gwinner and Peter Berthold we have learned that migratory songbirds dispose of innate dispositions for migratory restlessness and migratory fueling (for reviews see Gwinner, 1986; Bairlein and Gwinner, 1994; Berthold, 1996; Gwinner, 1996). Hand-reared naïve captive birds reveal nocturnal restlessness as well as migratory body mass gain roughly at the same time as their wild conspecifics despite living in an artificial environment without external cues. In addition, between-species and within-species variation of the amount of migratory restlessness reflect overall migration distance. In line with this, short-distance migratory songbirds accumulate smaller amounts

of migratory fuel than long-distance migrants. Migratory fueling is mainly achieved by increasing food intake, increasing assimilation efficiency of ingested food, selecting particular diets and nutrients, and through metabolic and physiological adjustments (Bairlein, 1990; Ramenofsky, 1990; Bairlein, 2002; Bairlein, 2003; Jenni-Eiermann and Jenni, 2003; Ramenofsky et al., 2003; McWilliams et al., 2004; Ramenofsky and Wingfield, 2006; Lyons et al., 2008).

Despite these fundamental findings and the optimal migration theory (Alerstam and Lindström, 1990), comparatively little is known about external factors such as food availability, weather, competitors, parasites or diseases that might influence migration in particular with respect to migratory fueling in free-ranging birds

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(e.g. Moore and Kerlinger, 1987; Moore and Yong, 1991; Moore et al., 2003). Moreover, this has not yet been resolved in an integrated approach linking captive studies revealing the innate migration program with field studies demonstrating the realized migration behavior. Understanding the interplay between genes (intrinsic factors) and environment (extrinsic factors) is crucial for understanding the adaptability of migrating birds in a rapidly changing world.

2 The Wheatear Model

As the model species for an integrative approach to study migratory fueling we selected a small songbird, the northern wheatear *Oenanthe oenanthe* (thereafter wheatear). The species has a nearly circumpolar distribution and presents a fascinating migration system, as all breeding wheatears spend the northern winter in northern sub-Saharan Africa. It was speculated for a long time (Conder, 1989) but only recently revealed by light-level geolocation (Bairlein et al., 2012) that even the Canadian and Alaskan breeding birds spend the non-breeding season in Africa. The latter show a migration distance of annually about 30,000 km, the longest of any songbird reported so far. The wheatear is a typical nocturnal migrant when flying over land, but needs to perform long non-stop flights when flying over water.

On migration it occurs in a variety of habitats including meadows, arable land, beaches and other habitats with sparse vegetation (Glutz von Blotzheim and Bauer, 1988; Cramp, 1988). In its western breeding range, three subspecies are distinguished. The subspecies *seebohmi* is confined to the Atlas Mountains of Morocco while the nominate *oenanthe* wheatear (thereafter *oenanthe* wheatear) breeds in Great Britain and in an area ranging from continental Europe via Siberia as far east as Alaska (Cramp, 1988). The ‘Greenland Wheatear’ *O. o. leucorhoa* (thereafter *leucorhoa* wheatear) breeds on Iceland, Greenland and in eastern Canada. It is one of the few passerine migrants regularly covering distances of more than 1,000 km over sea.

During both fall and spring migration, the two northern subspecies occur together at stopover sites in northern and western Europe including the small German island of Helgoland in the North Sea. There, *oenanthe* wheatears of Scandinavian origin mingle with *leucorhoa* wheatears breeding in Greenland and Iceland (Dierschke and Delingat, 2001). Whereas Scandinavian birds face sea crossings of 50–500 km when flying towards the East and North, much longer flights are necessary for *leucorhoa* wheatears to reach stopover sites in

Scotland (c. 800 km) or the breeding areas (up to 4,000 km) (Schmaljohann et al., 2011; Schmaljohann and Naef-Daenzer, 2011; Bairlein et al., 2012).

Field studies on wheatears are facilitated by it being a species of open landscapes and comparatively easy to catch using baited spring traps. Once color-banded, they are easy to observe at stopover sites owing to their habitat choice and visibility (Dierschke and Delingat, 2001). Moreover, they can be attracted to remote-controlled baited balances placed in their habitats so that data on refueling can be gathered without re-trapping (Fig. 1; Schmaljohann and Dierschke, 2005).



Fig. 1 Color-ringed juvenile northern wheatear perched on a digital balance placed in the field in Wales Alaska (H. Schmaljohann)

Wheatears can also be easily kept in captivity under controlled conditions to study the endogenous basis of their migratory behavior (Maggini and Bairlein, 2010). Furthermore, captive breeding allows estimating the heritability of migratory traits. These circumstances and the general habits of wheatears provide a unique opportunity for taking a comparative approach for examining intrinsic disposition and extrinsic factors that control stopover behavior and decisions of a long-distance migrant species.

3 Innate Migration Program

The migration behavior of wheatears is governed by innate mechanisms. Migratory activity, as revealed by nocturnal migratory restlessness as well as migratory fueling, are under endogenous control (Maggini and Bairlein, 2010; Bulte and Bairlein, 2013). Hand-reared naïve birds, taken from wild nests and kept individually in controlled indoor conditions at a constant photoperiod of 12 hrs light and 12 hrs dark, constant tempera-

ture and constant food, revealed seasonal body mass variation corresponding to the time of migration and fueling in wild birds (Fig. 2; Maggini and Bairlein, 2010).

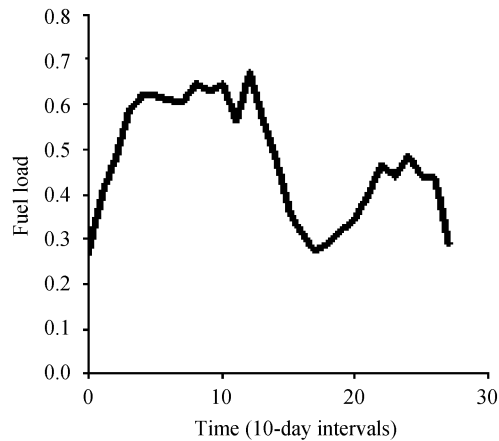


Fig. 2 Seasonal variation of fuel load of first year hand-raised captive Icelandic northern wheatears *Oenanthe oenanthe leucorhoa* [after Maggini and Bairlein (2010)]

Interval P1 starts at the age of 60 days when the birds were transferred from LD14:10 to LD 12:12.

In addition, the pattern and amount of migratory body mass gain is population-specific. Keeping wheatears from different populations with different migration routines in identical captive condition, so-called “common garden” experiments, revealed fueling which reflects their population-specific differences in migration routes and strategies. Icelandic birds showed a greater increase of their body mass in fall than Norwegian or Moroccan birds (Maggini and Bairlein, 2010). This indicates preparation for the initial ecological barrier crossing in Icelandic birds which is absent in the two other populations (Maggini and Bairlein, 2010). In all three populations, body mass increased to a greater extent in fall than in spring, whereas nocturnal activity was higher in spring than in fall (Maggini and Bairlein, 2010). This suggests that the endogenous program responds to specific seasonal needs, with more time invested in storing fuel for the journey in fall than in spring and more time invested in flying to reach the migratory goal faster in spring than in fall. Contrary to expectations, the timing of onset of body mass increase and nocturnal restlessness in spring did not differ between populations (Maggini and Bairlein, 2010). This might be explained by the lack of external cues, most likely photoperiod, which are responsible for the fine tuning of the expression of migratory behavior (Gwinner, 1986). When we kept the birds under a simulated

photoperiod that reflected the one they would have experienced during migration in the wild, differences in seasonal onset of body mass gain and migratory restlessness between the populations became more evident than under constant photoperiod (Maggini, 2009). These observations confirm that there is a strong population-specific endogenous control of the events relating to migration in wheatears which does not depend on a changing photoperiod, though photoperiod may fine-tune migration in the natural world (Gwinner, 1986). They also gave evidence that overall migration distance is not the only factor driving selection on the evolution of endogenous population-specific differences of migratory traits (Gwinner, 1986), but the geographic components such as the presence of an ecological barrier plays a role too (Maggini and Bairlein, 2010).

Wheatears breeding in Alaska travel for 14,500 km across Asia and the Arabian Peninsula to winter in eastern Africa (Bairlein et al., 2012). When kept in captivity indoors in the same setting as the other populations, Alaskan birds also revealed spontaneous seasonal patterns of migratory fueling and nocturnal migratory restlessness (Bulte and Bairlein, 2013). However, as compared to the other populations, their amount of fall migratory restlessness was significantly higher. In comparison with birds from Iceland, Alaskan birds showed a higher peak value and a longer lasting period of migratory restlessness. Hence, the amount of migratory restlessness is positively correlated with the length of the migration route of the corresponding wild populations. These results are in agreement with the findings in other migrants (for review see Berthold, 1996). However, the amount of migratory fueling was much smaller than expected for the extremely long migration distance in Alaskan wheatears. These birds showed just half the amount of fuel load observed in Icelandic birds (Fig. 3; Bulte and Bairlein, 2013). However, the patterns of migratory fueling during fall differed between both populations. While Icelandic wheatears exhibited a steep fueling increase and high levels of fueling early in the season, Alaskan birds started with low fueling rates and reached their highest fuel load later in the season (Bulte and Bairlein, 2013). This relates most likely to differences in their migratory challenges. The Icelandic wheatears have to cross a large part of the North Atlantic during early migration, while the Alaskan birds migrate mostly over benign land that offers feeding opportunities en route. At the end of fall migration both populations have to cross the Sahara desert. This appears to be also reflected in their similar fueling pattern

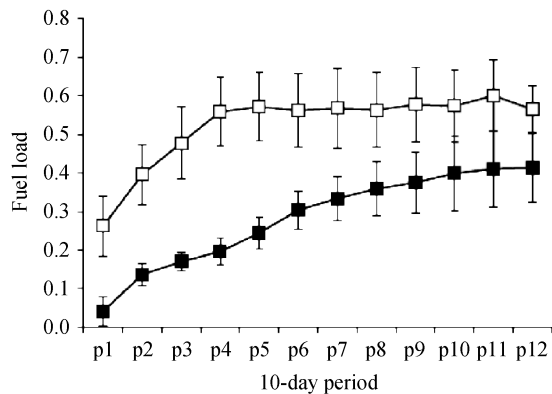


Fig. 3 Seasonal pattern of average fuel load (in relation to lean body mass) of Alaskan wheatears (filled squares) and Icelandic northern wheatears (open squares)

Error bars 95 % confidence interval of the mean value. P1–P12: Five-day periods starting since the start of the experiment in mid August. The differences are significant (repeated measures ANOVA, $F = 17.45$, $P < 0.001$; after Bulte and Bairlein 2013).

towards the end of their fall migrations. Thus, while the endogenous pattern of migratory restlessness corresponds to the migratory distance, migratory fueling appears to reflect the environmental conditions the populations are facing during their journeys.

In many migratory bird species, males arrive at the breeding grounds before females, and wheatears are no exception. Male wheatears migrate earlier in spring (Spina et al., 1994, Dierschke et al. 2005) and arrive at the breeding grounds earlier than females (Currie et al., 2000; Pärt, 2001). The evolutionary causes of protandry have been debated quite rigorously (Morbey and Ydenberg, 2001; Coppack and Pulido, 2009), but it remained open whether protandry has an endogenous component as well. We were able to show that captive male wheatears kept under constant conditions for their first year of life started their spring migratory activity and migratory fueling significantly earlier than females, even in the absence of environmental cues (Maggini and Bairlein, 2012). This indicates that protandry in the wheatear has an endogenous basis.

4 Realized Migration

4.1 Cost of migration

Migrants spend less time and energy during flight than during stopover. The ratios were theoretically predicted to be close to 1:7 (time) and 1:2 (energy), see (Hedenström and Ålerstam, 1997). Extrapolation from a field study using doubly labeled water indicated that the energy expenditure during flight represented approximately 30% of the total energy expenditure during the entire migration (Wikelski et al., 2003). Estimating the

time and energy costs of the entire migration requires a high spatiotemporal resolution of migration and information about the meteorological conditions encountered en route. Such analyses have been impossible for small birds until the recent miniaturization of light-level geolocators. As movements with strong latitudinal components are less convenient to investigate than longitudinal movements (Hill 1994) East-West migration offers a better opportunity to locate migratory routes and stopover sites on a fairly accurate spatiotemporal scale (Bairlein et al., 2012; Schmaljohann et al., 2012b). For the Alaskan wheatears, which have a strong longitudinal component in their migration, we provided the very first estimates of the time and energy devoted to the flight and stopover stages on the entire migration. To do so, we modeled the total time and energy costs of migration for flying and resting by considering different physiological and aerodynamic approaches and the daily environmental conditions en route (Schmaljohann et al., 2012b). The ratio of time in migratory flight (on average 306 h) to time on the ground (1954 h) in fall was 1:6.35 (Schmaljohann et al., 2012b), close to the theoretical predictions (Hedenström and Ålerstam, 1997). In spring, this ratio was 1:3.25 (Schmaljohann et al., 2012b).

Calculating the energy costs for flying for the entire migration depends very much on the model chosen. Energy models and aerodynamic models revealed total flying costs of 2,000 to 5,500 kJ. Using a body mass model, the birds lost on average 115 g during their entire migratory flights, equivalent to 2,570 kJ on a dietary protein/fat ratio of 10:90 and 3,199 kJ on a protein/fat ratio of 5:95. For the entire time on the ground (stopover), the total energy costs were 5,085 kJ, resembling a total loss of 306 g (Schmaljohann et al., 2012b). The total energy cost for the entire fall migration appears to be divided between flying and stopping over at a ratio of approximately 1:2 (Schmaljohann et al., 2012b), which is close to theoretical considerations (Hedenström and Ålerstam, 1997) and extrapolation of a field study (Wikelski et al., 2003).

The total energy costs (flight and stopover combined) relative to the distance covered were significantly lower in spring than in fall. In spring, the bias towards energy and time costs during stopover diminished, indicating that the time for stopover was minimized, leading to an overall faster and energetically more economic migration with lower energy costs per migration unit in spring than in fall (Schmaljohann et al., 2012b).

4.2 Optimal migration strategies?

From an evolutionary point of view migratory birds

should minimize either the time spent on migration or their total energy expenditure, with predation risk as a further criterion to be considered (Alerstam and Lindström, 1990; Alerstam, 2011). The higher the fuel deposition rate the faster birds obtain the necessary fuel load for their next migratory stage. A major determinant of the overall migration speed is, hence, the fuel deposition rate of the bird. A high fuel deposition rate reduces the total time spent for stopover, which in turn minimizes the overall time of migration (Alerstam and Lindström, 1990; Lindström and Alerstam, 1992). Time-minimizers experiencing a high fuel deposition rate are expected to exploit the stopover site and depart with high fuel loads. If, however, their fuel deposition rate is low they resume migration regardless of fuel load. Consequently, departure fuel load is positively correlated with fuel deposition rate (Alerstam and Lindström, 1990; Lindström and Alerstam, 1992). In contrast, birds that minimize the overall energy costs of transport should depart from a stopover site independently of fuel deposition rate and stopover duration, but just carrying as much fuel as required for the next flight stage (Hedenström and Alerstam, 1997). Thus, the correlation between departure fuel load and fuel deposition rate may reveal the basic strategy a migrant is following on its journey.

We found indications that wheatears may differ in their migration strategy. In spring male *leucorhoa* wheatears behaved on Helgoland as expected for time-minimizers, whereas in *leucorhoa* females fuel deposition rate and departure fuel load did not correlate significantly indicating in general an energy saving strategy (Fig. 4; Dierschke et al., 2005; Delingat et al., 2006). However, departure fuel loads of *leucorhoa* females were higher than predicted for the minimization of overall energy costs of transport. Though sample size is small for *oenanthe* wheatears, spring data support predictions for energy minimization (Fig. 4). During fall migration first year wheatears of both subspecies behaved accordingly to the time minimization strategy both when leaving Iceland (Delingat et al., 2008) and Helgoland (Schmaljohann and Dierschke, 2005). In contrast, first outbound Alaskan wheatears behaved as expected for energy minimizers (minimization of the total energy cost of migration; Schmaljohann et al., 2013). Although departure fuel load was independent of fuel deposition rate and hence, in general accordance with an energy-minimization strategy, the juvenile Alaskan wheatears in fall and *leucorhoa* females in spring carried all considerable surplus fuel load at departure which was several times higher than would be

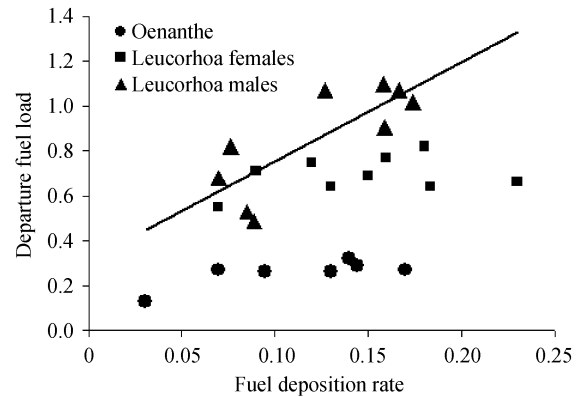


Fig. 4 Relationship between departure fuel load (in relation to lean body mass) and total daily fuel deposition rate in northern wheatears on Helgoland in spring [after Dierschke et al. (2005) and Delingat et al. (2006)]

While departure fuel load did not correlate significantly with daily fuel deposition rate in *oenanthe* and *leucorhoa* females respectively, reflecting a mostly energy minimizing migration strategy, the significant correlation in *leucorhoa* males reveals their time-minimizing strategy.

expected for a single-night flight. A similar phenomenon was observed at Fair Isle where *leucorhoa* wheatears heading to their breeding areas in spring carried a higher fuel load than necessary for the upcoming Atlantic crossing (Delingat et al., 2008). This speaks against the minimization of overall energy costs of transport, as carrying surplus of fuel load is energetically costly during flight (Hedenström and Alerstam, 1997). Surplus fuel load enables migrants to by-pass future stopover sites which is typical for time-minimizers (Alerstam and Lindström, 1990; Gudmundsson et al., 1991; Weber et al., 1994; Hedenström and Alerstam, 1997; Dierschke et al., 2005). It should be considered that differences in time and energy minimizing strategies may be only small, if search and settling times/costs are low (Alerstam and Lindström, 1990; Hedenström and Alerstam, 1997). These data may suggest that exploration times at new stopover sites are relatively short in wheatears (Delingat et al., 2006; Schmaljohann et al., 2012b).

The case of the wheatear demonstrates that even individuals within the same species do not necessarily behave accordingly to the same optimal migration strategy. The differences in strategy may be related to season, sex and subspecies, i.e., migration route or the type of barriers to be crossed.

4.3 Fueling and stopover

Birds spend up to about 85% of the entire migration period at stopovers in order to store or to replenish fuel for the next flight (Hedenström and Alerstam, 1997; Schmaljohann et al., 2012b). Consequently, under-

standing stopover and how birds adjust stopover decisions with respect to their migration strategy is crucial to an understanding of how migrating birds organize their journey. The rate of fuel deposition and departure fuel load are the two major determinants affecting departure decisions (Alerstam and Lindström, 1990).

Mean fuel loads of wheatears at various stopover sites in western Europe were found to be rather low as long as no significant ecological barrier is encountered. Flight range estimates suggest that these wheatears most likely refuel daily after each nocturnal flight depositing enough fuel for some five to seven hours flight, equivalent with a nocturnal flight range of 230 to 330 km (Delingat et al., 2006; 2008). *Leucorhoa* wheatears carried higher fuel loads than *oenanthe* wheatears, but differences were moderate suggesting that *leucorhoa* wheatears also refuel after each nocturnal flight when crossing continental Europe. It appears that in wheatears selection acts on migratory behavior to favor a ‘numerous-stops-and-flights strategy’ on migration over continental Europe (Delingat et al., 2006).

However, when facing an open sea crossing, migrants are faced with the need to generously refuel. On Helgoland, departure fuel loads of wheatears are significantly higher than arrival fuel loads, and individual *leucorhoa* birds exhibit fuel loads of more than 100% of lean body mass (Fig. 5; Dierschke et al., 2005; Delingat et al.,

2006). Moreover, *oenanthe* wheatears depart from Helgoland northbound with less fuel aboard, and they are less selective for weather conditions at departure than *leucorhoa* wheatears, possibly because the latter face longer migration distances and a more extent sea crossing en route to their breeding areas (Dierschke and Delingat, 2001; Dierschke et al., 2005; Schmaljohann et al., 2011; Schmaljohann and Naef-Daenzer, 2011). In contrast, in Alaskan wheatears, which face only a short sea crossing across the Bering Strait to the Russian mainland in fall, the departure probability increased with evening fuel load (Schmaljohann et al., 2013). Although most outbound young Alaskan wheatears resting on the American side of the Bering Strait carried sufficient fuel load for the short sea crossing, they performed rather lengthy stopovers to put on even more fuel likely as a safety margin for the subsequent Taiga crossing (cf Schmaljohann et al., 2012b).

Oenanthe and *leucorhoa* wheatears also differ in the extent of stopover and stopover duration. During spring passage on Helgoland, only 9% of male and 14% of female *oenanthe* resided on the island for more than one day, while in *leucorhoa* 40% of males and 30% of females stayed for at least one day (Dierschke and Delingat, 2001). The difference between subspecies was significant for both sexes. However, among birds not departing on the day of ringing, the stopover duration did not differ significantly between subspecies. Still, most *oenanthe* wheatears stayed for only one day, while most long-stayers were *leucorhoa* wheatears (Dierschke and Delingat, 2001).

4.4 Fueling and predation risk

Predation risk affects bird migration behavior (Lank et al., 2003). According to the optimal migration theory, predation risk is assumed to be mass-dependent (Lind et al., 1999; Kullberg et al., 2000), but see Dierschke (2003). Hence, optimal departure fuel load might be affected by predation risk in such a way that birds depart with lower fuel loads than predicted for time-minimizers, as predicted by stochastic dynamic modeling (Weber et al., 1998). In wheatears, predation risk did not directly influence birds’ departure decision, as predation risk did not differ between days when birds stayed on the island and days when birds decided to resume migration (Dierschke and Delingat, 2001; Schmaljohann and Dierschke, 2005). However, predation risk affected their fuel deposition rate: higher predation risk was associated with lower fuel deposition rate (Fig. 6; Schmaljohann and Dierschke, 2005). As wheatears behave as time minimizers in fall, a reduced

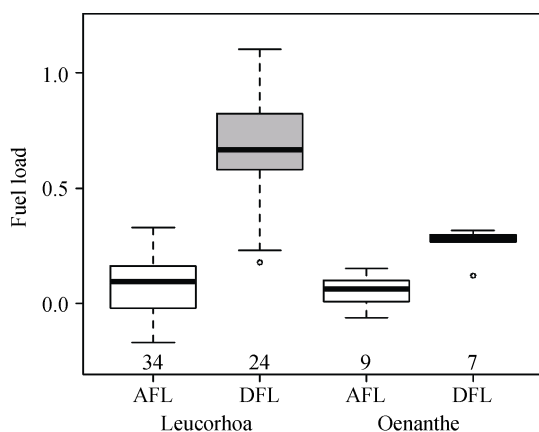


Fig. 5 Box plot of arrival fuel load (open boxes, AFL) and departure fuel load (grey boxes, DFL) *leucorhoa* and *oenanthe* northern wheatears on Helgoland during spring passage

In both subspecies, departure fuel load was significantly higher than arrival fuel load (Wilcoxon rank sum tests: $P < 0.0007$). Arrival fuel load did not differ significantly between the subspecies (Wilcoxon rank sum test: $W = 121$, $P = 0.34$). Departure fuel load was significantly higher in the *leucorhoa* subspecies than in the *oenanthe* northern wheatears (Wilcoxon rank sum test: $W = 12$, $P = 0.0002$) [after Dierschke et al. (2005)]. Fuel load is given relative to the lean body mass of the birds.

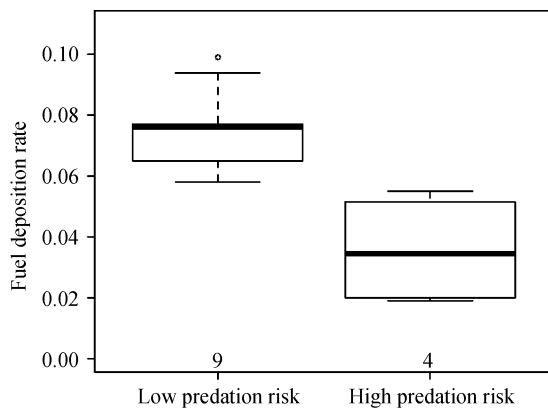


Fig. 6 Difference between total fuel deposition rate for northern wheatears having perceived a low averaged predation risk (< 1 raptor flyover per hour) and a high averaged predation risk (> 1 raptor flyover per hour) during their stopover on Helgoland

Wilcoxon rank sum test: $W = 36$, $P = 0.007$; sample size is given within the boxplot. Only northern wheatears staying more than 3 days beyond the day of arrival were considered (after Schmaljohann and Dierschke, 2005).

fuel deposition rate is supposed to increase bird's departure probability (see above, Optimal migration strategies). Hence, predation risk may influence stopover decision indirectly. However, departure fuel load was independent of the cost-benefit relation between predation risk and fuel deposition rate (Schmaljohann and Dierschke, 2005). Thus, it seems that predation risk does not necessarily modulate the optimal migration strategy adapted by a species at a stopover site.

4.5 Fueling and social rank

In migrants defending territories during stopover, social status can determine stopover behavior and fueling (Moore et al., 2003, and references therein). In wheatears during spring stopover on the island of Helgoland, social status dictated territorial behavior but the consequences of social status for fueling depended on food availability (Dierschke and Delingat, 2001; Dierschke et al., 2005; Arizaga et al., 2011). During spring stopover passage dominant birds defended territories while subordinates revealed extended vagrancy. In springs with low food abundance subordinates tended to have lower foraging rates, fly less and stopover at the site for shorter periods and revealed smaller fuel loads (on average 11% of lean mass) than dominants (22%), irrespective of sex and subspecies (Arizaga et al., 2011). However, fuel deposition rate did not differ between territorial and non-territorial birds when food was not limited. In such years the non-territorial subordinates compensated for restricted access to food resources with a more efficient exploitation by taking more food per

unit time leading to the same energy intake as that of dominant and territorial birds (Dierschke et al., 2005). Moreover, although male wheatears were more often territorial and on average attained a higher social rank than females, this did not result in higher refueling rates. Thus, there appears no evidence for competition between the sexes leading to differential timing of migration of male and female wheatears.

4.6 Fueling and weather

In the context of optimal migration strategies, the momentary individual decision to depart from a certain stopover site at the day-to-day level is modulated by environmental cues as well. Hence, migrants' short-term departure decisions might overrule species' general optimal migration strategies. In *oenanthe* wheatears, birds depart from Helgoland under more cloudy skies than *leucorhoa* wheatears in spring (Dierschke and Delingat, 2001). This is possibly a strategy adopted by *leucorhoa* wheatears to reduce the probability of encountering rain during the long sea crossing. An even more important variable is wind (Liechti and Bruderer, 1998). As wind speed is approximately the same order of magnitude or even greater than songbirds' air speed, the choice of favorable wind conditions for flying has a major effect on the birds' flight range (Liechti and Bruderer, 1998; Liechti, 2006). Departing at low wind speed was hypothesized to be a generally successful strategy (Liechti, 2006) because even if the wind direction changes with altitude, due to topographic modulation, the bird will only be flying with a slow headwind which is not unfavorable (Erni et al., 2002). Wheatears avoid strong headwinds, and they time their departure with favorable wind conditions when having generally low fuel loads indicating their capacity to take account of wind conditions (Delingat et al., 2008; Schmaljohann and Naef-Daenzer, 2011).

Regarding fuel deposition rate, the temperature on the ground is an important factor influencing food abundance (airborne insects) for insectivorous birds, which in turn affects the fuel deposition rate (Schmaljohann and Dierschke, 2005). Additionally, energy costs on the ground rise with decreasing ambient temperature (Wikelski et al., 2003; Schmaljohann et al., 2012b). Hence, resuming migration at relatively low temperatures can be a reaction to unfavorable feeding conditions and/or to the increasing energy costs on the ground, (Schmaljohann et al., 2012b). In Alaskan wheatears, the probability of departing from a stopover site increased significantly with decreasing surface temperature (Schmaljohann et al., 2013). Alternatively, a decrease in

temperature may indicate a change in air pressure and wind conditions, which often coincide with departure decisions (Liechti, 2006).

Using data from Alaskan wheatears tracked with light-level geolocators, we characterized the meteorological conditions, surface temperature, surface wind speed and surface precipitation for each individual noon and midnight fix. In fall, the departure decision was significantly associated with lower surface temperature and lower surface wind speed, whereas stopover was preferred at higher surface temperatures and higher surface wind speeds. None of the variables considered played a significant role in spring (Schmaljohann et al., 2012b).

4.7 Fuel load and nocturnal departure

When nocturnal migrants leave for their migratory flights and whether nocturnal departure times might be organized with respect to body condition, environmental cues (wind), the length of the night and the remaining migration distance is poorly known. This is, however, crucial in order to determine the potential nocturnal flight duration. Early nocturnal take-off and flight until sunrise maximizes the migrants' nocturnal travel range which, as a seasonal average, defines the overall number of stopovers needed during migration. Because more time is spent on the ground than flying (Schmaljohann et al., 2012b), the total number of stopovers significantly contributes to the overall speed and costs of migration (Alerstam and Lindström, 1990; Hedenström and Alerstam, 1997). In general, we found that take-off occurred after the end of nautical twilight (Schmaljohann et al., 2011; Schmaljohann and Naef-Daenzer, 2011) when the skylight polarization pattern may be used to calibrate the birds' compass systems (Cochran et al., 2004; Muheim et al., 2006; Chernetsov et al., 2011; Schmaljohann et al., 2013).

In *leucorhoa* wheatears departing from Helgoland, fuel load and the northward component in the departure direction each explained 20% of the variation in the nocturnal take-off time (Schmaljohann and Naef-Daenzer, 2011). Lean birds might depart either early or late at night to aim for nearby stopover sites and possibly decide several times during the night whether departure conditions are sufficient to set off from Helgoland. *Leucorhoa* wheatears with high fuel loads, i.e., long potential flight vectors flying in the principal seasonal migration direction may have a shorter time window for their departure decision during the first half of the night only (Schmaljohann and Naef-Daenzer, 2011).

In contrast to European wheatears showing a wide

scatter of nocturnal departure times, Alaskan wheatears departed within a relative small time window shortly after sunset and at a relatively high sun elevation from an Alaskan stopover site in fall (Schmaljohann et al., 2013). The general time window in which migrants can decide to depart is smaller when nights are shorter. Thus, a simple rule might be to take off early when nights are short. This overall pattern is modified by the fact that nocturnal departure time is also influenced by body condition (Schmaljohann and Naef-Daenzer, 2011).

4.8 Fuel load and departure direction

Migrants should depart from a stopover site in the seasonally appropriate migration direction (Åkesson et al., 2001; Åkesson et al., 2002; Schmaljohann et al., 2013). However, cage experiments have shown that lean birds orient away from a barrier, whereas physically fit migrants are less likely to detour from the principal migratory direction if a barrier is ahead (Sandberg, 1994; Sandberg and Moore, 1996; Sandberg, 2003; Deutschland and Muheim, 2009). Such behavior could explain the frequently observed phenomenon of reverse migration, in which birds fly in seasonally inappropriate migratory directions (Lewis, 1939; Alerstam, 1978; Åkesson et al., 1996; Åkesson, 1999; Phillips, 2000; Williams et al., 2001; Zehnder et al., 2002; Komenda-Zehnder et al., 2002). We showed that free-flying *leucorhoa* wheatears departed with headings towards their breeding grounds only with sufficient fuel load aboard while lighter birds did so only under favorable tail wind conditions (Fig. 7; Schmaljohann and Naef-Daenzer, 2011). With high fuel loads and favorable wind conditions, birds were likely to depart for a long non-stop flight across the sea. This choice represents a risky but direct (and thus fast) migratory route towards the breeding areas on Iceland, Greenland and in eastern Canada. In contrast, birds that set off under unfavorable conditions, i.e., low fuel load and bad weather, flew a safer route towards the nearby mainland within a 50–100 km range. As the minimum sea barrier to be crossed correlated with the physical condition of the birds, visual cues were likely used in the departure direction decision (Schmaljohann and Naef-Daenzer, 2011). Adaptive behavioral adjustments of migratory direction are critical for crossing ecological barriers (Alerstam, 2001; Henningsson and Alerstam, 2005). The *leucorhoa* wheatear's variation of departure direction in relation to fuel load and wind conditions reveals the capacity for such behavioral responses (Schmaljohann and Naef-Daenzer, 2011) and indicated that the relevant phenotypic trait was a behavioral response to both in-

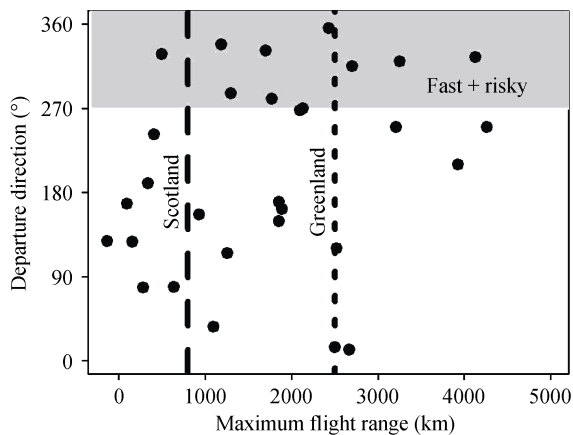


Fig. 7 Departure directions over the maximum flight range of Greenland/Iceland northern wheatears *Oenanthe oenanthe leucorhoa* departing from Helgoland in spring

Maximum flight range was estimated by the departure fuel load of the birds and considering their current wind profit towards Iceland (circular-linear correlation: $n = 30$, $F_{2,30-3} = 7.88$, $R^{c-1} = 0.23$, $P = 0.030$). The shaded area indicates the ‘fast and risky’ direct way across the North Sea. Dashed line indicates the farthest distance across the North Sea towards Great Britain (800 km) and dotted line the distance towards the nearest breeding areas on Greenland (2500 km) (after Schmaljohann and Naef-Daenzer, 2011).

ternal information (body condition) and external information (wind support). Furthermore, *leucorhoa* wheatears incorporate a physiological safety margin, in terms of fuel, when selecting a route for their next migration stage (Schmaljohann and Naef-Daenzer, 2011).

4.9 Fueling and corticosterone

Several studies found that exogenous corticosterone affects food intake and even fattening. However, whether endogenous corticosterone actually facilitates migratory fueling in wild birds is at present unclear and results are contradictory (Eikenaar et al., 2013, and references therein). We therefore conducted a study with wheatears on Helgoland, measuring corticosterone levels in both *oenanthe* and *leucorhoa* birds during their simultaneous spring stopovers and relating them to their rate of fueling. If corticosterone promotes refueling we expected that (a) *leucorhoa* wheatears should have higher corticosterone levels than *oenanthe* wheatears, because *leucorhoa* birds deposit more fuel, more rapidly than *oenanthe* birds, and (b) fuel deposition rate should be positively correlated with corticosterone level. However, our results did not reveal a stimulating effect of corticosterone on migratory fueling in wheatears (Eikenaar et al., 2013). Corticosterone levels were lower in *leucorhoa* than *oenanthe* wheatears, and the actual fuel deposition rate was negatively correlated with corticosterone level. We also observed a positive correlation between corticosterone level and fuel stores. These

findings suggest that rather than promoting migratory fueling corticosterone may function as a readiness cue, with levels increasing towards departure from the stop-over site (Eikenaar et al., 2013) as suggested previously by Landys-Ciannelli et al. (2002) and Lohmus et al. (2003).

5 Conclusions

Avian migratory behavior has been studied for centuries either in the wild or captivity (e.g. Berthold, 1996, 2001; Alerstam, 2008). However, in a few species both field and lab studies have been integrated. On the one hand, there are various studies exploring endogenous migratory traits in small songbirds in captive setting. On the other hand, migratory behavior in the wild is mainly studied on the individual level in larger species, because they are more easily observed.

We aimed to overcome these challenges with the northern wheatear by combining tracking technologies, experimental stopover studies, common garden experiments and captive breeding. These approaches provide the opportunity to compare behavior in detail at various stopover sites along species’ migration route indicating how birds manage their journeys in free-ranging natural conditions being confronted with various environmental challenges in the framework of innate behavioral and physiological pre-dispositions. By this, a significant contribution to a better understanding of the so-called “migratory syndrome” (Piersma et al., 2005) could be made.

A common feature of the syndrome is fueling to accommodate infrequent and often unpredictable opportunities to feed. As shown in the wheatear, it is a complex trait which is under internal control but influenced by environmental conditions. Its understanding needs a comparative integrated approach to investigate the genetic and physiological architecture by linking field and captive studies. This is of biological importance with conservation application as many migratory species are in serious decline. However, fueling does not only shape and determine the migratory journey it also can carry over as breeding success depends to a large degree on body reserves obtained already on the wintering grounds or during stopover (e.g. Bairlein and Henneberg, 2000, Smith and Moore, 2003, Drent et al., 2006). Therefore, effective conservation of migratory species needs knowledge about when and where and to what extent fueling is required. Furthermore, understanding the interplay between internal and environmental control of migratory behavior may also have implications

for a better understanding of the micro-evolutionary consequences of climate driven changes in migratory birds (e.g. Bairlein and Hüppop, 2004; Pulido and Berthold, 2004, 2010).

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