

Routes to genes: unravelling the control of avian migration—an integrated approach using Northern Wheatear *Oenanthe oenanthe* as model organism

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Abstract Numerous studies in both the field and laboratory illustrate factors involved in the endogenous, intrinsic and environmental control of avian migration, but we are lacking an integrated individual-based approach, connecting field and laboratory studies in a single species. The Northern Wheatear *Oenanthe oenanthe* appeared very feasible for an integrated individual-based one-species approach in the study of the control of bird migration as it can be studied individually in the field as well as kept indoor under controlled ‘common-garden’ conditions. We here present a brief overview of the results collected in our wheatear studies on the intrinsic disposition and extrinsic factors that control migratory behavior in an obligate migratory species.

Keywords Migration · Endogenous rhythms · Migratory restlessness · Zugunruhe · Fueling · Protandry · Corticosterone · Competition · Wind

Introduction

In birds, migration makes up a significant part of the annual life cycle. The control of migration is a complex interplay of intrinsic and extrinsic factors (Ramenofsky and Wingfield 2006). Migratory songbirds carry innate dispositions for migratory restlessness and migratory fueling, which are

governed by endogenous annual rhythms (for reviews, see Gwinner 1986, 1990, 1996, 2009; Bairlein and Gwinner 1994; Berthold 1996). Numerous studies on a diverse set of species revealed that a complex set of extrinsic cues and environmental conditions such as food availability, weather, competitors and predators (for reviews see Alerstam 1990; Newton 2008; Berthold 2012; Rappole 2013) modulate the intrinsic template into what we can see as day-to-day realized migration of free-flying birds (Fig. 1; Bairlein 2008). Understanding migration and revealing different migration strategies consequently require an integrated approach of jointly studying intrinsic and extrinsic factors and mechanisms controlling migration. Furthermore, annual life cycle events need to be linked as conditions at the breeding area might influence behavior during migration and at the wintering grounds and/or vice versa (Marra et al. 1998). Understanding the interplay between genes (intrinsic factors) and environment (extrinsic factors) is therefore crucial for a holistic understanding of bird migration.

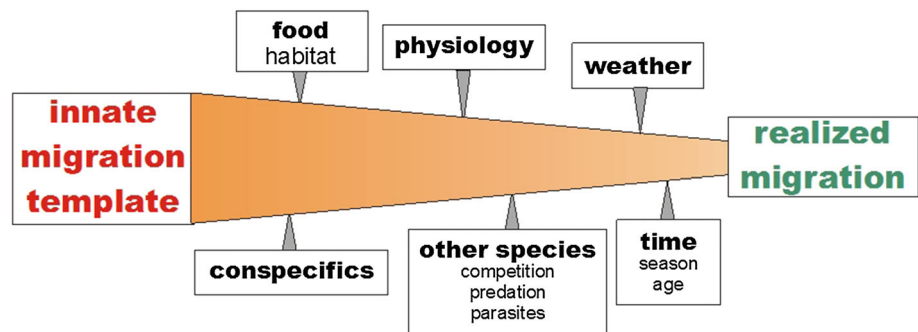
Despite numerous studies of various aspects of the control of migration in many different species (Berthold 1996; Berthold et al. 2003; Newton 2008), we are lacking an integrated individual-based approach, connecting field and laboratory studies in a single species. This is mainly due to the fact that larger migrants, such as storks, raptors, ducks and shorebirds, are comparatively easy to study in their natural environments but are difficult to keep under controlled captive conditions, while several of the passerine migrants such as warblers, thrushes or finches that are comparatively easy to maintain in captivity are difficult to study individually in the wild. The Northern Wheatear *Oenanthe oenanthe* (wheatear hereafter) possesses a number of characteristics that makes it highly suitable for an integrated individual-based one-species approach in the

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Fig. 1 A complex set of factors is involved in shaping an innate migration template into realized migration. The order of the factors does not imply a hierarchy of relevance (from Bairlein 2008)



study of the control of bird migration and hence our model species.

The wheatear has a nearly circumpolar distribution and presents a fascinating migration system, as all breeding populations spend the northern winter in the Sahel and savannahs of northern sub-Saharan Africa. It was speculated for long (Conder 1989) and recently revealed by light-level geolocation (Bairlein et al. 2012) that even the birds breeding in Canada and Alaska winter in Africa, as do European populations (Schmaljohann et al. 2012a; van Oosten et al. 2014). Alaskan wheatears annually migrate some 30,000 km, the longest songbird migration reported so far. The wheatear is a typical nocturnal migrant (Schmaljohann et al. 2011, 2013; Schmaljohann and Naef-Daenzer 2011). When crossing the Atlantic on their way to their breeding areas, they have to perform long non-stop flights (Schmaljohann and Naef-Daenzer 2011; Bairlein et al. 2012). 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 *O. o. seebohmi* is confined to the Atlas Mountains of Morocco while the nominate *O. o. oenanthe* wheatear (*oenanthe* wheatear hereafter) 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* (*leucorhoa* wheatear hereafter) breeds in Iceland, Greenland and eastern Canada. It is one of the few passerine migrants regularly covering distances of at least >1000 km in one flight bout over sea.

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



Fig. 2 Free-flying wheatears are easily attracted to mealworms offered in the field. Wheatears regularly use these “feeding stations” during their stopover. By placing a balance underneath the dish, the individual changes in body mass of color-ring wheatears can be studied. (Photo: H. Schmaljohann)

Helgoland with c. 800 km from/to Scotland and up to 4000 km from/to their Arctic breeding grounds (Schmaljohann et al. 2011; Schmaljohann and Naef-Daenzer 2011; Bairlein et al. 2012). The co-occurrence of the two wheatear subspecies on Helgoland provides an ideal and near-experimental basis for comparative research on this species’ migratory behavior and physiology.

In contrast to other insectivorous songbird migrants foraging in dense vegetation, such as warblers, the preference of wheatears for open habitats makes them comparatively easy to catch using mealworm-baited spring traps. Once color-banded, they are easy to observe and identify on the individual level at stopover sites owing to their habitat choice and visibility (Dierschke and Delingat 2001). Moreover, because wheatears can be attracted to remote-controlled mealworm-baited balances, data on refueling can be gathered without re-trapping (Fig. 2; Schmaljohann and Dierschke 2005).

Wheatears are also easily kept in captivity under controlled conditions to study the endogenous basis of their migratory behavior (Fig. 3; Maggini and Bairlein 2010). Captive breeding allows estimating the heritability of



Fig. 3 A Northern Wheatear in a registration cage. Migratory restlessness is recorded automatically with a motion-sensitive microphone (attached to the cage wall). Each time a bird moves this generates an impulse that is transmitted to the recording devices. (Photo: C. Eikenaar)

migratory traits and cross-breeding of populations with different migration characteristics in order to investigate the genetic background of migration behavior. Furthermore, wheatears caught at stopover sites adapt well to temporary confinement, as they immediately start to feed and thus to refuel. This allows studying migratory behavior of wild birds under controlled conditions (Eikenaar and Schmaljohann 2015). We here present a (non-exhaustive) overview of the results collected in our wheatear studies on the intrinsic disposition and extrinsic factors that control migratory behavior.

Endogenous control and intrinsic factors

Migratory restlessness

Although known from a number of migrant passerine species that first outbound young migrants are equipped with an innate knowledge about timing, distance, direction and energetic demands of migration based on endogenous annual rhythms (for reviews, see Gwinner 1986, 1996, 2009; Bairlein and Gwinner 1994; Berthold 1996; Bairlein 2002; Berthold et al. 2003), we needed to show that this also holds for wheatears. Therefore, we took under license nestling wheatears from wild nests of various populations, hand-reared them and kept them afterwards individually in controlled indoor conditions without access to environmental cues. In both autumn and spring they showed population-specific nocturnal migratory restlessness during approximately the same period as their respective wild conspecifics migrate. Thus, like other passerines studied, wheatears possess an innate migratory disposition, which is under the control of an endogenous rhythm. Furthermore, it is population-specific with wheatears migrating longer

distances in the wild showing more nocturnal migratory restlessness than shorter distance migrants (Maggini and Bairlein 2010). For example, Alaskan birds that travel 14,500 km to eastern Africa (Bairlein et al. 2012) showed a higher peak value and longer period of migratory restlessness than birds from Iceland (Bulte and Bairlein 2013) that travel about 7000 km (Fig. 4). Hence, the amount of migratory restlessness is positively correlated with the length of the migration route of the corresponding wild populations, indicating that the innate amount of migratory restlessness mirrors overall migration distance. These results are in agreement with the findings in other migrants (for review, see Berthold 1996).

Since the work of Gwinner (1986) and Berthold (1996), many studies have used migratory restlessness as a proxy for birds' motivation to migrate. However, the temporal match between nocturnal migratory restlessness in captive birds and actual migration of wild conspecifics was shown at the species or population level. The assumption that, also at the individual level, migratory restlessness is an accurate proxy for the motivation to migrate meanwhile remained

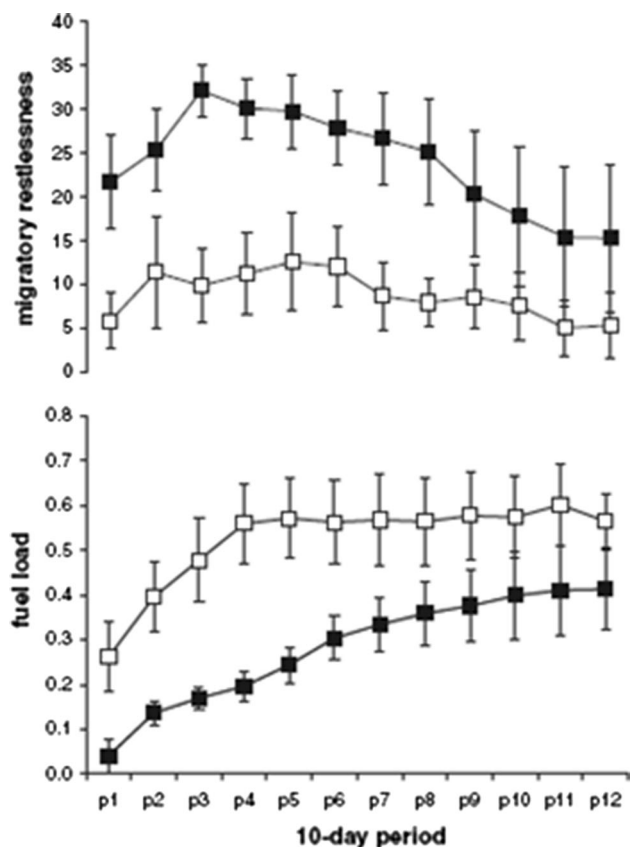


Fig. 4 Migratory restlessness (upper panel) and fuel load (lower panel) of captive Northern Wheatears from Alaska (open squares) and Iceland (filled squares), respectively, during autumn migration (p1 the first 10-day period of the experiment corresponds to mid August; from Bulte and Bairlein 2013)

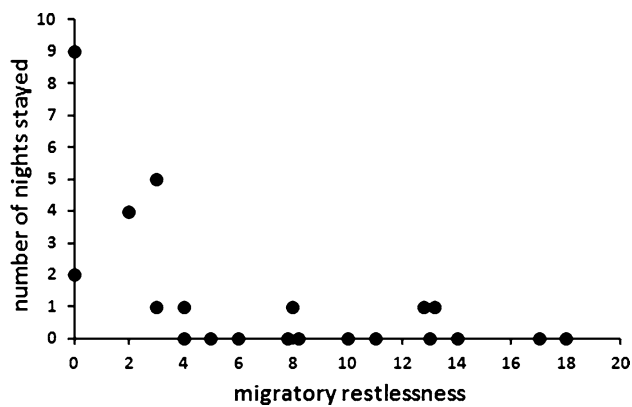


Fig. 5 Number of nights birds stayed on Helgoland after release from temporary captivity in relation to the amount of previous night nocturnal migratory restlessness (from Eikeenaar et al. 2014c)

untested. We therefore measured migratory restlessness in a set of wheatears at a stopover site during one night and released all birds the next day. By fitting the birds with a radio transmitter, we were able to determine exactly how long after release the birds stayed at the stopover site. We found that individuals showing very little migratory restlessness remained at stopover beyond the night following release, whereas most individuals showing more restlessness departed the night after being released (Fig. 5; Eikeenaar et al. 2014a). This result validates the use of migratory restlessness as a proxy for the motivation to migrate at the level of the individual.

Spatial adjustment of migration

Measuring average fuel loads of wheatears at various stopover sites across their western European migration route in spring revealed that they travel with low to moderate fuel loads, but still sufficient to fly for about 7 h a night. Furthermore, wheatears refuel every day after nocturnal flights, not preparing for long non-stop flights as long as no significant ecological barrier is encountered (Delingat et al. 2006). When facing an open-sea crossing, wheatears accumulate much more fuel, with fuel loads sometimes reaching more than 100 % of lean body mass (Dierschke et al. 2005; Delingat et al. 2006). Therefore, the question is by which cues migrating birds know where the ecological barriers are and by which cues intensive refueling is triggered. Studies in Thrush Nightingales (*Luscinia luscinia*; Fransson et al. 2001) and European Robins (*Erithacus rubecula*; Kullberg et al. 2007) revealed that extensive fueling prior to barrier crossing is triggered via the current magnetic conditions.

We subjected captive-bred naïve juvenile wheatears of Norwegian parents to either a simulated gradually changing magnetic field corresponding to what the birds would

have experienced during their first outbound migration from the south of Norway to their wintering grounds in western Africa or a stationary constant magnetic field of northern Germany. Fueling and migratory restlessness showed a different reaction to the magnetic simulation along the bird's migratory journey. The amount of migratory restlessness declined with consecutive southern latitudes as compared to the birds with the stationary magnetic field, revealing that the wheatears take the current position and remaining flight distance into account to adjust their migratory activity. In contrast to Thrush Nightingales, the temporal course and intensity of fueling were similar for both treatments and not affected by the local earth magnetic field of the stopover site along their autumn journey (Bulte et al. in preparation). The difference between both species most likely reflects their differences in migration behavior. While Thrush Nightingales need to store large amounts of fuel prior to the Sahara crossing because of the lack of feeding opportunities in the desert, wheatears have been observed feeding even in the desert (personal observation) and consequently may not require similar high fuel loads to Thrush Nightingales. The wheatear's innate fueling capacity appears to prepare birds with a sufficient fuel load for the upcoming migratory flight combination with other environmental cues (Schmaljohann and Naef-Daenzer 2011).

Protandry

In many migratory bird species, males arrive at the breeding grounds before females (e.g., Morbey and Ydenberg 2001; Tøttrup and Thorup 2008; Coppack and Pulido 2009), a phenomenon called protandry, and wheatears are no exception. Male wheatears migrate earlier in spring (Spina et al. 1994; Dierschke et al. 2005; Corman et al. 2014) and arrive at the breeding grounds earlier than females (Conder 1989; Currie et al. 2000; Pärt 2001; Buchmann 2001; Arlt and Pärt 2008). In wheatears, protandry has an endogenous component with captive males starting their spring migratory activity and their migratory fueling significantly earlier than females (Maggini and Bairlein 2012).

Migratory fueling

As with migratory restlessness, seasonal body mass variation in naïve hand-reared wheatears kept in constant conditions corresponds to the time of migration and fueling in wild birds (Maggini and Bairlein 2010), thus being under endogenous control as well. In addition, the pattern and amount of migratory body mass gain are population-specific. Wheatears from different populations with different migration routines kept in a “common garden” set-up

exhibited spontaneous fueling, which reflects their population-specific differences in migration routes and strategies. However, in contrast to migratory restlessness, the innate capacity of migratory body mass gain (fueling) does not reflect migration distance, but rather reflects whether the birds encounter ecological barriers such as long stretches of open sea. Icelandic birds showed a greater body mass increase in autumn than Norwegian and even Alaskan birds (Maggini and Bairlein 2010; Bulte and Bairlein 2013), despite the latter traveling to eastern Africa (Bairlein et al. 2012), which is almost three times the distance of the Icelandic birds.

Migratory fueling in wheatears is inherited and under genetic control. While it has been shown in other migrants that migratory restlessness is genetically controlled and inherited (Berthold and Querner 1981), it has been unknown whether this is also the case for migratory fueling. To assess genetic control of migratory fueling we, therefore, cross-bred birds from populations with different migratory fueling in captivity and compared the migratory fueling of the “hybrid” offspring with their respective parents (Bulte et al. 2015). In all cases, the “hybrids” showed intermediate fueling capacities compared to the respective parent populations, showing, for the first time, that migratory fueling is under genetic control as well.

Intrinsic subspecies differences in refueling

Field studies revealed that the stopover fuel deposition rate (FDR) is different between *oenanthe* and *leucorhoa* wheatears with higher FDR in *leucorhoa* than *oenanthe* (Bairlein et al. 2013). Captive studies revealed that the two subspecies differ in the underlying physiological trait as well (Corman et al. 2014). Both sexes of *oenanthe* wheatears showed significantly lower FDR than their corresponding *leucorhoa* sexes and took lower amounts of food. Also, in *leucorhoa* wheatears the mass specific fuel deposition rate (FDR/g food intake) was higher than in *oenanthe* wheatears (Fig. 6). Thus, *leucorhoa* wheatears appear to have higher food assimilation efficiency enabling faster refueling and thus faster migration than *oenanthe* wheatears.

Fuel reserves and nocturnal migratory restlessness

Fuel reserves upon arrival at stopover and the accumulation of fuel affect stopover departure decisions (Jenni and Schaub 2003). However, whether the amount of fuel accumulated at stopover predicts a migrant’s motivation to depart has not been studied. Therefore, we studied this in temporarily contained wheatears that were captured at spring stopover (Eikenaar and Schläfke 2013). Most fat birds (large fuel reserves) showed much nocturnal migratory restlessness, indicating that they were motivated to

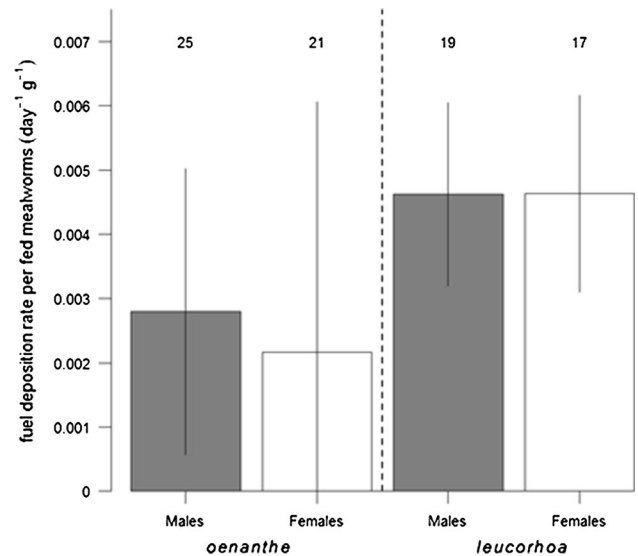


Fig. 6 Fuel deposition rate per gram fed mealworms in migratory wheatears caged for 3 days. Data for male (grey) and female (white) *oenanthe* (left) and *leucorhoa* (right) wheatears are shown as mean \pm standard deviation. Sample sizes are given at the top of the figure (after Corman et al. 2014)

depart. Lean birds (small fuel reserves) on the other hand often showed little restlessness, indicating that they were set on staying and accumulating fuel. Moreover, birds that fueled while in captivity also increased their restlessness and thus their motivation to depart (Eikenaar et al. 2014a), whereas birds that did not accumulate fuel did not show an increase in restlessness. These results provide strong evidence for the importance of fueling dynamics in migrants’ departure decisions.

Corticosterone and its actions during migration

The role of corticosterone, the main glucocorticoid hormone in birds, in the regulation of avian migration is much debated (for review, see Wingfield et al. 1990; Cornelius et al. 2013). Corticosterone, at baseline and moderately elevated levels, is thought to have a permissive effect on food intake, and affects locomotor activity and energy mobilization during the predictable life-history stages (Landys et al. 2006 and references therein). Food intake affects the rate of refueling at stopover, and departure involves an increase in both locomotion and energetic demands. Consequently, we studied the relationship between corticosterone and migratory (re)fueling and stopover departure decisions. Field and laboratory studies on stopover refueling in wheatears revealed that both food intake and FDR are negatively correlated with both total and free plasma corticosterone levels (Eikenaar et al. 2013, 2014b). This may seem maladaptive because corticosterone would decrease the refueling rate, thereby extending stopovers

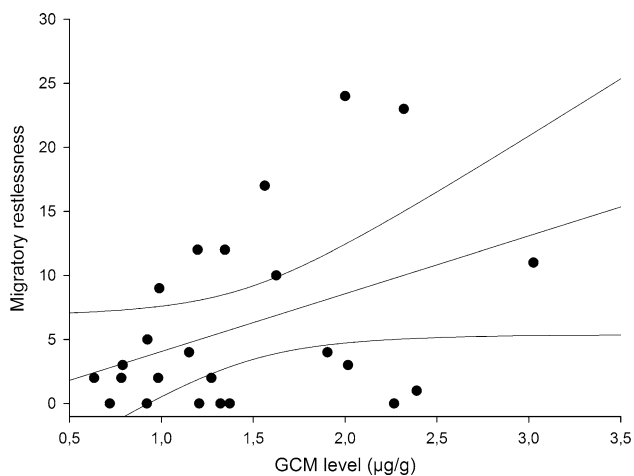


Fig. 7 Glucocorticoid metabolite levels and simultaneously measured nocturnal migratory restlessness in refueling long-term captive Northern Wheatears (from Eikenaar et al. 2014c)

and prolonging migration. However, Eikenaar et al. (2014b) argued that, as corticosterone levels are not downregulated during refueling, these negative correlations are probably not causal. The negative correlation between corticosterone and food intake is perhaps explained by considering the results from other studies that suggest that, rather than being associated with refueling, corticosterone is involved in the regulation of departure from stopover. First, a comparative study on two Northern Wheatears subspecies revealed that corticosterone levels are higher in the subspecies that makes shorter stopovers and thus is more likely to depart at any time (Eikenaar et al. 2013). Second, in wheatears, caught and temporarily caged at stopover, migratory restlessness was positively correlated with corticosterone level (Eikenaar et al. 2014c). Third, in refueling long-term captive wheatears, migratory restlessness was positively correlated with concurrently measured glucocorticoid metabolite levels in droppings (Fig. 7; Eikenaar et al. 2014c). Finally, the likelihood of actual departure from stopover, established using radio-telemetry, tended to increase with increasing corticosterone level (Eikenaar et al. 2014c).

Collectively, the results of these studies are consistent with the hypothesis that, by increasing locomotor activity, baseline corticosterone is involved in the regulation of departure of migrants at stopover. Corticosterone clearly does not promote refueling at stopover, at least not in the wheatear.

Morphology and migration

The flight performance in birds is influenced by the aerodynamic properties of its wings and body (e.g., Norberg 1990; Fiedler 2005). Within a species, flying with more

pointed wingtips increases the air speed and aspect ratio, thus supporting long-distance migratory flights. This is also the case in wheatears. Birds migrating longer distances show longer and more pointed wings than shorter distance migrants (Delingat et al. 2011; Förschler and Bairlein 2011), revealing that selection favors aerodynamic properties that enable fast and efficient flying (Fiedler 2005; Baldwin et al. 2010). We further studied whether the nature of the migration route shapes wings' aerodynamic properties. If so, wing pointedness (which is independent of body size) should be more pronounced in *leucorhoa* than in *oenanthe* wheatears, and birds with more pointed wings should arrive at stopover in spring earlier. Indeed, the *oenanthe* wheatears, even the Alaskan *oenanthe* wheatears, showed less pointed wings than *leucorhoa* wheatears, although the migration distance of the latter is much shorter than in Alaskan *oenanthe* wheatears. Furthermore, *leucorhoa* males had more pointed wings and a higher aspect ratio than their females. *Oenanthe* males had significantly lower aspect ratios than *leucorhoa* males, while females of both subspecies did not differ in their aspect ratios (Corman et al. 2014). The aerodynamic properties of the wing did not influence the timing of *oenanthe* wheatears at the Helgoland stopover site, but the arrival date was significantly influenced by the aerodynamic traits in *leucorhoa* birds, with early individuals showing more pointed wings, thus being more efficient and faster flyers than late ones (Corman et al. 2014). Aerodynamic properties in *leucorhoa* wheatears lead to a fast and efficient migration, favoring a sea crossing. The trade-off is likely lower flight maneuverability in comparison to *oenanthe* wheatears. The less risky migration route, i.e., no long sea barrier crossing, in *oenanthe* wheatear may have favored higher flight maneuverability for foraging (less pointed wings) in trade-off an energetically slightly more costly flight than in *leucorhoa* wheatears. It therefore seems that not the migration distance itself, as long hypothesized, but the existence/non-existence of severe ecological barriers presents a significant selection pressure in land birds supporting low costs of flight (Corman et al. 2014). On a Mediterranean Island during spring migration, *oenanthe* wheatears with more pointed wings arrived later in season than individuals with less pointed wings (Maggini et al. 2013). Here, stable hydrogen isotope ratios revealed that the earlier birds might breed in "close" vicinity of the study area, whereas late individuals are assumed to breed further north in central and northern Europe, including the Baltic Sea area (Delingat et al. 2011; Maggini et al. 2013) and thus migrating much later. This geographic differentiation is, however, absent on Helgoland as *oenanthe* wheatears passing Helgoland breed mostly in western Scandinavia (Dierschke et al. 2011) likely with less geographic variation in arrival (Haftorn 1971; Bakken et al. 2006).

Extrinsic factors

Timing of nocturnal departure

In nocturnal migrants time of departure determines the potential nocturnal flight duration. The earlier nocturnal take-off is, the longer the potential nocturnal flight and consequently nocturnal travel range. Longer nocturnal flights also reduce the number of stopovers needed during migration. Therefore, nocturnal departure is an important factor shaping the overall speed and costs of migration. However, when exactly nocturnal migrants take off and whether nocturnal departure times are organized with respect to intrinsic and extrinsic factors, such as body condition, environmental factors (wind), the length of the night and remaining migration distance, are poorly known.

In wheatears, take-off occurred after the end of nautical twilight on Helgoland (Schmaljohann et al. 2011; Schmaljohann and Naef-Daenzer 2011) when the skylight polarization pattern may be used to calibrate the birds' compass systems (Muheim et al. 2006; Chernetsov et al. 2011; Schmaljohann et al. 2013). In *leucorhoa* wheatears departing from Helgoland in spring, fuel load and the northward component in the departure direction each explained about 20 % of the variation in the nocturnal take-off time (Schmaljohann and Naef-Daenzer 2011). *Leucorhoa* wheatears with high fuel loads, i.e., long potential flight vectors, flying in the principal seasonal migration direction departed in the first half of the night only (Schmaljohann and Naef-Daenzer 2011). Lean birds on the other hand departed at no certain time within the night to aim for nearby stopover sites. Lean birds likely decide several times during the night whether departure conditions are sufficient to resume migration (Schmaljohann and Naef-Daenzer 2011).

In contrast to European wheatears showing a wide scatter of nocturnal departure times, Alaskan wheatears departed within a relatively small time window shortly after sunset and at a relatively high sun elevation from an Alaskan stopover site in autumn (Schmaljohann et al. 2013). The time window in which migrants decide to depart might be shorter when nights are shorter. Thus, birds might simply set off earlier in the night when nights are short. This general behavior is possibly influenced by the fact that nocturnal departure time is affected by body condition (Schmaljohann and Naef-Daenzer 2011).

Migratory departure and wind

Wind has been reported to influence departure decisions in migrants significantly (Liechti 2006), but observations are inconsistent. While many studies have found that migrants favor departing under favorable wind conditions (e.g.,

Åkesson and Hedenström 2000; Dänhardt and Lindström 2001; Erni et al. 2002; Yamaguchi et al. 2012), others have found no effect of wind on departure likelihood (Fransson 1998; Thorup et al. 2006; Sapir et al. 2011; Smolinsky et al. 2013). In a few studies migrants even departed in headwinds (Buurma et al. 1986; Bulyuk and Tsvey 2006).

In wheatears on Helgoland in spring wind conditions did not play a major role in the Scandinavian *oenanthe*, which even departed during headwind conditions, but the departure decision of *leucorhoa* birds is partly explained by wind (Dierschke and Delingat 2001). For both subspecies, an overcast sky seemed to be more important than wind, showing that visibility is an important factor in the decision to depart. This was further illustrated when combining wind and cloud cover. The percentage of departing *leucorhoa* birds was considerably lower with a completely overcast sky, and when both weather variables were unfavorable, only a few *leucorhoa* departed. By contrast, most Scandinavian birds departed whatever the weather (Dierschke and Delingat 2001). On Iceland, autumn departure of *leucorhoa* wheatears coincided with prevailing tail winds. The daily proportion of departing birds correlated with tailwind components at 1000 mb (reflecting c. 100 m above sea level) and 850 mb (c. 1500 m above sea level), showing that wheatears facing an ecological barrier select wind conditions supporting their oceanic travel (Delingat et al. 2008).

At an Alaskan stopover site wind did not significantly influence wheatears' departure decisions, likely because variation in wind conditions was too low to influence departure probability (Schmaljohann et al. 2013). However, wheatear's departure probability increased with decreasing temperature, which may be a reaction to the increase in energy costs on the ground with decreasing temperature. Changes in temperature may also coincide with a shift in pressure system and wind conditions; however, the daily tailwind component did not change with temperature or with season (Schmaljohann et al. 2013).

Assessing the role of wind for the departure of migrants is complicated because of the many confounding factors related to wind. Furthermore, current methods either suffer from inaccuracy in determining whether or not an individual has resumed migration, or, when accurate, are expensive (e.g., large-scale automated telemetry systems). Therefore, we also used a novel approach to study the effect of wind on stopover departure decisions (Eikenaar and Schmaljohann 2015). Wheatears caught during stopover were temporarily caged to measure their nocturnal migratory restlessness. We then related the degree of nocturnal restlessness to wind conditions prevailing at the time of capture. Amount of nocturnal migratory restlessness went up with more favorable wind conditions toward the seasonally appropriate migration direction (Fig. 8). Hence, we

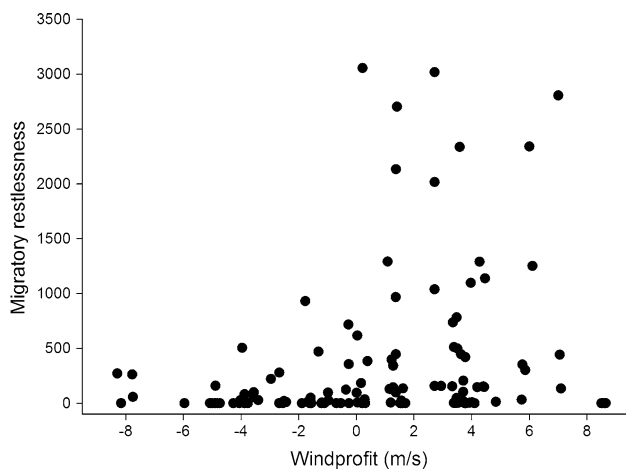


Fig. 8 The effect of surface wind profit on migratory restlessness the night following capture in Northern Wheatears during stopover on Helgoland (after Eikenaar and Schmaljohann 2015)

can estimate the influence of wind as experienced during stopover on the departure decision of birds by considering birds' nocturnal migratory restlessness as an approximation for their departure probability. These results also suggest that nocturnal migrants are able to use information collected during the day for their decision to depart in the night.

With the observation that wheatears facing an ecological barrier are selecting favorable winds for the crossing (Delingat et al. 2008; Schmaljohann and Naef-Daenzer 2011), we revisited the hypothesis that Canadian Northern Wheatears may sometimes cross the northern Atlantic in a direct flight to their western African wintering grounds (Thorup et al. 2006). For that we modeled nonstop trans-Atlantic migration of *leucorhoa* wheatears from eastern Canada to western Africa. In an individual-based model, we estimated costs of flight considering modeled wind data of several altitudes for autumn from 1979 to 2011. Modeled wheatears made it nonstop to western Africa on about 60 % of departure days when starting autumn migration with a high fuel load of 1.0 and migrating at altitudes of ~ 3000 m reached with a mean tailwind support of 4.9 ms^{-1} (Bulte et al. 2014).

Migration strategy, stopover and refueling

Except when facing ecological obstacles such as an extended sea crossing, wheatears migrate with low to moderate fuel loads and regular stopovers (Delingat et al. 2006). During migration, most species alternate flight bouts with stopovers, during which they rest and replenish the fuel used during flight (refueling). These migrants spend most of their migration time at stopover sites (e.g., Schmaljohann et al. 2012b); thus, overall migration speed depends

mainly on the number and duration of stopovers. The rate at which fuel stores are replenished (fuel deposition rate, FDR) is thought to affect stopover duration and is, therefore, considered to be one of the most important determinants of the overall migration time (Alerstam and Lindström 1990; Alerstam 2011).

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). Migrants minimizing time on migration (time-minimizers) experiencing a high FDR are assumed to stopover for a relatively long time period so that they depart with high fuel loads. In the case that birds experience low FDR, i.e., slow overall migration speed, they are expected to set off from the stopover site, to either search for a better site or actually resume migration. If birds behave in such a way, their fuel load at departure is positively correlated with FDR, as suggested for time minimizers (Alerstam and Lindström 1990; Lindström and Alerstam 1992). Birds minimizing the overall energy costs of transport (energy minimizers) are assumed to leave a stopover site irrespective of the current FDR. Energy minimizers are thought to fuel until a certain fuel load is gained that would be sufficient for the next flight bout of that bird (Hedenström and Alerstam 1997). Here, the departure fuel load is supposed to be unrelated to FDR. Simplified, an existing or lacking correlation between departure fuel load and FDR indicates the “migration strategy” of a bird on its move.

In wheatears on Helgoland, the correlation between departure fuel load and FDR depends on subspecies and sex (Dierschke et al. 2005; Delingat et al. 2006; Bairlein et al. 2013), reflecting different migration strategies in *oenanthe* versus *leucorhoa* wheatears and in males and females, respectively. In spring male *leucorhoa* wheatears behaved on Helgoland as suggested for time-minimizers, whereas *leucorhoa* females revealed a migration strategy more in line with an energy-saving strategy, as the departure fuel load was not related to FDR. However, departure fuel loads were higher than predicted for the energy-minimizing strategy, because fuel loads were as high as in males (Dierschke et al. 2005). During autumn migration juvenile wheatears in general behaved as predicted by the time minimization strategy when leaving Iceland (Delingat et al. 2008) and Helgoland (Schmaljohann and Dierschke 2005). Alaskan wheatears in autumn (Schmaljohann et al. 2013) and *leucorhoa* females on Helgoland in spring (Dierschke et al. 2005) or at Fair Isle in spring (Delingat et al. 2008) carried high departure fuel loads, which were higher than expected for a single nocturnal flight bout. This contradicts the strategy of minimizing the overall costs of transport, under which birds are not supposed to carry any

surplus fuel because this is energetically costly (Hedenström and Ålerstam 1997). Surplus fuel load may give birds a higher flexibility in the selection of stopover sites, which seems especially important in unpredictable environments.

Variation in FDR may result from environmental factors such as food availability and weather as well as from intrinsic factors such as molt and body mass (reviewed in Jenni and Schaub 2003; Ålerstam 2011). Furthermore, the motivation to feed may depend on the remaining distance to migrate and likely on the quantity of fuel consumed during the previous flight. To assess whether the amount of fuel loss prior to refueling influences FDR, we combined field data with data from a fasting-refueling experiment on our long-term captive wheatears. FDR was higher in *leucorhoa* that have burned more fuel to get to our study site (see above) than in *oenanthe* wheatears. In the captive study, birds were fasted for different periods, and the resulting variation in the extent of fuel loss explained most of the variation in subsequent FDR. This indicates that FDR is modulated on top of the current environmental and endogenous conditions by fuel loss prior to refueling (Eikehaar et al. 2014d).

Stopover fueling and the role of predation and competition, respectively

FDR depends on food availability (Dierschke and Delingat 2001; Dierschke et al. 2003), which in turn depends on intrinsic habitat factors and on weather. Furthermore, extrinsic factors, such as the presence and quantity of predators and competitors, also influence FDR. In wheatears, the predation risk did not have a direct effect on the departure decision (Dierschke and Delingat 2001; Schmaljohann and Dierschke 2005) but affected refueling with lower FDR as predation risk, as overflying raptors, increased (Schmaljohann and Dierschke 2005). Besides the presence of predators, competitors may also influence FDR as the social status (dominance rank) of an individual may determine access to food resources. Intraspecific aggressive interactions between color-ringed wheatears were predominantly won by the initiator, by males and by larger birds, whereas fuel load and subspecies did not affect the outcome (Dierschke et al. 2005). Although compared to females, males were more often dominant at the feeding stations or held territories, refueling patterns could not be explained by dominance (Dierschke et al. 2005). Unable to settle and defend a territory, subordinates were mostly vagrant and used stopover sites only shortly. Possibly these subordinates were chased out by dominant wheatears (Arizaga et al. 2011). However, subordinate or non-territorial wheatears did not refuel at a lower rate or depart with lower fuel loads than dominant or territorial birds when

supplied with mealworms at feeding stations (Fig. 2). Their restricted access to feeding stations was made up with larger doses of food taken per visit, leading to the same energy intake as that of dominant and territorial birds (Dierschke et al. 2005). Therefore, competition during stopover does not necessarily need to play a significant role in shaping the differential timing of migration of male and female wheatears when food is plenty. In habitats with low food abundance (Delingat and Dierschke 2000), however, subordinates tended to forage at lower rates (Arizaga et al. 2011).

Field studies on the role of competition for fueling are commonly affected by confounding factors that cannot be controlled for, such as food abundance or weather. Therefore, we studied the role of dominance status under controlled conditions in captivity as well. Two individuals each were simultaneously placed in an indoor aviary with food provided at a feeder where only one bird of the pair was able to use the feeder at a time. During the period of autumn migration adults displaced first-year birds and males displaced females from the feeder, respectively, while body size, fuel load and subspecies did not show significant effects (Arizaga and Bairlein 2011). This intrinsic competition may facilitate the time-minimizing migration strategy of male wheatears.

Outlook

The wheatear proved to be an ideal model species to combine field and laboratory studies to elucidate the complexity of the control of migration in a single-species approach. It revealed that it is feasible to track individual birds during migration, to quantitatively study stopover behavior, ecology and physiology, and to keep birds in controlled captive conditions to study endogenous and intrinsic factors involved in the control of migration. Our studies show that the migration of wheatears—and likely many other of the long-distance migratory species—is governed by endogenous, intrinsic and environmental factors, respectively. It enables studying the interplay between genes and the environment and elucidating the evolutionary adaptability of a migrant species in a single-species approach. Using new molecular genetics technology such as next generation sequencing (Morozova and Marra 2008; Schuster 2008) will also allow a more focused approach to revealing the underlying mechanisms of the spontaneous seasonal body mass cycle, for example, which is so prominent in wheatears. However, future studies also need to address in more detail the required nutritional quality of stopover sites for rapid refueling and timely and successful migration. During spring, these conditions could even carry over to subsequent breeding (Smith and Moore 2003). Therefore, future studies need to integrate migration

and breeding performance as well. High breeding site faithfulness of wheatears and new tracking technology make this feasible (Schmaljohann et al. 2012a).

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