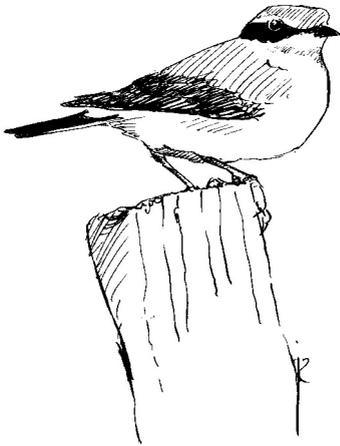# Daily stopovers as optimal migration strategy in a long-distance migrating passerine: the Northern Wheatear *Oenanthe oenanthe*

Julia Delingat[1], Volker Dierschke[2], Heiko Schmaljohann[3], Bettina Mendel[2] & Franz Bairlein[1]

Selection for early arrival is expected to shape optimal stopover decisions in migrating birds to minimise time spent on migration. Optimality models predict that fuel loads at departure from stopover sites and stopover duration should depend strongly on search and settling costs as well as on individual fuel deposition rates. In previous years little attention was paid to natural search and settling costs. In the Northern Wheatear *Oenanthe oenanthe*, a nocturnal long distance migrant, we found evidence for low search and settling costs suggesting that these birds have the capacity to gain body mass from the first day of stopover. Positive correlation between fuel deposition rates and departure fuel loads in males met model predictions for time minimising strategies with an expected global variation in fuel deposition rates and search and settling costs of less than one day. Assuming such low search and settling costs, a time minimising migrant experiencing a stopover site with average fuel deposition rates of 4% of lean body mass is expected to depart with fuel loads less than 17% of its lean body mass. Data on fuel loads from different stopover sites in Europe show that Northern Wheatears generally fulfil these model predictions. Such low fuel loads are expected to force the birds to rest and refuel daily.

Key words: spring migration, optimal migration strategies, Northern Wheatears, search and settling costs

[1]Institut für Vogelforschung, An der Vogelwarte 21, 26386 Wilhelmshaven, Germany; [2]University of Kiel, Forschungs- und Technologiezentrum Westküste, 25761 Büsum, Hafentörn, Germany; [3]Swiss Ornithological Institute, 6204 Sempach, Switzerland; *corresponding author (jdelingat@gmx.de)

INTRODUCTION

For migrating birds the right timing and arrival before competitors at breeding grounds has been shown to be an important factor affecting breeding success (e.g. Currie *et al.* 2000, Forstmeier 2002, Ollivier *et al.* 1999, Smith & Moore 2005). In addition to fitness benefits gained by early arrival it seems especially important for females to arrive in good condition leaving reserves for reproduction

(Sandberg & Moore 1996, Farmer & Wiens 1999, Smith & Moore 2003). As the timing and condition at arrival plays such an important role in breeding success we expect strong selection acting on migratory behaviour to increase either speed of migration or the condition at arrival or a combination of both. During the last decade various models about optimal behaviour in migrating birds have been developed (reviewed by Alerstam & Hedenström 1998, Houston 1998). As birds on migration spend most time on stopover sites for refuelling between consecutive flights (e.g. Hedenström & Alerstam 1997), selection pressure is expected to have an effect on stopover strategies to optimise either time or energy costs on migration. The importance of avoiding predation during migration has also been discussed (e.g. Alerstam & Lindström 1990, Schmaljohann & Dierschke 2005), but will not be considered in this paper.

Food availability at stopover sites and the consequential gain in body mass per day (fuel deposition rate) are expected to play a major role in optimal behaviour decisions. For time minimising migrants a positive correlation between fuel deposition rate and departure fuel loads is expected, while energy minimising migrants should leave a stopover site with a constant optimal fuel load regardless of the experienced fuel deposition rate (Alerstam & Lindström 1990).

Search and settling costs are another important factor affecting predicted optimal fuel loads, stopover duration and the number of flights during the entire migration (Alerstam & Lindström 1990, Alerstam & Hedenström 1998). These costs arise if a bird experiences an initial phase of no or low body mass gain or even mass loss when reaching a new stopover site. Search and settling costs can arise e.g. from difficulties in establishing feeding territories (Rappole & Warner 1976) or physiological constraints due to reduction of organs or muscles after long non-stop flights (Biebach 1998, Bauchinger & Biebach 2001, Guglielmo *et al.* 2001). Evidence for natural search and settling costs in passerine migration over land, when no barriers have to be crossed, is however controversial (Schwilch & Jenni 2001).

Theoretical optimality models suggest an optimal overall organization of migration to minimise the time spent on migration, which is influenced by fuel deposition rate and search settling costs at new stopover sites. Following model predictions an increase in fuel deposition rate and increased search and settling times lead to increased optimal fuel loads and thus to longer stopovers and longer flights between each stopover (e.g. Alerstam & Hedenström 1998, Weber *et al.* 1999).

Based on this theoretical background, we evaluate search and settling costs and stopover behaviour of migrating Northern Wheatears (Wheatear hereafter) at different stopover sites with respect to different constraints of subspecies and sexes. In order to test whether Wheatears are time or energy minimisers we focus on model predictions from Weber *et al.* (1999). In their model they discuss the importance of different expectations of future stopover site quality in time minimising birds: (1) Migrants expecting that the currently experienced variation in fuel deposition rate is only a local phenomenon should react strongly to a superabundant food resource (local-variation-model). They are expected to have a fixed baseline fuel deposition rate along their migration route. (2) In contrast, birds expecting that future stopover sites will provide similar fuel deposition rates as the current stopover site (global-variation-model) should show less pronounced reactions to superabundant food resources. Weber *et al.* 1999 also predicted that the higher the search and settling costs, the steeper is the slope of the relationship between fuel deposition rate and departure fuel load.

One aim of this study is to discover the optimal organisation of migration over the European continent, in terms of optimal duration of flights and stopover periods. By means of empirical data on departure fuel loads at various stopover sites we test predictions from optimality models for time minimising and energy minimising strategies and estimate the length of flights between each stopover.

METHODS

Study species and field methods

The Wheatear is a nocturnal long-distance migrant, which has a nearly circumpolar distribution. On migration they can be found in a variety of habitats like lowlands, meadows, arable land, beaches and other habitats with low or scarce vegetation to bare soil or rocky areas (Glutz & Bauer 1988). In the northern breeding range two subspecies are distinguished, which both overwinter in Africa. The nominate subspecies *O. o. oenanthe* breeds in Great Britain and in an area ranging from continental Europe via Siberia as far east as Alaska (Cramp 1988). The Greenlandic subspecies *O. o. leucorhoa* breeds in Iceland, Greenland and eastern Canada. The latter belongs to the few passerine migrants covering regularly distances of more than 1000 km over either the North Sea or the east Atlantic, for example from the southern coast of Greenland or Iceland to Scotland.

During spring migration 2002 we collected data on stopover length, fuel deposition rate and departure fuel loads on Ventotene, an Italian island (40°47'N, 13°25'E), on Fair Isle in the northern North Sea off the Scottish coast (59°32'N, 1°39'W) and on Helgoland, a German offshore island in the south eastern North Sea (54°11'N, 7°55'E). In 2003 the study was completed at the German North Sea coast in Wilhelmshaven (53°58'N, 8°11'E) (Fig. 1). During this study period we trapped 388 Wheatears with spring traps at these four sites. The birds were sexed and aged according to Svensson (1992), measured (wing length to the nearest 0.5 mm) and weighed to the nearest 0.1 g with electronic scales at Helgoland and to the nearest 0.5 g with Pesola spring scales at the other sites. Fat score was determined using a scale from 0–8 according to Kaiser (1993). Each bird was individually marked with a combination of three to four colour-rings and an aluminium ring from the appropriate ringing centre. The birds were assigned to either subspecies by wing length: males with wing length exceeding 102 mm and females exceeding 97 mm were assigned to the Greenlandic/Icelandic subspecies *O. o. leucorhoa*,
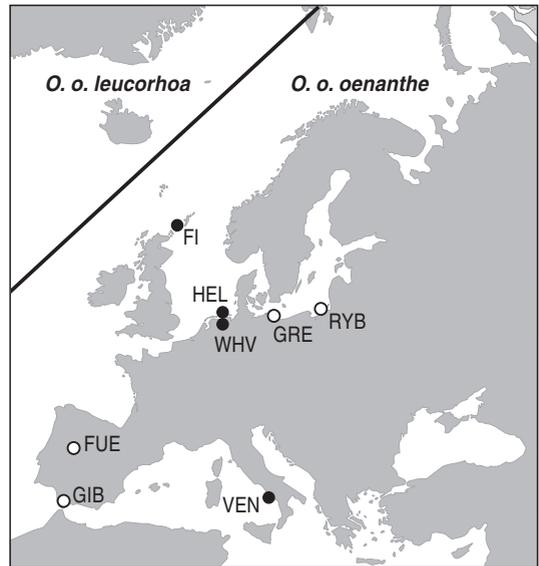
Figure 1. Study sites in Europe. Black dots indicate study sites where we gained data on fuel deposition rates and departure fuel loads. White dots indicate sites from where we obtained body mass measurements from standard ringing projects. The bold black line indicates the border between the distribution of the two subspecies *O. o. leucorhoa* and *O. o. oenanthe*. FI = Fair Isle, HEL = Helgoland, WHV = Wilhelmshaven, GRE = Greifswalder Oie, VEN = Ventotene, FUE = Fuentes de Nava/Laguna de la Nava, GIB = Gibraltar, RYB = Rybachy.

whereas males with wing length below 99 mm and females below 96 mm were assigned to the subspecies *O. o. oenanthe* (Svensson 1992). Individuals with wings of intermediate length were not assigned to either subspecies.

As body mass changes during stopovers are generally difficult to obtain by capture and recapture efforts, we offered bowls with mealworms in the four study areas to the birds. These bowls were fixed on digital scales and the body mass of birds visiting these feeders could be read from a distance to the nearest 0.1 g, using binoculars or telescopes. On Helgoland the scales were observed daily during most of the daylight hours, whereas at the other three sites this was done for 3–9 hours daily.

Fuel deposition rates and departure fuel loads

For calculating fuel deposition rates (*FDR*) and departure fuel loads (*DFL*) as proportion of lean body mass (*LBM*) we first calculated standardised body mass (*sBM*) and *LBM* for each bird. Data for these calculations were collected at the above mentioned study sites including also data from Helgoland from 1998–2002, resulting in a data set of 865 Wheatears. As body mass (*BM*) correlates significantly with wing length we used the equation of the following regression based on birds with a fat score of 1:

$$BM = 0.276 * WL_i - 4.159$$
$$(r = 0.537, P < 0.001, n = 150),$$

with WL_i as the individual wing length measured in mm.

By using the slope of the regression we could calculate standardised body mass (*sBM*):

$$sBM = BM_i + 0.276 *(WL_{mean} - WL_i),$$

with BM_i being the individual measured body mass. Mean wing length WL_{mean} was 97.4 mm ($\pm 3.9, n = 865$).

The average *sBM* of all birds with fat score 1 was 22.7 g ($\pm 1.7, n = 150$).
Using these results we calculated *LBM* for each bird as

$$LBM = 22.7 - 0.276 * (97.4 - WL_i).$$

FDR was then calculated as body mass gain (or loss) within 24 hours (± 2 hours) or a multiple of 24 hours divided by *LBM* and the number of days between the measurements. We included all observed fuelling rates from the first day of capture until departure.

For estimates of departure fuel loads (*DFL*) we took only body mass measurements into account that were gained after 16:00 h of the day the bird was seen for the last time. *DFL* was calculated by subtracting *LBM* from last body mass measurement and dividing this by *LBM*.

Sample size for *FDR* in this study is higher than for *DFL* because not all birds, from which *FDR* was calculated, could be measured at their day of departure.

Search and settling costs

For Wheatears migrating over the European conti-

nent, we do not expect a reduction of the gastrointestinal tract during their nocturnal flights, because – unlike those birds where a reduction of the intestines was observed when crossing for example the Sahara dessert (Biebach 1998) – they are not obliged to fly long distances non-stop. For other nocturnally migrating passerines it is shown that nocturnal flights frequently last less than a whole night (Bruderer & Liechti 1995, Bulyuk & Tsvey 2006), which is unlikely to afford any reduction of organs needed for refuelling during stopover.

It can be assumed that on their spring migration over continental Europe, Wheatears have no sizeable barriers to cross and that suitable stopover sites can be found within every 20–50 km. Therefore search and settling costs are more likely to arise from competition for feeding territories or the time needed to become familiar with new stopover sites. In order to investigate whether search and settling costs arise from the time required to find food and to become familiar with new stopover sites we relocated 13 Wheatears trapped in the morning hours at a stopover site in Wilhelmshaven on the North Sea coast to other potential stopover sites more than 3 km away. When the birds were released it was measured how much time elapsed before each started to feed. All birds were released within one hour of being trapped. Additionally we analysed data from the supplementary feeding experiment on Helgoland, in order to see whether fuelling rates were lower at the beginning of their stopover. To find out possible search and settling costs and *FDR* under conditions without supplementary food, *FDR* was also calculated from birds that were recaptured within 24 hours after first capture without using feeders at Ventotene (2002) and at Helgoland (1998–2000).

Fuel loads and flight ranges

To estimate fuel loads of migrating Wheatears in Europe, we used data from birds trapped at the above mentioned field sites in 2002 and 2003 and included data from previous ringing projects on Helgoland from 1998–2002.

Additionally we were able to access data on wing length and body mass obtained in standard ringing projects from Rybachy (55°05' N, 20°44' E), Fuentes de Nava (42°05' N, 04°47' W), Greifswalder Oie (54°15' N, 13°55' W) and Gibraltar (35°57'N, 5°36'W) (Fig. 1). Fuel loads were calculated in the same way as *DFL* but are referred to as 'fuel loads', because these measurements were not all taken in the evening hours and it is likely that some birds gained some more fuel before their final departure. All birds included in this analysis were not retrapped or observed (in the case of colour marked individuals) at the stopover site after the body mass measurements were taken. As there is no evidence that these birds stayed longer at the stopover site, we conclude that on average the potential difference between fuel loads and final *DFL* is small.

Flight ranges were computed with Flight for Windows, Version 1.15 (Pennycuick 2005). We calculated flight ranges for an average Wheatear of the subspecies *O. o. oenanthe* with wing length of 95 mm. Wing span and wing area were measured in 26 Wheatears resulting in a wing span of 0.270 m and a wing area of 0.0122 m^2 for a bird with a wing length of 95 mm.

We assumed a flight altitude of 500 m and used defaults of the program for all other factors, such as basal metabolic rate: 0.394 W, body drag coefficient: 0.1, profile power constant: 8.4, conversion efficiency: 0.23, minimum energy from protein: 5%. When calculating the flight ranges for given fuel loads the birds were expected to land when they reach *LBM* (22 g for a bird of 95 mm wing length).

For statistical analysis we used SPSS 11.5 for Windows. When appropriate, means are reported ± 1 SD.

RESULTS
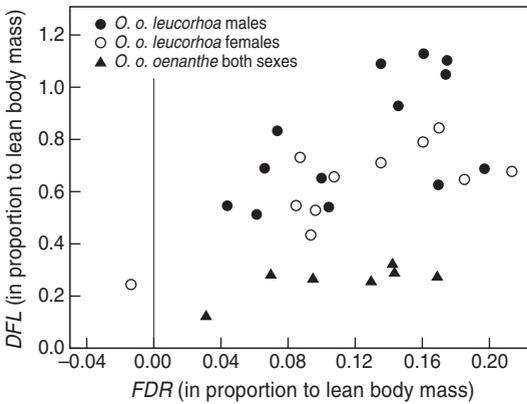
Fuel deposition rates and departure fuel loads
Data on male Wheatears of the subspecies *O. o. oenanthe* from Ventotene, Wilhelmshaven and Helgoland showed a positive correlation between
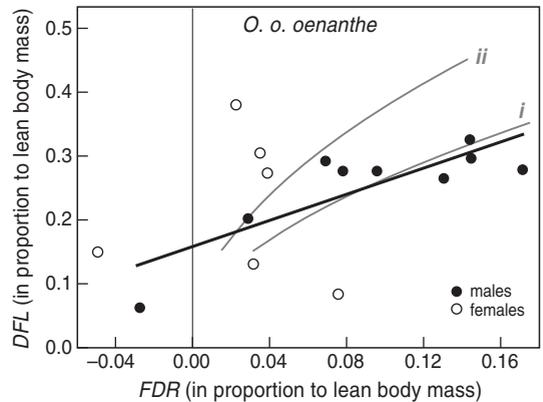
Figure 2. Relationship between departure fuel load (*DFL*) and fuel deposition rate (*FDR*) in Wheatears during spring migration at three different sites (Ventotene, Wilhelmshaven, Helgoland, not separately indicated). Birds were attracted to balances with supplementary food. The black line indicates the significant correlation for males (r_s = 0.68, *P* = 0.042, *n* = 9). There was no correlation for females (r_s = –0.37, *P* = 0.468, *n* = 6). Curve (i) shows predicted fuel loads for expectation of global variation with search and settling time costs of 0.5 days and curve (ii) for search and settling times of one day (derived from Weber *et al.* 1999).

DFL and *FDR*, suggesting time minimising strategies in males (Spearman's correlation: males: r_s = 0.68, *P* = 0.042, *n* = 9) but not in females (r_s = –0.37, *P* = 0.468, *n* = 6) (Fig. 2). Both sexes together did not show a significant correlation (r_s = 0.39, *P* = 0.147, *n* = 15). Mean *FDR* of those birds receiving supplementary feeding was 0.07 ± 0.06, *n* = 20. Mean *DFL* was 0.24 ± 0.09, *n* = 15. *FDR* in males was higher than in females (*U*-test: *Z* = 19, *P* = 0.019, n_{males} = 10, $n_{females}$ = 10), mean *FDR* for males was 0.1 ± 0.06, *n* = 10; for females 0.04 ± 0.04, *n* = 10. *DFL* did not differ significantly (*U*-Test: *Z* = –0.471, *P* = 0.637, n_{males} = 9, $n_{females}$ = 6).

The data on male *O. o. oenanthe* support model predictions for time minimisation with expectations of global variation in *FDR* and search and settling costs of less than one day following Weber *et al.* (1999) (Fig. 2).

Figure 3. Relationship between departure fuel load (*DFL*) and total fuel deposition rate (*FDR*) in Wheatears of both subspecies on Helgoland and from two birds from subspecies *O. o. leucorhoa* on Fair Isle (not separately indicated in the figure). All birds had access to feeders with *ad libitum* mealworms. While preparing for the crossing of the North Sea *O. o. leucorhoa* deposits significant higher fuel loads than *O. o. oenanthe* which does not have to prepare for such a non-stop flight (see text).

For the subspecies *O. o. leucorhoa* we can only present data from stopovers at Helgoland and two birds from Fair Isle (Fig. 3). These birds use the two stopover sites to prepare for the imminent crossing of the North Sea and made use of the supplementary food. Since predictions on optimal fuel loads from theoretical models do not include the crossing of a barrier (Alerstam & Lindström 1990), we were unable to compare observed fuel loads with model predictions like in Fig. 2. However, a correlation between *FDR* and *DFL* could be shown in *O. o. leucorhoa* too when pooling the sexes (Pearson: $r_p = 0.59$, $P = 0.002$, $n = 24$), while either sex showed nearly significant correlations (Spearman: males $r_s = 0.53$, $P = 0.064$, $n = 13$; females: $r_s = 0.58$, $P = 0.060$, $n = 11$). *FDR* and *DFL* did not differ between sexes (*FDR*: $Z = -0.316$, $P = 0.752$, $n_{males} = 15$, $n_{females} = 16$, *DFL*: $Z = -1.535$, $P = 0.125$, $n_{males} = 13$, $n_{females} = 11$).

Regarding only the supplementary feeding experiment on Helgoland we were able to show that both subspecies could accumulate fuel at the same speed (mean *FDR* of *O. o. leucorhoa*: 0.13 ±

0.05, $n = 26$; *O. o. oenanthe*: 0.11 ± 0.05, $n = 10$; *U*-Test: $Z = -1.20$, $P = 0.23$) but showed significant differences in their *DFL* (*O. o. leucorhoa*: 0.73 ± 0.22, $n = 22$; *O. o. oenanthe*: 0.26 ± 0.06, $n = 7$; *U*-Test: $Z = -3.62$, $P < 0.001$).

Search and settling costs

Birds which were relocated at the German coast near Wilhelmshaven during the morning hours of their stopover, started feeding in the new surroundings within minutes.

Mean time between being released and feeding was 13 min (range 1–34 min, $n = 8$). Five birds disappeared from sight after being released.

Analyses of body mass gain of Wheatears trapped at Helgoland during the supplementary feeding set up in 2002 showed an average body mass gain of 3.6 g (± 1.6, $n = 32$) between the day of ringing and the following day (Fig. 4). Only one bird lost body mass within the first day of its stay (–0.3 g). Instead of search and settling costs of one or more days, we see highest mass gain rates at the beginning of the stopover and a decline towards the fifth day of stopover (Fig. 4).

For testing the influence of the day of stopover on body mass changes we analysed body mass changes in those 10 birds from Fig. 3 which stayed
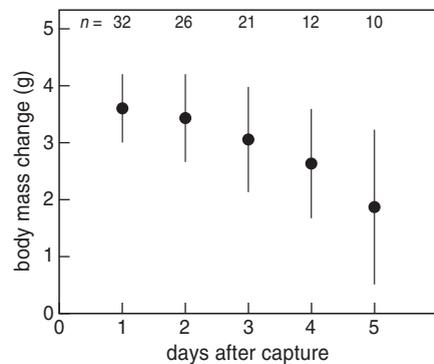
Figure 4. Body mass change in 24 hours intervals of Wheatears during stopover at Helgoland with supplementary food supply. Differences in body mass are calculated from 24 h intervals from day of capture until first day of stay and from first day of stay until second and so on. Whiskers mark 95% confidence interval.
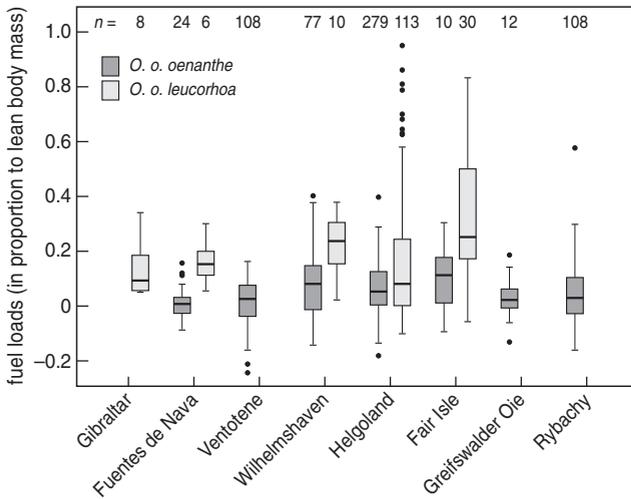
Figure 5. Fuel loads of Wheatears trapped on spring migration. For location see (Fig. 1). Boxes present 5, 25, 50, 75 and 95% percentiles and outliners (dots). Note that both subspecies were not captured at all ringing sites. Although sample size was small at some sites data are presented here as box plots too.

at least five days on Helgoland. For these birds, data on body mass changes were available for each day in 24 hour intervals. Comparing median values of body mass change from each day indicates a decline of daily body mass gain over time although the results were not significant (Friedman-Test: $\chi^2 = 8.5$, $P = 0.075$, $n = 10$).

Data from Wheatears recaptured within 24 hours ($\pm$ 3 hours) after first capture at Ventotene in 2002 and at Helgoland in the years 1998–2000 (including data on autumn migration), showed an average body mass gain of 0.9 g during the first day (minimum 0.0 g, maximum 1.3 g, $n = 9$), which represents an average *FDR* of 0.04. These birds were not supplied with *ad libitum* mealworms.

Fuel loads and flight ranges
If Wheatears minimise time and can indeed refuel immediately after landing at new stopover sites, we would expect them to avoid long stopovers and large fuel stores as long as they migrate over land according to optimality models (e.g. Alerstam & Lindström 1990). Assuming expected global variation of *FDR* and search and settling costs of 0.5 days, Wheatears with a current *FDR* of 0.04 can be expected to depart with optimal *DFL* of 0.17 (derived from curve (i) in Fig. 2 following Weber *et al.* 1999).
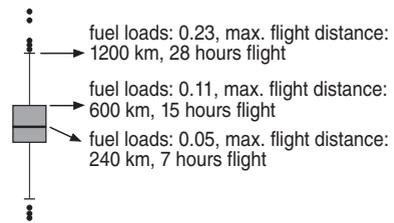
Figure 6. Fuel loads of *O. o. oenanthe* on migration in Europe. Box plot shows 5, 25, 50, 75 and 95% percentiles of fuel loads from *O. o. oenanthe* ($n = 618$). Mean value of fuel loads as well as values for 75 and 95% percentiles are presented right of the box plot. For these three values maximum flight ranges and approximate time spent flying were calculated using Flight for Windows, version 1.15 (Pennycuick 2005).

We analysed data from 618 Wheatears of the subspecies *O. o. oenanthe* and 167 Wheatears of the subspecies *O. o. leucorhoa* from all sites shown in Fig. 1.

Regarding fuel loads of Wheatears of the subspecies *O. o. oenanthe* at various stopover sites in Europe we found mean fuel loads of 0.05 ($\pm$ 0.1, $n = 618$). 95% of all birds showed fuel loads below 0.23 with variances being highest at the North Sea (Wilhelmshaven, Helgoland and Fair Isle) (Figs 5 and 6).

O. o. leucorhoa showed higher but still moderate fuel loads when migrating over land and pronounced variances when approaching the sea crossing at Helgoland and Fair Isle. Single birds of subspecies *O. o. leucorhoa* on Helgoland reached fuel loads of more than 90% of *LBM* without supplementary feeding. Both subspecies and location had an influence on fuel loads of migrating Wheatears, whereas the combination of both did not show any effect (Table 1). Differences between locations were explained by high fuel loads at Fair Isle, which differed significantly from all other sites (*post-hoc* Tukey-HSD: *P* < 0.001 for all pairs of locations including Fair Isle and no significant differences between all other sites).

The distribution of fuel loads among all Wheatears of the subspecies *O. o. oenanthe* on spring migration analysed in this study (*n* = 618) was used to estimate flight ranges during migration and to calculate how often these birds would have to rest and refuel (Fig. 6). These flight range estimates showed that probably most birds trapped during migration were in the condition to perform a 'night-long' flight. Mean fuel loads were 0.05, which would be sufficient for a 7 hours flight. 75% of all *O. o. oenanthe* showed fuel loads below 0.11, and consequently they could fly less than approximately 600 km in 15 hours. Only the upper 5% showed fuel loads of more than 0.23, which would provide sufficient energy to fly about 1200 km in 28 hours.

Table 1. Global linear model testing for influence of subspecies and location on fuel loads. Four stopover sites at which each subspecies could be captured are included (Fuentes de Nava, Wilhelmshaven, Helgoland and Fair Isle). Homogeneity of variances was not given (Levene-Test: $F = 16.9$, $P < 0.0005$).

|	Sum of squares (Type III)	*df*	*F*	*P*
Subspecies	0.809	1	38.448	< 0.001
Location	0.295	3	4.680	< 0.01
Subspecies x location	0.124	3	1.971	0.117
Error	11.377	541		

DISCUSSION

Optimal bird migration models

Evidence for selection on fast migration was supported by a positive relationship of *FDR* and *DFL* for *O. o. oenanthe* males in this study and on the species level by other studies (e.g. Lindström & Alerstam 1992, Dänhardt & Lindström 2001, Schmaljohann & Dierschke 2005). As the data set is rather small, especially for females (*n* = 6), we cannot exclude that the results would be different with bigger sample sizes.

In the case of Greenlandic Wheatears on Helgoland, data on *FDR* after third day of stopover showed similar results (Dierschke *et al.* 2005) and support the evidence for sex related differential migration in spring.

However, the difference between optimal fuel loads for time minimising strategies and energy minimising strategies are small when assuming low search and settling costs. Positive correlation between *FDR* and *DFL* as observed for males supports the evidence for selection on both fast migration strategies and minimisation of total energy costs of migration (Hedenström & Alerstam 1997). Following model predictions, low search and settling times would also imply low optimal fuel loads both for time and energy minimisers (Alerstam & Hedenström 1998, Weber *et al.* 1999). In the case of selection for time minimising strategies with low search and settling times as presented in Fig. 2 curve (i), we would expect high fuel loads only at stopover sites with very good feeding conditions or before a barrier.

The optimal organisation of the migratory route would thus result in a strategy with low fuel loads, short migration steps during the night and daily interruptions for refuelling, because optimal fuel loads would not be sufficient to fly continuously for one night, the next day and the next night without refuelling. Therefore interruption during daytime and resumption of migration during night appear to be the fastest strategy for migration in this case. Fig. 7 demonstrates that the most efficient way to save time on migration would be to use each night for migration and
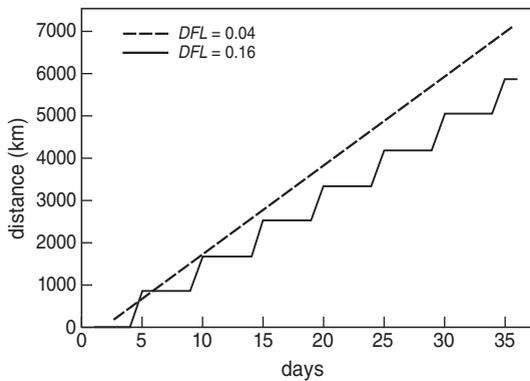
Figure 7. Theoretical migration speed demonstrated for two scenarios:
Dashed line: Departure from stopover sites after one day of refuelling with *DFL* of 0.04, resulting in a flight range of 210 km covered in less than 6 hours per night ('numerous-stop-and-flight-strategy').
Black line: Departure from stopover after four days of refuelling with *DFL* of 0.16, resulting in a flight of approximately 840 km in 20 hours. For both cases we assume a daily *FDR* of 0.04 and no search and settling costs when arriving at a new stopover site. The numerous- stop-and- flight strategy with short migratory steps every night would lead the birds faster to their breeding grounds than a strategy with longer stopovers.

refuel daily. In the illustrated case it is shown that without search and settling costs a migration with *DFL* of 0.04 and short flights of approximately 210 km every night would be faster than staying at a stopover site for four days to accumulate fuel loads of 0.16 and to fly 840 km non-stop afterwards. In both cases we assumed that the birds experience an average *FDR* of 0.04 and the approximate flight ranges for *DFL* of 0.04 and 0.16 were calculated as described above. The average *FDR* of 0.04 that we found in birds that were not supplementally fed appears to be in agreement with other studies on similar sized passerines (Lindström 1991).

Search and settling costs
The main problem in estimating real search and settling times and costs is the lack of certainty whether the day of capture is actually the day of

arrival. With high trapping effort, colour marking, intense observations and study areas that allowed counts of newly arrived birds, we hoped to overcome these problems. We therefore believe that our calculations of body mass change within the first 24 hours after ringing in most cases represent body mass changes on the first day after arrival. Evidence for immediate mass gain starting from the first day of stopover was found in other species as well (e.g. Carpenter *et al.* 1983, Bairlein 1987, Moore & Kerlinger 1987). Our experiment with relocated Wheatears shows that they are able to get used to new surroundings within a short time and start feeding quickly. The supplementary feeding experiment supports the assumption that they are also able to start to accumulate reserves shortly after arrival. However, body mass changes in supplementary feeding experiments are generally higher than in most natural situations. In the case of the Wheatear we were able to show that some natural habitats such as beaches at Helgoland seem to provide similar good feeding conditions as our artificial feeders (Dierschke *et al.* 2003). On Fair Isle the results were similar: Wheatears were feeding on naturally abundant *Tipulidae* larvae between the offered feeders and gained mass quickly (Delingat 2003).

Evidence for initial body mass loss has, however, been found in other species. Causes for this phenomenon like handling effects, illness and competition were discussed (Lindström 1995, Schwilch & Jenni 2001). Especially after sustained non-stop flights time is needed for the physiological switch from flying to refuelling and for restoring proteins in organs and muscles (e.g. Lindström *et al.* 1999, Bauchinger & Biebach 2001).

In the case of the Wheatear, evidence for search and settling costs caused by competition could not be found in supplementary feeding experiments (Dierschke *et al.* 2005). However, effects of competition on search and settling costs might be different when food resources are limited. Low fuelling rates as a consequence of food based competition in passerine migrants were confirmed by other studies (Moore & Yong 1991, Rappole & Warner 1976).

Declining fuelling rates at subsequent days of stopover like in our study were also found in Whitethroats *Sylvia communis* (Fransson 1998) and in caged Thrush Nightingales *Luscinia luscinia* that had access to food *ad libitum* for at least 13 hours per day but are inconsistent with fuelling patterns with daily feeding times of 10 hours and less (Kvist & Lindström 2000). More field experiments and observations are needed to clarify the frequency and causes of initial mass loss and the course of *FDR* during stopovers in migratory birds in the wild.

With regard to optimal stopover behaviour both low search and settling times and a decline in fuelling rates are expected to lead to short stopovers and a numerous-stop-and-flight-strategy.

Flight ranges and migration performance
The low fuel loads that we found at the various stopover sites are in agreement with model predictions. Following the model from Weber *et al.* (1999) we expected a fuel load of 0.17 assuming an average *FDR* of 0.04 and search and settling times of 0.5 days. Regarding fuel loads of *O. o. oenanthe* we found even lower values with mean *DFL* of 0.05.

The fact that some birds showed even negative values for fuel loads like in Fig. 5 arises probably in most cases from our calculations for *LBM*. We defined *LBM* as body masses of birds with a fat score one (Kaiser 1993). This body condition is usually shown by Wheatears during the breeding season (own observations). We intended to calculate how much fuel they deposit on top of this 'breeding condition' for migration. Obviously a fat score of one still provides some resources that can be used for migration and those birds in our study migrating with zero fuel loads (equal to fat score one) or even negative values are using up these last resources. Additionally, not only fat but also protein is used during migratory flights to produce energy (Biebach 1998, Bauchinger & Biebach 2001, Klaassen *et al.* 2000, Guglielmo *et al.* 2001, Schwilch *et al.* 2002). We could frequently observe Wheatears carrying no visible fat resources when passing Helgoland during migration onset. In

some calculated fuel loads morning body masses were included. Therefore, fuel loads were probably underestimated, since birds could have gained easily energy (body mass) before final departure. Due to these uncertainties that include also variations in body size affecting calculations for *LBM* or in estimates of flight costs in migrating birds (Klaassen *et al.* 2000, Kvist *et al.* 2001) flight ranges may have been underestimated in our study. However, we believe that moderate changes in flight ranges would not affect the general pattern of a numerous-stop-and-flight-strategy.

Considering the fuel loads of Wheatears of the subspecies *O. o. oenanthe* it seems that most birds during migration over the European continent deposit sufficient fuel to fly at least a few hours each night. Only very few birds, especially in southern Europe, deposited fuel stores to migrate more than two successive nights without refuelling during the day. 95% would have to refuel after one night of migration before dusk the following day at the latest.

Flight range estimates suggest that Wheatears in general refuel every day after nocturnal flights and do not prepare for longer non-stop flights as long as no barrier has to be crossed. Such a daily-rest-nocturnal-flight strategy with low search and settling costs and low fuel loads is to be expected in several nocturnally migrating passerines with modest demands on stopover site quality. Low fuel loads for passerine nocturnal migrants on migration over continental Europe indeed seem to be a frequently observed pattern both in spring and autumn (e.g. Bairlein 1991, 2003, Schaub & Jenni 2000). Further support for a migration in short steps is found by radio telemetry and radar studies which show that some nocturnal passerine migrants migrate just for some hours per night (Åkesson *et al.* 1996, Bruderer & Liechti 1995).

Data on Greenlandic/Icelandic Wheatears suggest that this subspecies in general also migrates over continental Europe using short flights. Only an imminent barrier crossing forces them to deposit large fuel loads, exceeding by far those that were observed for *O. o. oenanthe* (Figs 3 and 5). With data from Wheatears subject to supplemen-

tary feeding at Helgoland we were able to show that both subspecies could deposit fat at the same speed, exceeding even the theoretical prediction (FDR_{max} = m $^{-0.27}$, Lindström 1991). But *O. o. leucorhoa* reacted much more strongly to high *FDR*: the higher the *FDR* the higher the departure fuel loads. *O. o. oenanthe* probably avoids higher fuel loads than necessary for the next flight and leaves the island soon even while experiencing high *FDR*. *O. o. leucorhoa* has to stay longer than *O. o. oenanthe* to gain the required higher fuel loads for an imminent barrier crossing, which is a general observed pattern at Helgoland (Dierschke & Delingat 2001, Dierschke *et al.* 2005).

Regarding the importance of arrival date and condition at the breeding grounds for migrating passerines it seems that selection on migratory behaviour supports a numerous-stops-and-flights strategy on migration over continental Europe. However the effect of weather on stopover decisions must not be underestimated and might lead to shorter or longer stopovers under favourable or unfavourable wind conditions than predicted by the above mentioned optimality models.

Daily stopovers and nocturnal flights as suggested by the observed fuel loads and flight range estimates would indeed fulfil model predictions for time and energy minimised migration as long as search and settling times are short (e.g. Alerstam & Lindström 1990, Hedenström & Alerstam 1997, Alerstam & Hedenström 1998, Weber *et al.* 1999).

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SAMENVATTING

Een vroege aankomst in het broedgebied is voor veel vogelsoorten een voorwaarde om succesvol te broeden. Het is daarom te verwachten dat vogels zo kort mogelijke tussenstops inlassen tijdens de voorjaarstrek en doortrekken zodra ze voldoende lichaamsreserves hebben opgeslagen. Theoretische modellen voorspellen dat de duur van de tussenstop en de grootte van de lichaamsreserves bij vertrek afhangen van de snelheid waarmee een individu lichaamsreserves aanlegt en van de zogenaamde zoek- en aanloopkosten (bijvoorbeeld de tijd die nodig is om een voedselterritorium te bemachtigen of om het verteringsstelsel goed te laten functioneren na een lange vlucht). Aan het probleem van de zoek- en aanloopkosten is tot nu toe weinig aandacht besteed. De Tapuit *Oenanthe oenanthe* is een langeafstandtrekker die 's nachts vliegt. Er zijn aanwijzingen dat de soort lage zoek- en aanloopkosten heeft, dus de vogels hebben de mogelijkheid om lichaam-sreserves aan te leggen zodra ze ergens landen. Waarnemingen lieten zien dat tussen de snelheid waarmee mannetjes van de Tapuit lichaamsreserves opsloegen en de grootte van de reserves bij vertrek een positief verband bestond, wat klopte met voorspellingen van modellen die gebaseerd waren op heel geringe zoek- en aanloopkosten. Aannemende dat de zoek- en aanloopkosten zo laag zijn als verondersteld (minder dan een dag), dan is te verwachten dat een trekvogel die de verblijftijd zo kort mogelijk houdt en een dagelijkse gewichtstoename van 4% van het vetvrij lichaamsgewicht haalt, vertrekt met lichaamsreserves van hooguit 17% van het vetvrij lichaamsgewicht. Gegevens van lichaamsreserves afkomstig van verschillende pleisterplaatsen in Europa laten zien dat Tapuiten lijken te voldoen aan deze voorspelling. Dit zou betekenen dat de vogels elke nacht een stuk vliegen om vervolgens overdag bij te tanken en te rusten.

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