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Obligatory barrier crossing and adaptive fuel management in migratory birds: the case of the Atlantic crossing in Northern Wheatears (*Oenanthe oenanthe*)

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Abstract Behaviour on migration was often suggested to be selected for time-minimising strategies. Current optimality models predict that optimal fuel loads at departure from stopover sites should increase with increasing fuel deposition rates. We modified such models for the special case of the east Atlantic crossing of the Northern Wheatear (*Oenanthe oenanthe*). From optimality theory, we predict that optimal time-minimising behaviour in front of such a barrier should result in a positive correlation between fuel deposition rates and departure fuel loads only above a certain threshold, which is the minimum fuel load ($f_{\min}$) required for the barrier crossing. Using a robust range equation, we calculated the minimum fuel loads for different barrier crossings and predict that time-minimising wheatears should deposit a minimum of 24% fuel in relation to lean body mass (m_0) for the sea crossing between Iceland and Scotland. Fuel loads of departing birds in autumn in Iceland reached this value only marginally but showed positive correlation between fuel deposition rate (FDR) and departure fuel load (DFL). Birds at Fair Isle (Scotland) in spring, which were heading towards Iceland or Greenland, were significantly heavier and even showed signs of overloading with fuel loads up to 50% of lean body mass. Departure decisions of Icelandic birds correlated significantly with favourable wind situations when assuming a migration direction towards Spain; however, the low departure fuel loads contradict a direct non-stop flight.

Keywords Barrier crossing · Flight costs · Optimal migration · *Oenanthe oenanthe* · Fuel loads

Introduction

Migratory birds show a multitude of adaptations that enhance their migration performance in relation to residents. These adaptations involve wing morphology, physiological plasticity of metabolic organs and behavioural programmes (Alerstam et al. 2003). The behavioural strategy set involves the adaptive responses to the fuel deposition rate encountered at stopovers and the associated fuel load and timing of departure. Optimality theory of bird migration assumes one of alternative currencies being subject to selection, and depending on the currency assumption, different optimal behaviours may be deduced (Alerstam and Hedenström 1998). Field experiments have shown that behaviour in migratory birds is mostly consistent with an overall time-minimisation strategy (Lindström and Alerstam 1992; Schmaljohann and Dierschke 2005; Bayly 2006; Hedenström 2007), which is equivalent to a strategy that maximises the overall speed of migration (Alerstam and Lindström 1990; Hedenström and Alerstam 1997). This involves the adjustment of departure decisions so that the fuelling opportunities are exploited in line with the time-selected strategy, which is manifested as a positive relationship between the current fuel deposition rate (FDR) and the relative departure fuel load (DFL). This is contrasted with the energy minimisation strategy, where the DFL should be independent of FDR. In simple optimality

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models for time-minimising migration, the optimal DFL depends on the FDR and search/settling time and energy costs associated with arrival at a new stopover site (Alerstam and Lindström 1990; Hedenström and Alerstam 1997).

Fuelling at a stopover can be seen as the accumulation of potential flight distance. A tailwind will increase the utility of the current fuel load, while a headwind will devalue its utility (Weber et al. 1998; Weber and Hedenström 2000). Migratory birds are therefore expected to pay attention to the current wind situation, and mainly depart with tail winds or at least avoid departing into headwinds (reviewed by Liechti 2006). Radar studies show that migration intensity is highest when birds encounter tail winds in their preferred migration direction (Alerstam 1990; Erni et al. 2002). A further complication is that stopover sites are not available everywhere, and depend on the species-specific distribution of suitable habitats for fuelling. Long-distance migrants are almost certainly bound also to encounter ecological barriers, where stopover for refuelling is not possible. When confronted with a significant barrier, such as a major desert or a sea crossing, the behaviour has to be modified as compared to migration across ecologically suitable habitats. One solution is to migrate along a detour and thus avoiding the barrier crossing or cross it where the non-stop distance is reduced (Alerstam 2001). However, in some cases, this may not be an option if there are no detour alternatives. Then, the migrant has to prepare for a long direct flight. This implies that a certain threshold of fuel load has to be deposited regardless of the current fuelling situation. But how should the behaviour change when preparing to cross a barrier? In this study, we focus on a classic migratory system—the Icelandic and Greenlandic populations of the northern wheatear (*Oenanthe oenanthe*, wheatear hereafter). These populations of the wheatear migrate across the North Atlantic on both autumn and spring migration, and the Greenlandic population supposedly uses different routes between the seasons (Snow 1953; Alerstam 1990). Wheatears were studied when preparing for migration on Iceland in autumn and on Faire Isle, off the Scottish north coast, in spring. Theoretical estimates of flight range on the basis of fuel load are a fundamental component of optimal migration theory (Alerstam and Hedenström 1998). Here we derive a robust range equation based on mass loss rates in flying birds, which we believe has advantages in relation to alternative methods based on flight mechanics. This equation is used to estimate flight ranges of wheatears studied in Iceland and Scotland, and it is also used to explore the possibility of a direct flight between the Nearctic and West Africa in autumn (cf. Thorup et al. 2006). The aim of this paper was to test if birds preparing to cross an ecological barrier, in this case more than 1,000 km across the Atlantic Ocean, follow a time-minimising strategy or not.

Flight range

To estimate flight ranges of birds leaving their stopover site to cross the North Atlantic, we derive new equations to calculate mass loss during flight. The potential flight range in powered flight follows a diminishing return function of added fuel (Pennycuick 1975). Let the relative fuel load $f=(m-m_0)/m_0$, where m is departure mass including fuel and m_0 is the lean mass of the bird. Depending on the assumption of how drag increases due to fuel accumulation and its effect on frontal area, the flight range equation is $Y = c\left(1-(1+f)^{-1/2}\right)$ if the frontal area increases in direct proportion to added fuel mass (Alerstam and Lindström 1990), and $Y = 0.5c\ \ln(1+f)$ if added fuel does not affect the frontal area (Alerstam and Hedenström 1998). An alternative way of deriving a flight range equation is to use the empirical result that the rate of mass loss in flying birds is a constant proportion of the current mass. In studies of small passerine migrants, the rate of mass loss is close to 1% of the mass per hour flight time in the thrush nightingale (*Luscinia luscinia*) (Kvist et al. 1998), which is of similar size to the wheatear. Two available field estimates of mass loss in the wheatear yielded 0.75 and 1.3% h^{-1}, respectively (Nisbet 1963). Other estimates indicate that 1% h^{-1} is a realistic assumption for other small birds as well (Hussell and Lambert 1980; Alerstam 1981). Let us therefore assume

$$\frac{dm}{dt} = -0.01m, \tag{1a}$$

where dm/dt is the rate of change in body mass. The variables can be separated and written in integral format as

$$dt = -100\int\frac{dm}{m}. \tag{1b}$$

After integration from departure mass $(1+f)m_0$ to arrival mass m_0, the flight duration is

$$T = 100\cdot\ln(1+f),\ [\text{hours}] \tag{2}$$

which, in turn multiplied by airspeed U [km/h], gives the flight range equation as

$$Y\ = 100\cdot U\ \ln(1+f).\ [\text{km}] \tag{3}$$

This equation thus refers to the distance in relation to the surrounding air, while tailwinds will increase the range over ground and headwinds will reduce the range over ground. Alternative methods of calculating the potential flight range in migratory birds involve the use of aerodynamic models (Pennycuick 1989), which rest on assumptions of various morphological and physiological properties of the birds.

There is some controversy regarding some of these assumptions (Hedenström 2002); especially the magnitude of the body drag coefficient is not known with great precision. Therefore, the empirically derived range equation above should be more reliable than alternative methods because it depends on direct measurements of fuel consumption rates.

According to aerodynamic theory, birds should adjust their airspeed in relation to body mass, which means that, during long flights, when body mass is reduced due to fuel consumption, the airspeed should be lowered (Pennycuick 1978). Birds may also compensate for cross-winds to various degrees with concomitant changes of speed in the preferred track direction and flight costs (Liechti et al. 1994; Alerstam and Hedenström 1998). Our formula assumes a fixed airspeed taken as an average for the whole flight and ignores effects due to wind drift compensation because these effects will be small in comparison with the overall range estimates.

Fuel requirements for different Atlantic and North Sea crossings are calculated assuming an airspeed of 13 m/s (47 km/h) in still air as measured using radar by Bruderer and Boldt (2001). Distances and initial departure directions were calculated using great circle routes (Imboden and Imboden 1972).

Methods

Field work and biometrics

For collecting field data, wheatears were trapped at two sites along the north-east Atlantic flyway. From 5 to 28 May 2002 wheatears were trapped at Fair Isle (59°32′ N, 1° 39′ W), a small island between the Shetland Islands and the Orkneys off north-east Scotland, and from 8 until 30 August 2002 on Heimaey, Iceland (63° 26′ N, 20° 17′ W), one of the Vestman Islands south of Iceland. In the following text, these sites will be referred to as Scotland and Iceland, respectively.

All birds were trapped with baited (either mealworms or maggots) spring traps and measured and banded immediately after capture with an individual combination of three colour rings and one metal ring. The birds were sexed and aged according to Svensson (1992). Wing length (maximum wing length, method 3, Svensson 1992), was measured to the nearest 0.5 mm and the birds were weighed to the nearest 0.1 g with an electronic balance. Fat score was determined using a scale from 0 to 8 according to Kaiser (1993), where 0 means no visible subcutaneous fat and 8 a fat layer that covers the ventral side of the bird completely.

Two subspecies of the northern wheatear were passing through Scotland during the study period: the nominate subspecies *O. oenanthe oenanthe* and the bigger subspecies *O. oenanthe leucorhoa*, respectively. The latter one is supposed to breed in Iceland, Greenland and east Canada, while the nominate form is widespread over Europe, Asia and as far east as Alaska (Cramp 1988). Because only the subspecies *leucorhoa* migrating towards Iceland or Greenland was of interest for this study, we distinguished subspecies by wing length as follows: males exceeding 102 mm and females exceeding 97 mm were considered as subspecies *leucorhoa* (Svensson 1992). Data on migrants of the nominate subspecies *oenanthe* were not analysed in this study. A differentiation by wing length between birds of either Icelandic or Greenlandic origin was, however, not possible due to a considerable overlap (Salomonsen 1934). In spring, males and females are easily distinguished due to their dimorphic colouration, while juveniles on autumn migration are not distinguishable on plumage characteristics (Svensson 1992). Therefore, most birds trapped during autumn migration on Iceland could not be sexed.

Body mass changes throughout stopover of individually marked birds were recorded by remote weighing with electronic balances, baited with either maggots or mealworms, from 09:00 hours until 21:00 hours local time, depending on weather conditions. The weight on the display of the balances was read using a telescope from distances of 10–50 m.

To estimate fuelling rates and relative DFLs for individual birds, we calculated a relationship between lean body mass (m_0) and size. A linear regression ($R^2=0.502$, $p<0.001$, $n=102$) of body mass vs wing length of wheatears with fat score 0 (no visible fat) trapped at different stopover sites in Europe resulted in the equation

$$m_0[\mathrm{g}] = 0.50[\mathrm{g/mm}] * \mathrm{Wing}[\mathrm{mm}] - 26.51 \qquad (4)$$

This implies, for example, that an average Icelandic wheatear with a wing length of 102.7 mm (average of 96 wheatears trapped in this study in Iceland was 102.7 mm, sd=2.55 mm) has a lean body mass of 24.8 g. Smaller birds have a lower and larger birds a higher lean body mass than 24.8 g. However, the individual lean body mass not only depends on size but it can differ depending on whether birds are preparing for migration or if they just arrived after a migratory flight. This is illustrated by wheatears collected during spring in 1968 at the, then quite barren, volcanic island Surtsey (Gudmundsson 1970). Birds classified as having no visible fat, and consequently lean, had an average body mass of 20 g. This is almost 5 g lower than the average calculated lean mass for birds in our study. However, when comparing birds of corresponding fat classes collected before autumn migration on Iceland with those making landfall on Surtsey during spring migration, it appeared that the autumn birds were 8 g heavier than spring birds (Gudmundsson 1970). Birds approaching the end of a migratory flight have also consumed some non-fat tissue mass (cf. Piersma 1998, Bauchinger and Biebach 2001), which is the reason for these differences in lean body mass estimates. Because we are concerned with flight ranges of birds, we have based our estimates on the regression equation derived here, which is derived from birds caught before migratory flights.

After calculating the size-corrected lean mass m_0 for each bird according to the formula above (Eq. 4), fuel deposition rate (hereafter FDR) was calculated as body mass gain during 24 h (±2 h), or a multiple of 24 h divided by m_0 and the number of days between the measurements. If birds were weighed on several days, the measurements with the largest time span between measurements were used as a representative value for FDR. This approach is identical to other studies using mass gain as an estimate for fuel accumulation (e.g. Fransson 1998, Dänhardt and Lindström 2001, Bayly 2006). Mass changes prior to migration are generally assumed to represent fat and non-fat components such as protein (e.g. Lindström and Piersma 1993, Mc Williams et al. 2004). A rapid mass gain could potentially be also due to water ingestion, which could be the case if birds are dehydrated. This is very unlikely during spring and autumn at the sites used in this study, but it could potentially introduce a bias at desert sites.

To calculate relative departure fuel loads (hereafter DFL), only the last body mass measurements obtained on the last day the bird was observed were taken into account. Both study sites were searched for colour-marked individuals daily to record if birds had left after the last body mass measurement. Resighting probability for nine *leucorhoa* birds staying in Scotland was 86%, and that for 18 birds staying on Iceland was 83% (number of days with observations divided by number of days between ringing and last observation for all birds pooled). When calculating DFL, we refer either to birds that used our feeders (fed birds, hereafter) and whose weight before departure could be read on the balance display, or to unfed birds that were only trapped once but were not seen again in the study area. Those birds that disappeared after capture were assumed to have departed, and their body mass at capture is probably close to their departure weight. Therefore, we used weight at capture in these birds to calculate DFL for unfed birds. Birds that were observed in the study area at days following capture but did not feed at the balances and departed with unknown weights were not included in the analyses. DFL was calculated as $(m-m_0)/m_0$ with m as the last body mass measurement before departure.

Because some of the measurements were taken in the morning hours, and the birds presumably gained body mass until departure in the evening, DFL might have been underestimated in some cases. Our calculation of lean body mass (m_0) using regression of fat score 0 and wing length as reference does not imply that m_0 is a strict fat-free body mass, but instead, the birds might have visceral fat reserves that can be used up during extreme migratory flights. Therefore, our estimates of DFLs represent conservative estimates of maximum flight ranges. Sample sizes for testing correlation of FDR and DFL differ from sample sizes for mean DFL and FDR. This is partly due to the fact that some birds from which we obtained FDR could not be weighed on the day of departure, so their DFL remained unknown. Also, some birds could not be weighed on a 24-h schedule to obtain FDR but weights shortly before departure could be obtained in these birds, so DFL could be calculated.

We calculated wind assistance at departure from Scotland from 5 to 28 May and for Iceland for each day between 8 and 31 August 2002. Tailwind components (TWC) were calculated as $V_w \cos(\varphi_T - \varphi_w)$ where V_w is the wind velocity [m/s], φ_T is the migration direction and φ_w is the wind direction. Migration direction refers to the initial course of a great circle between possible destinations (see Table 1). Daily wind direction was calculated from wind vectors obtained from NCEP Reanalysis data provided by the National Oceanic and Atmospheric Administration Cooperative Institute for Research in Environmental Sciences (NOAA-CIRES) Climate Diagnostic Center from their web site at http://www.cdc.noaa.gov. Data consisted of Uwind vectors (eastward wind component) and Vwind vectors (northward wind component) measured daily at 1,000 mb (approximately 100 m above sea level) and 850 mb (approximately 1,500 m above sea level) at 24:00 h. These altitudes represent possible migration altitudes at a time close to possible departures by the birds (cf. Åkesson et al. 1996a). The wind data contain daily analysis values interpolated to a 2.5°×2.5° regular latitude/longitude grid calculated for the geographical position of the icelandic island of Heimaey and the scottish island Fair Isle, respectively.

Table 1 Barrier distance, initial migration direction and required fuel loads to cross the North Atlantic from Iceland (Heimaey, 63°26′ N, 20° 17′ W) in different initial directions along great circles are shown

Goal	Barrier distance (km)	Direction	Required relative fuel load
Scotland (58° N 5° W)	1,022	119°	0.24
Norway (60° N 5° E)	1,374	95°	0.34
Spain (43° N 8° W)	2,403	155°	0.67

Assumed airspeed is 13 m/s. Fuel loads are presented in relation to m_0, which is a size-corrected parameter estimated from birds with fat score 0.

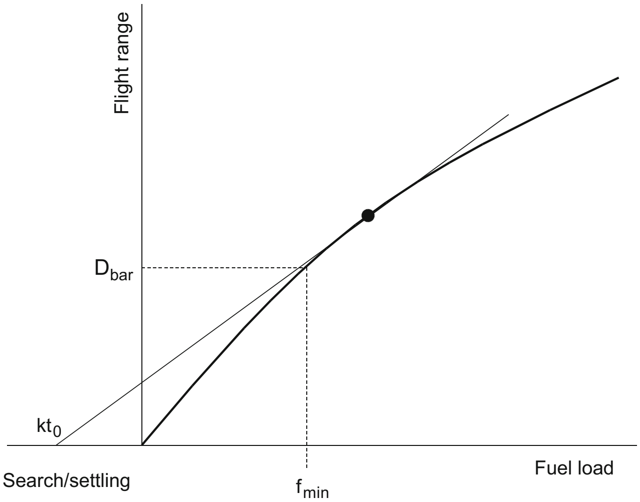

Fig. 1 Potential flight range in relation to relative fuel load. For a given search settling time which is connected with an initial mass loss (kt_0), the optimal DFL can be found by drawing a tangent from kt_0 to the gain curve. The optimal departure load to maximize speed of migration is indicated by a *black dot*. In front of a barrier with a given distance (D_{bar}), the optimal fuel load will always be above a minimum fuel load (f_{min}) required to cross the barrier

Results

To determine the optimal DFL for a bird in front of a barrier of distance D_{bar}, a modification to the standard situation is required as illustrated in Fig. 1. It will never be optimal to depart with less fuel than needed to cover the barrier distance D_{bar}, unless the bird can count on a tail wind (cf. Weber et al. 1998). Therefore, with very low FDRs, the optimum departure load is f_{min}, while beyond a threshold FDR, the DFL follows the usual time minimisation criterion, obtained graphically by constructing a tangent as shown in Fig. 1. For minimising energy cost of transport, the DFL will always be f_{min}, i.e. exactly that required to cross the barrier, irrespective of FDR.

We used the above-mentioned flight range equation (Eq. 3) to calculate fuel requirements for a scenario of different barrier crossings for birds leaving Iceland in autumn. Three different possibilities to cross the east Atlantic or the northern North Sea by departing from southern Iceland were considered:

(a) Towards Scotland
(b) Towards southern Norway
(c) Towards Spain

The relative fuel requirements differ between 0.24 for a flight to Scotland and 0.67 for a flight directly to Spain, with an intermediate value for a flight to Norway of 0.34 (Table 1). For birds leaving Fair Isle, Scotland, in spring, the shortest distance to reach the east coast of Iceland (ca 64° 45′ N, 14° 0′ W, 860 km; departure direction 317°) would require a relative fuel load of approximately 0.20.

Derived from these calculations, we expect Icelandic wheatears to deposit a minimum DFL of 0.24, even if FDR is low, and to deposit more fuel only in cases of high FDR (Fig. 2). For predicting a relationship between FDR and DFL above this threshold we refer to data published by (Schmaljohann and Dierschke 2005). They found a positive correlation in FDR and DFL in northern wheatears (including subspecies *oenanthe* and *leucorhoa*) on stop-over, following model predictions (Weber et al. 1999), with the expectation of global variation in FDR along the migration route and search settling times of 1–3 days at each new stopover site.

On Iceland, we obtained both FDR and DFL for 11 birds using the feeders. Excluding the only bird that lost weight, there was a positive correlation between FDR and DFL (Fig. 2; r_s=0.81, p=0.005, n=10). This is justified because the model does not allow for negative mass gains, unless they are search/settling costs (cf. Hedenström and Alerstam 1997). The difference in the slope of the empiric data and in the predicted curve was not significant (Fig. 2; t test for differences between empirical and hypothetical regression coefficients: t_8=1.00, p>0.05,). DFL varied from 0.11 to 0.58 (mean=0.30, sd=0.14, n=13) and FDR varied between −0.04 and 0.11 (mean=0.05, sd=0.04, n=13). Sample sizes for FDR and DFL are bigger than in Fig. 2 because we could not obtain DFL from all birds from which we obtained FDR and vice versa.

In Scotland in spring, we obtained FDR and DFL in four female birds and one male which were visiting the

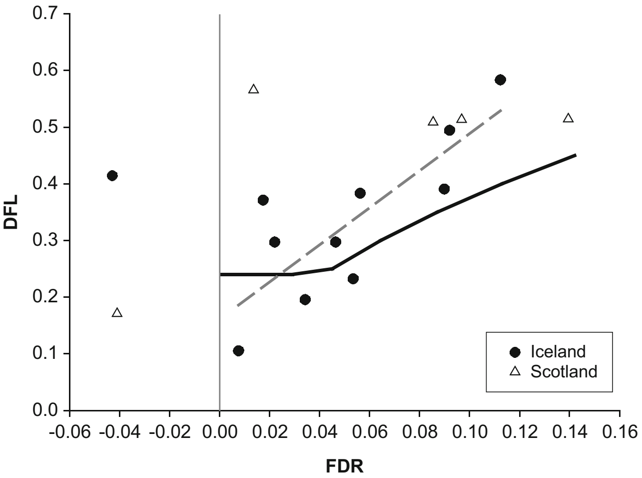

Fig. 2 Relationship between DFL and FDR in wheatears leaving Iceland in autumn (*black dots*) and Scotland in spring (*white triangles*).The *black solid line* shows predicted relationship of DFL and FDR for optimised time minimising migration strategies of birds facing a barrier of 1,000 km extension. The steepness of the predicted correlation between FDR and DFL arises from data on autumn migration of northern wheatears published by Schmaljohann and Dierschke (2005). The *grey broken line* indicates significant correlation in Icelandic birds, when excluding the bird with negative FDR, while no correlation could be shown for the birds in Scotland (see text)

feeders. The range of FDR was −0.04 to 0.14 (mean=0.06, sd=0.07, n=5) with DFL varying from 0.17 to 0.57 (mean=0.45, sd=0.16, n=5). In these birds, the correlation between FDR and DFL was, however, not significant (r_s=0.4, p=0.505, n=5).

Barrier distance and fuel loads

Data on unfed wheatears trapped on Iceland and departing after capture without using the feeders showed mean relative DFL of 0.13 (sd=0.08, n=75). In spring, unfed wheatears leaving Scotland showed significantly higher relative DFL with a mean of 0.25 (sd=0.21, n=25) (U-test: Z=−2.601, p=0.009) than the Icelandic autumn birds. Birds using the artificial feeders showed significantly higher DFL at both sites when compared with unfed birds (U-test: Iceland Z=−4.16, p<0.001, n_{fed}=13, n_{unfed}=75, Scotland: Z=−2.09, p=0.037, n_{fed}=5, n_{unfed}=25) (Fig. 3).

While both fed and unfed birds in Scotland during spring migration seem to reach the DFL of 0.20 required to cross the northeast Atlantic, birds in August on Iceland did so only marginally (Fig. 3). Among 13 Icelandic birds that were using the feeders, eight reached the marginal DFL of 0.24 to reach the Scottish coast.

To test whether departure decisions were made to achieve support from tailwinds, we tested whether the daily proportion of departing birds correlated with tailwind components at 1,000 mb (×100 m above sea level) and 850 mb (×1,500 m above sea level). For Scotland, we assumed a migration direction of 317°, which should bring the birds on the shortest way to Iceland (×860 km). For Iceland, we consider the three possible migration directions given in Table 1. There was no significant correlation between the proportion of departing birds in Scotland and tailwind components neither at 1,000 mb nor at 850 mb ($r_{\mathrm{p1,000\ mb}}$=0.175, p=0.475; $r_{\mathrm{p850\ mb}}$=0.104, p=0.672; n=19 days). For departures in autumn on Iceland, we found a significant correlation assuming a migration direction towards Spain at both heights ($r_{\mathrm{p1,000\ mb}}$=0.627, p=0.002; $r_{\mathrm{p850\ mb}}$=0.507, p=0.016; n=22 days). There were no significant correlations between departure decisions and wind assistance assuming flight directions towards Norway and Scotland (Norway: $r_{\mathrm{p1,000\ mb}}$=−0.003, p=0.990; $r_{\mathrm{p850\ mb}}$=−0.353, p=0.107; Scotland: $r_{\mathrm{p1,000\ mb}}$=0.351, p=0.109; $r_{\mathrm{p850\ mb}}$=0.060, p=0.790, n=22 days). The results for departures from Scotland towards Iceland and from Iceland towards Spain corresponding to tailwinds at 1,000 mb are presented in Fig. 4. We plotted the daily number of birds present and the number of birds that departed at the next night together with the tailwind components for each day during the study period. If bars for present and departing birds are of the same length, this means that 100% of the present birds departed the following night. “Present birds” means, in this case, the total number of trapped birds at each day plus the number of already present colour-marked birds trapped at previous days. During spring migration, the birds experienced on average tailwind components of 5.5 m/s at 1,000 mb and 7.2 m/s at 850 mb, respectively. They had to face light headwinds only on three nights. The most favourable period started after 17 May. Hardly any bird landed at the study site after that day and those birds that were trapped after 17 May all departed the following night, thus taking advantage of tailwinds up to 15 m/s (Fig. 4). On Iceland, the wind situation was less favourable, with average tailwind components of 3 m/s at 850 mb for departures towards Norway and, on average, headwinds towards Spain. No birds seemed to leave the study site especially in a period from 20 to 26 August with prevailing storms and precipitation.

Taking DFLs plus wind conditions at the night of departure into account, we calculated a possible flight range for each bird. For each night, the height (1,000 mb or 850 mb) with the most favourable tail wind component was chosen and birds with departure weights below our calculated m_0 were considered to have a flight range of 0 km. Those birds that departed from Scotland had an average flight range of 1,451 km (sd=1,104 km, n=30), and 60% of them could have reached Iceland. Those birds leaving Iceland in autumn and heading towards the Iberian Peninsula had an average flight range of 753 km (sd=546 km, n=88). Two birds would have been able to reach the Iberian Peninsula in a non-stop flight assuming a steady wind situation like that at departure. However, because the prevailing winds came from the west and southwest, an eastward drift would have enabled those birds with a flight range of at least 1,000 km (21 birds out of 88) to reach the northwest coast of Scotland or Ireland.

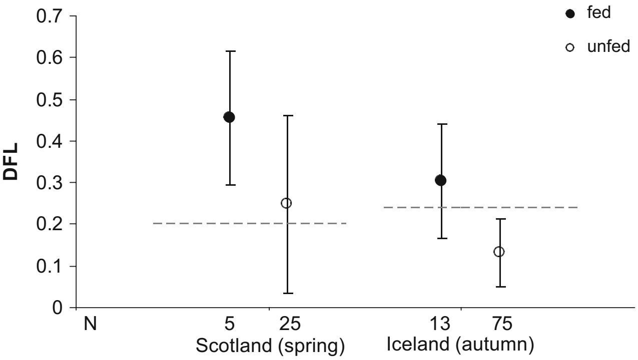

Fig. 3 DFLs of wheatears at Fair Isle, Scotland, during spring migration and birds at Heimaey, Iceland, during autumn migration 2002. *White symbols* represent mean fuel loads from unfed birds that departed after capture; *black symbols* represent fed birds that were weighed at feeders at days following capture. *Whiskers* mark standard deviation. The *horizontal dotted line* indicates the minimum required fuel loads for the Atlantic crossing

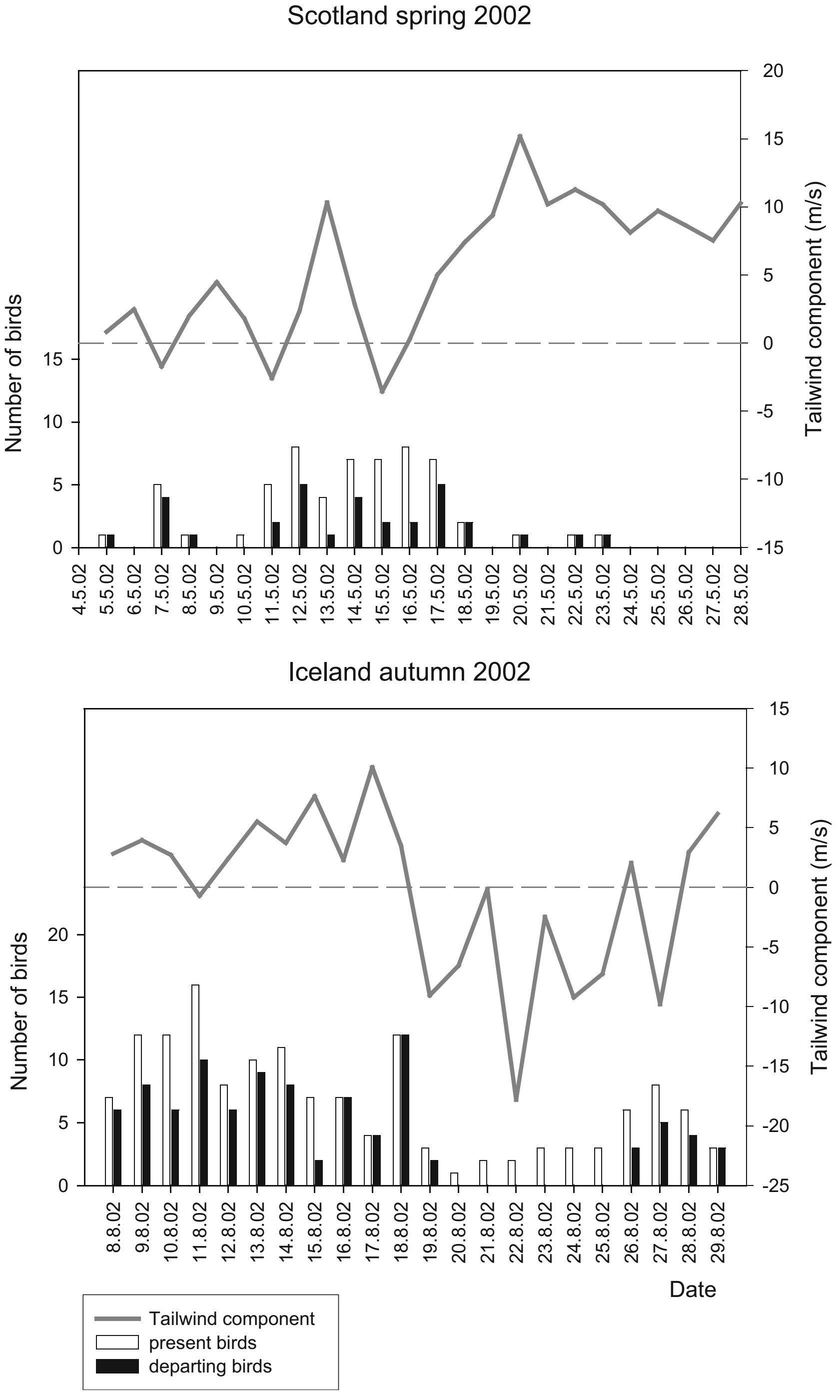

Fig. 4 Wind assistance (tailwind component) for birds heading from Scotland towards Iceland in spring and from Iceland, towards Spain in autumn measured at 24:00 hours and 10 m height daily from 5 May 2002 until 28 May 2002 and from 10 August 2002 until 31 August 2002 (*grey line*) and daily number of present colour-marked birds (*white bars*) and the fraction of departing birds (*black bars*)

Discussion

When birds are confronted with an ecological barrier, they must accumulate enough fuel to cover at least the distance across the barrier. Time-minimising migrants should also care about the rate at which this fuel is accumulated, which not uncommonly involves reverse migration to locate suitable stopovers (e.g. Åkesson et al. 1996b, but see Komenda-Zehnder et al. 2002). If the daily rate of fuel accumulation is beyond a threshold value at the relevant search/settling time costs, the optimal DFL will be higher than that required to cross the barrier distance (cf. Fig. 1).

At very low fuelling rates and short search/settling times, the optimal DFL will be exactly that required to cross the barrier, which is the reason for the horizontal part of the curve representing optimal DFL in Fig. 2. Therefore, if FDR is very low, there will be no response to variation within a range of FDR even though the birds are time-minimisers. However, beyond a certain FDR, the optimal response is increasing DFL in relation to FDR, as shown in Fig. 2, and the expectation is a positive correlation between FDR and DFL. The juvenile wheatears on Iceland showed a significant positive correlation between FDR and DFL, which, thus, is consistent with an overall migration strategy involving time as an important component. Stopover behaviours in agreement with time-selected migration appear to be quite general among passerine migrants (Hedenström 2007).

There is usually also a seasonal effect so that late birds exhibit elevated DFL compared with early birds (Bairlein 1998; Fransson 1998). This is further supported by data on nine wheatears caught in southern Iceland in October 1959 that showed a mean body mass of 38.1 g (reported by Gudmundsson 1970). Assuming average wing length measured in Icelandic birds in 2002 of 102.7 mm (sd=2.55 mm, n=96), 38.1 g represent a mean relative DFL of 0.53 (range: 0.41–0.60), which is higher than the average of 0.13 for birds caught but not using the feeders in the present study. Because a DFL of 0.13 is insufficient to reach the nearest land (cf. Table 1), it is unlikely that these birds departed with so little fuel unless with a strong tail wind assistance. Because the Icelandic study site was also frequently visited by predators (*Falco columbarius* and feral cats), a shift to a nearby stopover site on Heimaey appears as a possibility. Alternatively, these relatively lean birds performed reverse migration to mainland Iceland, where they continued fuelling. One of the latter explanations is probably the most likely one because a direct flight to Scotland would require a tail wind assistance of >10 m/s (with a relative fuel load of 0.13), and there was only one day during the whole study period when such winds occurred (cf. Fig. 4).

Interestingly, the supplementary fed wheatears recorded on spring migration at the site in Scotland did not show any significant relationship between DFL and FDR as expected for time minimisers, but instead, the birds accumulated high DFLs at about 0.50. Admittedly, there were only five birds in this data set, and one should therefore be careful in generalising. Data published by Williamson (1958) on wheatears passing Fair Isle, Scotland, in spring show mean weights of male *leucorhoa* of 31.0 g (sd=5.6 g, n=30) and for females of 30.2 g (sd=4.4 g, n=24). Assuming that these birds had similar mean wing length compared to those wheatears measured in our study at Fair Isle (males wing=104.6 mm, sd=2.4 mm, n=7 and females wing=101.6 mm, sd=2.32 mm, n=24), these mean weights would refer to a mean DFL for males of 0.20 and females of 0.25, respectively. These DFLs correspond to the minimum fuel requirements calculated in this study to reach Iceland (0.20 with no winds). Considering that our fed birds on Fair Isle had an average FDR of 0.06 and that FDR of unfed birds might be lower, the DFL of Williamson's (1958) birds with an assumed lower FDR support the predicted relationship between FDR and DFL for time-minimising wheatears (cf. Fig. 2). Our own data combined with the data in Williamson (1958), which include birds exceeding 40 g, suggest that some wheatears deposit more fuel than necessary to reach the next stopover site. The heavy birds in our study were females, and their behaviour was similar to female wheatears at another stopover on spring migration (Dierschke et al. 2005). The lack of a correlation between DFL and FDR could indicate that females behave according to an energy-minimising strategy (Dierschke et al. 2005). The DFL is, however, well beyond that required to fly between Scotland and Iceland (0.20 for an 860-km flight without winds). This argues against a pure energy minimisation strategy as noted by Dierschke et al. (2005). One should also remember that, during spring migration, the risk of encountering unfavourable head winds is greater than in autumn, which could inflate fuel loads as an insurance against such weather. Yet another difference is the age, where the spring birds are experienced birds having migrated at least once before. This could have influenced their DFL because they may already know the distance they are confronting. Another explanation for the high DFL in the spring birds could be that they aim for a direct flight to Greenland (minimum distance ca. 1,500 km, estimated fuel requirements: 0.37), thus skipping Iceland. Overloading and skipping of potential stopovers along the migration route are characteristic diagnostics of a time-minimising strategy (Gudmundsson et al. 1991; Weber et al. 1994). An additional reason for accumulating more fat than needed for the flight between the last stopover and the breeding area is to save some energy for needs upon arrival (Sandberg 1996; Sandberg and Moore 1996; Smith and Moore 2003). This is a common strategy among large birds such as geese, but it is also common in shorebirds (Drent and Daan 1980; Klaassen 2003; Morrison and Hobson 2004); however, the criterion for when to adopt such a strategy is scale-independent (Hedenström 2006). Also, some passerines breeding at high latitudes seem to arrive with considerable fuel reserves (Hedenström and Pettersson 1986; Sandberg 1996; Smith and Moore 2003). The ratio between FDR at the last stopover and the breeding site determine if it is optimal to bring some energy from migration (Hedenström 2006). Even if wheatears are not strictly capital breeders in the sense that energy from migration is directly shunted into the formation of a clutch, they might use saved energy for pre-breeding activities. In females these could be mate searching and nest building, and in males these could be territory establishment and costly flight displays.

The potential flight range for our fed autumn birds on Iceland suggest a direct flight to Scotland in still-air conditions, while a direct flight to the Iberian Peninsula, which has been suggested for Greenlandic wheatears (Snow 1953; Luttik and Wattel 1979; Alerstam 1990, Thorup et al. 2006), would require a tailwind assistance of 12 m/s. Not even the October birds reported by Gudmundsson (1970) would have reached the Iberian Peninsula in a direct flight without wind assistance (cf. Table 1), but a wind assistance of 2.7 m/s would be sufficient to allow a direct flight.

Following the flight range equation derived here (Eq. 3), wheatears leaving the southern tip of Greenland would require DFLs of approximately 0.9 for a 3,000-km non-stop flight to Spain. Assuming a wing length of 105 mm (Ottosson et al. 1990), such birds must gain a body mass of about 50 g to allow for such a long direct flight under calm condition. Such fuel loads were reported for caged Greenlandic wheatears fed ad libitum (Ottosson et al. 1990) and supplementary fed wheatears (*O. o. leucorhoa*) on migration (Dierschke et al., 2005) but seem to be recorded only exceptionally under natural situations on migration (e.g. 45 g reported by Gosler et al. 1998; DFL of 0.9 in Delingat et al. 2006).

Winds are generally exploited by migrating birds for good reasons (Richardson 1990; Liechti 2006). Winds are typically of the same order of magnitude as the migrants' own airspeeds, and so, the flight range could potentially be significantly increased. Wind-selective departures have been observed in other passerine species (e.g. Åkesson and Hedenström 2000). The wheatears in this study showed wind-related departure decisions. Even if the average wind conditions are unfavourable, birds may exploit windows of favourable winds. If departing from Iceland with westerly winds, wheatears aiming for Scotland and Norway will gain wind assistance because they will experience a wind component along the resulting flight track. While aloft, they seem to be capable of finding the altitude with the most favourable winds (Bruderer et al. 1995), and occasionally they may exploit extreme wind assistance (Liechti and Schaller 1999).

It has recently been argued that wheatears of Greenlandic or Nearctic origin may migrate directly to West Africa, which would ensure a 4,200-km non-stop flight (Thorup et al. 2006). This conclusion was made on the basis of flight range estimates using an aerodynamic model (Pennycuick 1989), which required a tail-wind assistance of approximately 5 m/s. The assumed relative fuel load at departure was 0.92 (Thorup et al. 2006). Using our range equation (Eq. 3), the Greenlandic birds would reach 3,066 km in still air, which is clearly less than the 4,200 km required to successfully reach West Africa. However, with a tailwind assistance of 4.8 m/s, this flight would be feasible. Hence, our range equation supports the conclusion by Thorup et al. (2006) that a direct flight between Greenland and West Africa is possible provided the wind assistance is constantly about 5 m/s and that natural stopover sites before the crossing provide conditions to reach body masses above 50 g.

In conclusion, it appears that wheatears behave according to an overall time-minimisation strategy in autumn. They do prepare for a sea crossing between Iceland and Scotland, but most likely not for a direct flight to the Iberian Peninsula or Northwest Africa. Also, the spring birds, although few individuals, exhibit DFLs suggesting a time-selected strategy possibly involving overloading of energy to save for arrival in the breeding area.

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