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Differential timing of spring migration in northern wheatears *Oenanthe oenanthe*: hurried males or weak females?

Received: 7 January 2004 / Revised: 20 October 2004 / Accepted: 2 November 2004 / Published online: 22 December 2004
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Abstract In a field experiment on the island of Helgoland (southeast North Sea), we investigated whether migration strategy or competition between the sexes cause the differential timing of spring migration of male and female northern wheatears (*Oenanthe oenanthe*) (males migrating earlier). The study included two subspecies, heading towards Greenland/Iceland and Scandinavia, respectively, and is based on colour-ringing and remote weighing of individuals. Despite food offered ad libitum, most Scandinavian birds left the island on the day of arrival or stayed only 1–3 days, whereas more than half of Greenlandic/Icelandic birds stayed for up to 12 days and refuelled rapidly. In the latter subspecies, males showed a positive correlation of departure fuel load and fuel deposition rate, resembling time-minimizers in optimal migration theory. In contrast, females departed irrespective of fuel deposition rate, with an approximately constant level of fuel stores. This level was lower than in males, but sufficient to enable by-passing of stopover sites en route, allowing us to regard females as time-minimizers also. Since females are not able to reach Greenland without additional refuelling elsewhere and

males appeared to have a larger potential for by-passing stopover sites, time-selection seems to be more pronounced in males and may be the reason for earlier migration of males. Intraspecific aggressive interactions between colour-ringed birds were predominantly won by the initiator, by males and by larger birds, whereas fuel load and subspecies did not affect the outcome. Although compared to females, males were more often dominant at the feeding stations or held territories, refuelling patterns could not be explained by dominance. Subordinate or non-territorial birds did not refuel at a lower rate or depart with lower fuel loads than dominant or territorial birds. In non-territorial birds, the 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. Therefore, competition during stopover could be eliminated as the reason for differential timing of migration of male and female wheatears, but this result may be species-specific.

Keywords Northern wheatear · *Oenanthe oenanthe* · Optimal migration · Stopover behaviour · Dominance

Communicated by W. Wiltschko

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Introduction

During migration from wintering grounds towards breeding areas, males precede females for several days in many passerine species (Gauthreaux 1982; Francis and Cooke 1986; Spina et al. 1994). This may be explained by sex-related differences in the situation of wintering grounds (Ketterson and Nolan 1983; Terrill and Berthold 1989), in departure times from wintering grounds (Moore et al. 1990; Wood 1992; Marra et al. 1998) and in migration speeds (Chandler and Mulvihill 1990; Swanson et al. 1999). The last may be caused by sexual differences in morphology, fuel deposition rate (FDR), dominance, migration strategies and risk-insurance. In willow warblers (*Phylloscopus trochilus*), differences in wing morphology suggest higher flight velocities in males (Hedenström and Pettersson 1986), but this difference appears to be quite

small. Apart from flight velocities, it has to be remembered that during migration the largest amounts of time and energy are consumed during stopover rather than during migratory flight (Hedenström and Ålerstam 1997). Hence, FDR at a stopover site is almost directly proportional to the migratory speed (Ålerstam and Lindström 1990). The earlier arrival of males compared to females then may be simply caused by physiological differences with higher FDR in males, but no such data are available. However, different refuelling patterns may also arise from dominance patterns among migrants at a stopover site (Rappole and Warner 1976; Lindström et al. 1990). Different phenology of males and females could result from a competition for resources during migration, i.e. that the dominance of males at stopover sites prevents a fast migration of females. In an experiment with captive pied flycatchers (*Ficedula hypoleuca*), it has been shown that females could not compete with males in a simulated stopover situation and were less successful in foraging (Mabey and Woodrey 1999; Moore et al. 2003). The lower foraging success of females suggests a lower refuelling rate and thus a lower speed of migration.

According to the theory of optimal bird migration (Ålerstam and Lindström 1990; Hedenström and Ålerstam 1997), migrants may optimize time or energy needed on their journey. If FDR is positively correlated with the departure fuel load (DFL), birds will be categorized as time-selected migrants which should migrate as fast as possible (speed-maximization and time-minimization). The central feature of this strategy is to leave a stopover site when the current FDR causes an instantaneous speed of migration that is lower than the average of the whole journey (because better conditions can be expected elsewhere). In contrast, birds minimizing the energy spent during migration leave a stopover site as soon as they have stored reserves needed for the flight to the next stopover site, irrespective of FDR and with more or less constant DFL (Ålerstam and Lindström 1990; Hedenström and Ålerstam 1997). The theory assumes that a strategy of time-minimizing requires a free choice of where to land and where to refuel. This assumption is not met when birds have to cross ecological barriers without any possibility of refuelling, but as discussed for shorebirds and waterfowl confronting a barrier, even time-minimizers would stay at a stopover site until they attained fuel stores sufficient to fly to the next stopover site (Ålerstam and Hedenström 1998). This means that until a certain level the departure decision is less influenced by FDR, but in contrast to energy-minimizers, birds minimizing the time spent on migration should stay beyond this level when experiencing above-average conditions in order to be able to by-pass low-quality stopover sites (Gudmundsson et al. 1991; Ålerstam and Hedenström 1998). As it is not known whether migrants precisely know their exact migration pathway including all stopover sites and weather conditions en route, at least part of extra fuel may also serve as insurance against both arriving at a stopover site with poor refuelling conditions, and being drifted off their course. Both kinds of risk are

independent of each other, but depend on weather conditions and are thus unpredictable.

A strategy of time-minimization may apply to many male passerine migrants, because it is often assumed that males migrate faster than females owing to a greater advantage of early arrival in the breeding area (Myers 1981; Gauthreaux 1982; Chandler and Mulvihill 1990). Evidence was found for acquisition of territories of higher quality, for better mating and breeding success and thus for higher fitness in early-arriving males of several passerine species (Møller 1994; Hasselquist 1998; Currie et al. 2000; Fortsmeier 2002; Smith and Moore 2004). Females can also increase their reproductive success through early arrival and earlier egg-laying (Perrins 1970; Cristol 1995; Hasselquist 1998; Smith and Moore 2004), but starting to breed too early has been shown to be disadvantageous (Visser et al. 1998). However, the stringency of time pressure may differ with regard to gender because, in contrast to males, females would take advantage of saving energy needed for reproduction after arrival in the breeding area (Sandberg 1996; Sandberg and Moore 1996; Spina and Pilaastro 1999; Moore et al. 2003). For female American redstarts (*Setophaga ruticilla*), Smith and Moore (2003) have shown higher reproductive success when arriving on the breeding grounds with more fat reserves. Arrival in the breeding grounds with a fixed amount of fuel stores fits a strategy incorporating the minimization of energy consumption during migration (see above). If sex-specific differential timing of migration is related to migration strategies, males and females should differ in FDR or DFL or in the relation between these two parameters at the same stopover sites.

Hence, differential timing in males and females may be related to stopover behaviour, in particular, as a result of sex-specific patterns of refuelling and dominance behaviour (Moore et al. 2003).

In order to investigate whether differential spring-migration phenology may result from different migration strategies or dominance patterns, we conducted a field experiment with northern wheatears (*Oenanthe oenanthe*) (wheatears hereafter) at a stopover site, the island of Helgoland. During spring migration, colour-ringed wheatears were supplied with ad-libitum food and weighed remotely throughout their stay. In line with the overall earlier arrival of males at stopover and breeding sites and the predictions of the optimal migration theory outlined above, we expected that departures of males should depend on the FDR, if DFL is high enough to reach the next stopover site, and thus to behave like time-minimizers. At least, males should obtain higher values of FDR or DFL than females, indicating a higher speed of migration or a higher potential of by-passing than in females. If different migration strategies are the reason for the differential timing of sexes, no correlation of DFL and FDR should occur in females. Their DFL would be sufficient to reach the next possible stopover sites in northern Germany and Denmark (50–150 km), Norway (450 km) or Scotland (850 km), probably with a surplus of fuel as risk-insurance. In the same experiment, we used the colour-ringed

birds to analyse the dominance pattern among these individuals stopping over on Helgoland simultaneously. As males and females are easily distinguished in spring, we intended to identify the role of sex in the competition over stopover resources, and expected subordinate birds to refuel at a lower rate than dominant individuals, leading to a lower speed of migration than in dominant migrants. Because male wheatears precede females during spring migration (Dierschke and Delingat 2003), this relation between speed of migration and dominance suggests that males are dominant over females. On Helgoland, wheatears occur in two subspecies, which differ in their migratory route as well as in body size, with some of the females of one subspecies being larger than males of the other subspecies (Dierschke and Delingat 2003). This allowed us to eliminate body size as the only factor determining the expected male dominance. If slower migration of females is caused by the dominance of males, then gender would be a more important factor in hierarchy than body size.

Methods

The field experiment was conducted on the small island of Helgoland (1.5 km², situated ca. 50 km off the German North Sea coast) along a line of boulders (used as kind of seawall) and in scattered short vegetation, where various arthropods are available for food (Delingat and Dierschke 2000). During the experiment, which lasted from 17 April to 26 May 2002, mealworms (*Tenebrio molitor*) were offered ad libitum to birds in six bowls, which were situated between 11 and 22 m apart. Close to the bowls or elsewhere at the study site, 226 wheatears were captured with spring traps baited with mealworms. Within 10–15 min until release, all birds were sexed by plumage coloration (Svensson 1992), measured (maximum wing length to the nearest 0.5 mm; Svensson 1992, length of third outermost primary P3 to the nearest 0.5 mm; Jenni and Winkler 1989, and other measurements not referred to in this study), weighed to the nearest 0.1 g with an electronic balance, and marked with individual combinations of one aluminium and four colour-rings. Wing length was used to categorize the birds as belonging to either subspecies: males and females with wing lengths exceeding 102 mm and 97 mm, respectively, were treated as belonging to the Icelandic/Greenlandic subspecies *O. o. leucorhoa*, whereas wing lengths below 99 mm (males) and 96 mm (females) indicated nominate birds from Scandinavia (Svensson 1992). Data from individuals falling into the intermediate ranges were generally used in the analyses, but not when subspecies differences were explored.

In order to describe the phenology, all wheatears present on the island were counted and sexed each day. In case high numbers did not allow us to sex all birds seen, the sex ratio of subsamples was applied to the whole sample. Subspecies could not be identified in the field. During the counts, the whole island was searched for marked birds in order to monitor the stopover length. A bird was considered to have departed on the day of its last resighting, and stopover length was expressed as the difference of last and first observation day (i.e. the number of nights spent on Helgoland). As the number of wheatears stopping over shows great fluctuations (Delingat and Dierschke 2000), the day of first capture was considered to be the day of arrival. In those 75 individuals staying at least 1 night, the resighting probability was 93% (for all birds pooled the number of days with observations divided by the number of days between ringing and last observation).

During the whole daylight period, the behaviour of the colour-ringed wheatears was observed at the study site. When visiting the bowls with food, the number of mealworms taken was counted in

order to determine the average meal size per visit. Total amounts of mealworms taken during the whole daylight period were not available, because not all bowls could be observed simultaneously. In the morning and evening, electronic balances were placed below the bowls. The weight on the display was read with a telescope from about 50 m distance just before a wheatear entered the bowl and when the bird was sitting on the bowl. Subtracting the former weight from the latter one gave the immediate body mass (for further details see Schmaljohann and Dierschke 2005). Owing to the large size differences among the wheatears, we compared fuel loads (FL) rather than body masses (BM). In a first step, lean body mass (LBM) was calculated as $LBM_i = 22.7 \text{ g} - x(WL_{\text{mean}} - WL_i)$ with the help of data from five spring migration seasons (1998–2002): wing length (WL; mean 97 mm, $n=855$), the average standardized body mass (22.7 g, SD 1.7 g, $n=153$) of wheatears with fat score 1 (only traces of fat visible; Kaiser 1993) and $x=0.28$ as the slope of the regression of body mass measured against wing length for the same birds ($R=0.598$, $P<0.001$). Fuel loads were calculated in relation to LBM by $FL = (BM - LBM) / LBM$ for several situations: arrival fuel load (AFL) at first capture, morning fuel load (MFL) from the first weighing in the morning, evening fuel load (EFL) from the last weighing in the evening, and departure fuel load (DFL) as the last EFL (assuming departure in the same evening or in the night after last weighing and last resighting).

The daily fuel deposition rate (FDR_d) was calculated as $FDR_d = EFL - MFL$ and the refuelling rate for the whole stay (FDR_{tot}) was the average of all daily values. For the latter calculation, the day of arrival was not considered because only few birds were captured early in the morning and arrivals usually happen throughout the day (Dierschke et al. 2003). Note that in contrast to similar studies (Lindström and Alerstam 1992; Weber et al. 1999), FDR only refers to refuelling during the daylight period and does not include the nocturnal loss of body mass.

To explore potential optimal migration strategies, DFL was plotted against FDR_{tot} . Models of time-minimization are based on different assumptions with either global variation of FDR (locally experienced variation reflects global variation along the migration route) or local variation of FDR (with fixed expected speed of migration). For wheatears in this study, we calculated the expected relationships between DFL and FDR_{tot} from the equations given by Weber et al. (1999). Following their study, we used recaptures from unmanipulated field studies in the spring migration seasons 1998–2001 ($n=7$) as the expected values for future sites ($FDR_{\text{tot}}=0.033$, $DFL=0.812$). The question of global or local variation is not discussed further in this paper, but the predicted curves are shown for comparison with other studies dealing with optimal migration theory. Since part of the forthcoming flights takes the wheatears over the sea, the general assumption in optimal migration theory of possible landing and refuelling anywhere and anytime is not fulfilled. But because there are several stopover sites available even for wheatears migrating across the northern Atlantic Ocean to Greenland, the free choice of stopover sites is projected to a larger scale in this case. For a bird with a high FDR at Helgoland, migration speed would be high if staying for some days and departing with high DFL in order to reach Iceland (1,800 km) or even Greenland (2,300 km, Fig. 1). However, a bird experiencing low FDR would do better to fly another 450 km to southern Norway or 850 km to northern Scotland and to refuel there more quickly. In other words, the relation between DFL and FDR is also a valid indicator of time-minimizing if the ecological barrier holds intermittent stopover sites, with high fuel loads allowing birds to bypass potential stopover sites (Gudmundsson et al. 1991).

Aggressive interactions were observed for the individuals involved and for the outcome. We only considered interactions in which at least one individual was recognized by its colour combination. Depending on the particular question, we excluded those interactions in which either the individual or the sex of the counterpart could not be identified. All interactions between two individuals on 1 day were summed up to a match. The winner of a match (e.g. 7 victories vs 3 losses) scored 2 points, a draw scored 1 point and a lost match scored 0 points (Lindström et al. 1990). For each individual, the daily average score of all matches was used as

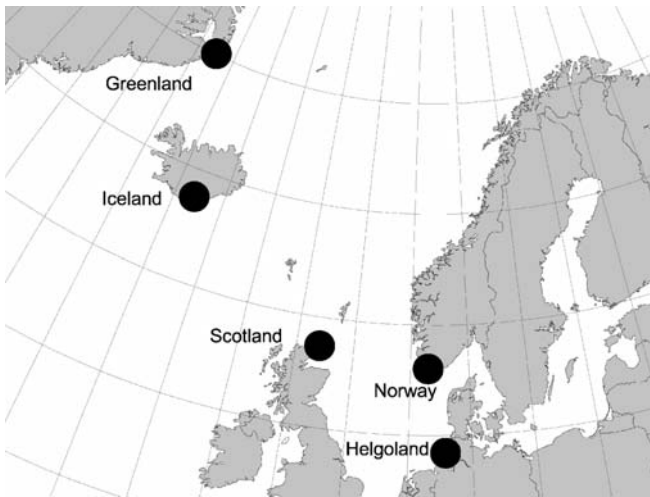
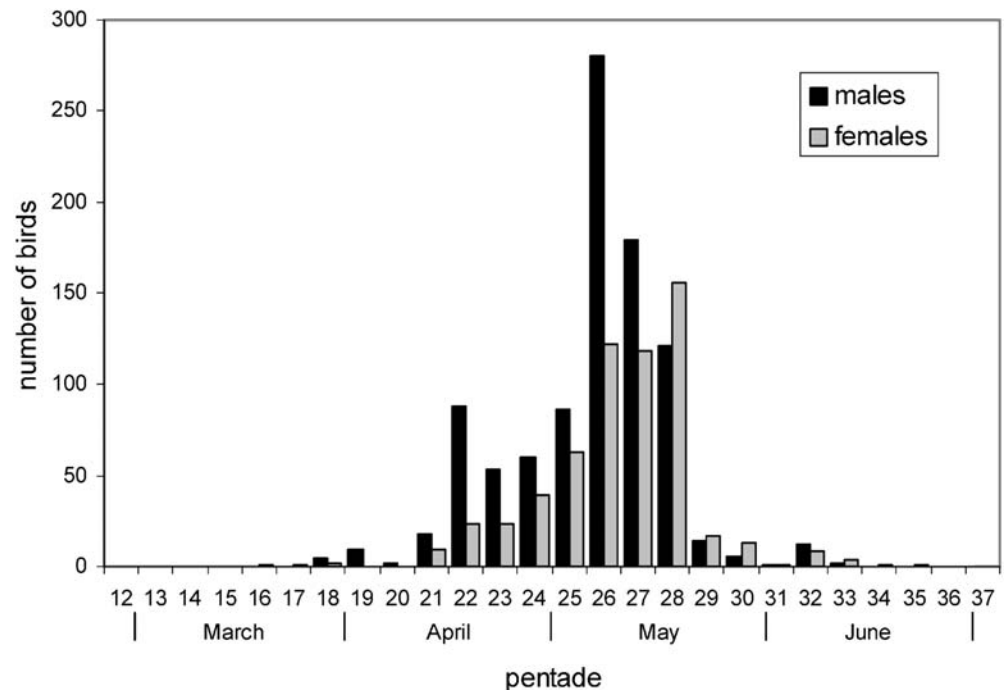


Fig. 1 Location of Helgoland and possible stopover sites en route to Greenland. The approximate direct distances from Helgoland are 450 km to southern Norway, 850 km to northern Scotland, 1,800 km to Iceland and 2,300 km to Greenland. Also possible are stopovers along the German and Danish coastline (50–100 km from Helgoland, not shown). A route to Greenland incorporating stopovers in Norway, Scotland and Iceland is 400 km longer than the direct route. Map projection is equidistant azimuthal with Helgoland as the projection centre.

a dominance index, and a total mean for the whole stay was calculated from the daily average values. Individuals that won half or more of their matches (dominance index 1–2) were treated as dominant birds, whereas those with the majority of matches lost (dominance index <1) were called subordinate birds. When birds defended one or more bowls against conspecifics for a period of at least 3 h, they were considered to be a holder of a territory, whereas those without such a behaviour were treated as non-territorial. Territoriality was not always equivalent to a high dominance index

Fig. 2 Number of male and female wheatears (totals per pentade) observed on Helgoland in spring 2002 ($n=936$ males and 602 females).



because take-overs or expulsions occurred frequently. Whether individual wheatears predominately attacked females was investigated by relating the sex ratio of attacked conspecifics to the sex ratio of birds present at the study site with the selection index of Jacobs (1974). For days with at least five colour-ringed individuals present at the study site, the dominance index was tested for correlation with wing length (as an indicator of body size), fuel load (as an indicator of motivation to feed) and preceding stopover length (as an indicator of prior residency), in order to analyse the influence of these parameters on the hierarchy among the wheatears stopping over (Spearman rank correlation).

Results

Phenology of migration

According to field observations, spring migration of wheatears lasted from late March to mid-June in 2002 (Fig. 2). Males appeared earlier on the island than females (median date: 8 May and 11 May, respectively; Mann-Whitney U -test: $Z=-7.179$, $P<0.001$). Trapping data (first captures) revealed an earlier migration of subspecies *leucorhoa* (median date: 1 May) compared to subspecies *oenanthe* (median date: 9 May; Mann-Whitney U -test: $Z=-5.56$, $P<0.001$). Differential timing of males and females could only be shown for *leucorhoa* (Table 1). Out of 226 colour-ringed wheatears, 75 (33.2%) stayed at least 1 day beyond the day of arrival. Residence rate was higher (53%, $n=80$) and stays were longer (mean 3.8 days, SD 2.4 days, $n=42$) in *leucorhoa* compared to *oenanthe* (residence rate: 16%, $n=101$, $\chi^2=25.9$, $P<0.001$; stopover length: mean 1.6 day, SD 0.8 day, $n=16$, Mann-Whitney U -test: $Z=-3.695$, $P<0.001$). Compared to an unmanipulated situation in the same habitat during the spring migration seasons 1998–2000, the percentage of birds not

Table 1 Median dates of trapping in male and female wheatears on Helgoland in spring 2002. Statistics refer to differences within subspecies (Mann-Whitney *U*-test)

	Males		Females		<i>U</i> -test	
	<i>n</i>	Median	<i>n</i>	Median	<i>Z</i>	<i>P</i>
<i>oenanthe</i>	62	8 May	39	9 May	-0.662	0.508
<i>leucorhoa</i>	38	28 April	42	3 May	-4.525	<0.001

departing on the day of arrival was more than twice as high, but significantly so only in *leucorhoa* males and females (Table 2).

Fuel deposition and migration strategy

During their stay, wheatears used the food offered ad libitum for fuel deposition. Most *leucorhoa* birds departed with a much higher fuel load compared to arrival, but males at least of *oenanthe* (data lacking for females) only slightly increased their stores (Fig. 3). The rate of refuelling (FDR_{tot}) was similar in male and female *leucorhoa* birds (males: mean 0.133, SD 0.043, $n=12$; females: mean 0.135, SD 0.049, $n=11$; Mann-Whitney *U*-test: $Z=-0.154$, $P=0.878$). FDR_{tot} of *oenanthe* seemed to be lower (males: mean 0.083, SD 0.097, $n=7$; females: mean 0.121, SD 0.101, $n=2$), but the difference to *leucorhoa* was not significant (males and females combined: $Z=-1.488$, $P=0.145$) due to the low sample size.

In *leucorhoa* birds with a stopover length exceeding 2 days (settled birds hereafter), departure fuel load ranged from 0.497 to 1.102 in males (mean 0.856, SD 0.240, $n=9$) and from 0.554 to 0.828 in females (mean 0.695, SD 0.083, $n=9$). DFL was neither correlated with wing length (males: $R_S=0.213$, $P=0.582$, $n=9$; females: $R_S=-0.538$, $P=0.135$, $n=9$) nor to dominance index (males: $R_S=0.567$, $P=0.112$, $n=9$; females: $R_S=0.233$, $P=0.546$, $n=9$). In the same subspecies, DFL of birds departing on the day of arrival ranged from -0.021 to 0.222 in males (mean 0.108, SD 0.122, $n=3$) and from -0.015 to 0.481 in females (mean 0.148, SD 0.165, $n=9$).

We compared the relation of DFL and FDR between males and females to explore possible differences in their refuelling and migration strategies. In males, DFL of settled birds was positively correlated with FDR, whereas females departed with almost the same level of fuel stores in all birds, irrespective of FDR_{tot} (Fig. 4). Too few

oenanthe wheatears stayed long enough to allow such a comparison.

Dominance and fuel deposition

During the 43 days of the study period, we observed 3,954 aggressive encounters that included at least 1 wheatear; 3,462 interactions were intraspecific, while the others were directed against 15 passerine species (most of them against white wagtail *Motacilla alba*, whinchat *Saxicola rubetra* and common redstart *Phoenicurus phoenicurus*). In total, 98.0% of the intraspecific encounters were won by the initiator. Detailed comparisons were possible in 446 interactions between 2 colour-ringed individuals. Significantly more aggressive encounters were won by the initiator, by larger birds and by males, whereas fuel load and subspecies were without a significant effect (Table 3). The majority of interactions were started by males (both subspecies) and *leucorhoa* females, but only a few *oenanthe* females were aggressive against conspecifics (Table 4). Compared to the sex ratio of wheatears present, females were attacked more often than males by both males and females (Fig. 5). Out of 81 encounters in which the females were larger than the males, 59 were initiated by males and 22 by females, indicating that size differences may be less important than gender in causing aggression. For 17 days with at least five colour-ringed birds present, we tested the dominance index for correlation with body size (wing length), fuel load and preceding stopover length. Because only very few significant correlations occurred (Table 5), none of these factors could explain the dominance pattern among the wheatears stopping over at the study site.

The social rank on the day of arrival probably influenced the departure decision. Of those birds that lost all aggressive encounters ($n=23$), only 44% stayed at least until the next day, whereas 87% ($n=30$) did so in birds with a dominance index of 1–2 (i.e. which won at least half of their encounters). Birds with a dominance index of 1–2 remained on Helgoland significantly more often than those with an index below 1 ($\chi^2=8.27$, $P=0.004$).

Many individuals established territories at the feeding stations. However, size (number of bowls defended) and location of the territories varied between days. Among the colour-ringed individuals that proved to feed at the bowls, 55% of the males ($n=60$) and 39% ($n=46$) of the females defended a territory for at least 3 h. The difference be-

Table 2 Proportions of the colour-ringed wheatears staying beyond the day of arrival on Helgoland during the field experiment in spring 2002 (additional food supply) and in the same habitat in spring 1998–2000 (no manipulation of stopover conditions; Delingat and Dierschke 2000 and unpublished data)

	Spring 2002 (experiment)		Spring 1998–2000		χ^2	<i>P</i>
	<i>n</i>	Staying	<i>n</i>	Staying		
<i>oenanthe</i> males	62	15%	50	6%	2.10	0.147
<i>oenanthe</i> females	39	18%	47	6%	2.78	0.096
<i>leucorhoa</i> males	39	54%	19	21%	5.60	0.018
<i>leucorhoa</i> females	41	51%	29	24%	5.19	0.023

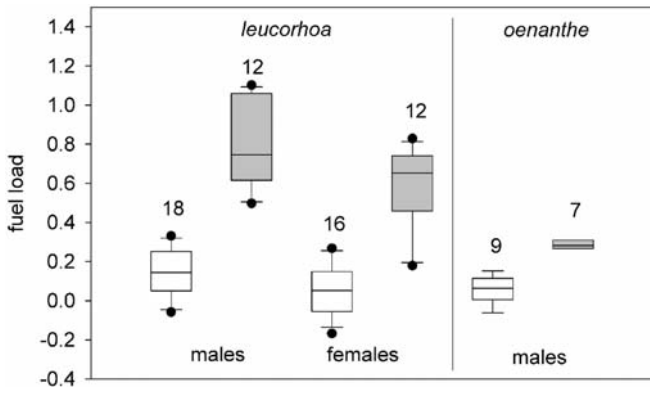


Fig. 3 Box plot of arrival fuel load (white) and departure fuel load (grey) of subspecies and sex classes (DFL only for birds staying at least 2 days). Boxes show the 5%, 25%, 50%, 75% and 95% percentiles as well as outliers (dots). Sample sizes are given above the boxes.

tween sexes is not significant ($\chi^2=2.03$, $df=1$, $P=0.154$). In those birds identified to subspecies, the percentage of territory holders was highest in *leucorhoa* males (65%, $n=20$), followed by *oenanthe* females (45%, $n=11$), *leucorhoa* females (39%, $n=28$) and *oenanthe* males (38%, $n=24$). Usually the bird coming first in the morning held the territory throughout the day. When more than one bowl was defended, the territory size decreased in the course of the day owing to take-overs by other individuals.

In birds staying at least 1 day, the fuel load at arrival and at departure did not differ between dominant and subordinate birds, as well as the stopover length, but the refuelling rate was higher in dominant individuals (Table 6). However, in a more detailed analysis, FDR_{tot} was independent of dominance index and thus social rank at the stopover site (Fig. 6). Furthermore, territory holders

did not refuel at a significantly higher rate than non-territorial birds (mean 0.143, SD 0.041, $n=21$ and mean 0.086, SD 0.096, $n=10$, respectively; Mann-Whitney U -test: $Z=-1.606$, $P=0.114$). For the latter comparison, it is of interest that non-territorial birds took more mealworms per visit at a bowl (mean 6.5, SD 2.0, $n=34$) than territorial birds (mean 4.5, SD 1.6, $n=49$; t -test $t=4.89$, $P<0.001$). In birds staying at least 1 day, the stopover length did not differ between territory holders (mean 3.3 days, SD 1.8 days, $n=24$) and non-territorial birds (mean 2.7 days, SD 2.2 days, $n=9$; Mann-Whitney U -test: $Z=-0.992$, $P=0.349$).

Discussion

As found in several other studies on passerine migrants in spring, male and female wheatears showed a differential timing of stopover on Helgoland in 2002. On a subspecies level this could be shown for Greenlandic/Icelandic birds only, but not for the nominate subspecies. It is possible that trapping effort was not distributed evenly enough over the spring migration period, missing females especially in late May and early June when this gender predominantly was seen in field observations (Fig. 2, see also Dierschke and Delingat 2003). Furthermore, owing to the large breeding area of the subspecies *oenanthe*, various breeding populations with slightly differing migration schedules may mask differences between sexes. Earlier migration of males even in the subspecies *oenanthe* was found elsewhere at stopover sites (Hantge 1958; Spina et al. 1994) and in arriving breeding birds (Currie et al. 2000).

Similar to the findings of an earlier field study on Helgoland (Dierschke and Delingat 2001), nominate wheatears stayed a shorter time than *leucorhoa* birds.

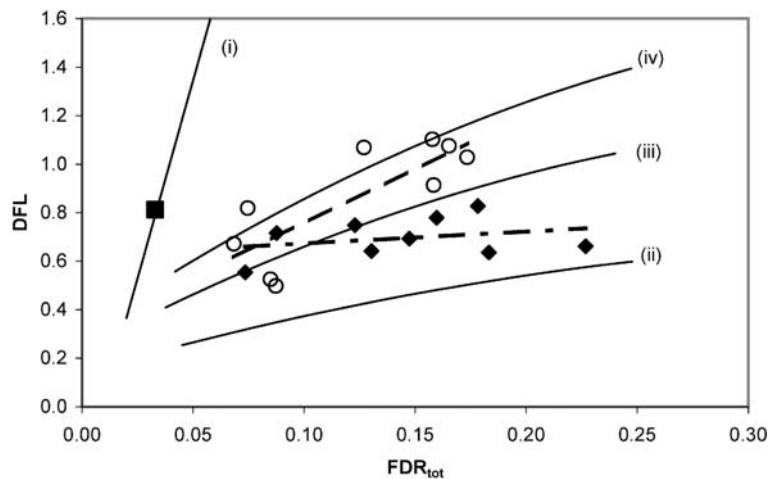


Fig. 4 Relationship between departure fuel load (DFL) and total fuel deposition rate (FDR_{tot}) in *leucorhoa* wheatears during spring migration on Helgoland (circles males, diamonds females). Curve i shows the predicted relationship assuming local variation (with $FDR=0.033$ and $DFL=0.812$ from recaptures without additional food supply 1998–2001 indicated by the square). Curves ii–iv are

the predicted relationships assuming global variation with establishment costs of 1 day (ii), 3 days (iii) and 5 days (iv). The correlation is significant for males ($R_S=0.669$, $P=0.049$, $n=9$; broken line) but not for females ($R_S=0.150$, $P=0.700$, $n=9$; dotted line shown for comparison). The two regression lines are not running parallel to each other (t -test: $t_{14}=3.090$, $P<0.01$).

Table 3 Outcome of intraspecific aggressive interactions among wheatears. For each pair, the deviation from evenly distributed wins and losses is tested

Winner	Loser	<i>n</i>	χ^2 -test (<i>df</i> =1)
Attacking bird	Attacked bird	421	$\chi^2=391$
Attacked bird	Attacking bird	10	$P<0.001$
Larger bird	Smaller bird	240	$\chi^2=5.13$
Smaller bird	Larger bird	175	$P=0.024$
<i>leucorhoa</i>	<i>oenanthe</i>	30	$\chi^2=0.08$
<i>oenanthe</i>	<i>leucorhoa</i>	27	$P=0.780$
Higher fuel load	Lower fuel load	152	$\chi^2=0.68$
Lower fuel load	Higher fuel load	138	$P=0.410$
Male	Female	179	$\chi^2=42.99$
Female	Male	46	$P<0.001$

Although nominate birds made use of the ad-libitum food supply and attained a similar FDR_{tot} , their DFL was lower compared to their Greenlandic/Icelandic conspecifics. When discussing subspecies differences in migration strategy, it has to be remembered that *oenanthe* wheatears are already close to their breeding grounds when stopping over on Helgoland. Carried fuel stores may be sufficient for the forthcoming (and perhaps last) flight, making much overloading unnecessary. Based on the results of a continent-wide ringing project with passerines, Schaub and Jenni (2001) concluded that a good food supply does not necessarily lead to maximum refuelling rates unless birds are confronted with an ecological barrier that requires a high fuel load for crossing (see also Bairlein 1991). Whereas the former seems to be valid for some of the Scandinavian wheatears, the latter definitely applies to Greenlandic/Icelandic wheatears refuelling at high rates on Helgoland (compare also to the theoretical maximum FDR of 0.06 day^{-1} ; Lindström 1991). Many of them departed with very large stores exceeding their lean mass by 50–110%. The heaviest birds weighing more than 50 g (54.2 g at the maximum) match those wheatears departing from Greenland in autumn with an estimated flight range of at least 3,400 km (Ottosson et al. 1990). Unfortunately, fuel loads higher than 0.6 do not allow any application of the flight range model “Flight 1.12” (Pennycuik 1989, 2002). However, most birds staying for several days should be able to reach Iceland in a non-stop flight, because a fuel load of half the maximum (ca. 0.6) would allow approximately half the flight range (i.e. 1,700 km, nearly the distance between Helgoland and Iceland, which

is about 1,800 km). Those *leucorhoa* birds departing with lower fuel stores are supposed to stopover en route in Scotland or even in southern Norway (Bernhoft-Osa 1958), the latter area indicated by some birds adopting a northward course in release experiments on Helgoland (Dierschke and Delingat 2003).

In settled *leucorhoa* wheatears (length of stay >2 days), males and females differed in their pattern of FDR_{tot} and DFL. When projecting the theory of optimal migration (Alerstam and Lindström 1990) to a larger scale with fixed distances between possible stopovers en route to Greenland (see Methods), the positive correlation of these two parameters in males indicated that they behaved like time-minimizers, i.e. they optimized their migration with respect to a high speed. Furthermore, the data suggest that the males update their expected FDR to currently experienced conditions (global variation type of time-minimizing, Weber et al. 1999) with an establishment time of 3–5 days (Fig. 4). In spite of the lack of opportunity to stopover anywhere and anytime, the flight range of almost all males allows us to maintain the classification as time-minimizers, because they are able to reach Iceland or even Greenland in a single flight, and can by-pass closer stopover sites such as southern Norway or northern Scotland easily. The very high departure fuel loads of some males resemble those of wader species breeding in the same Arctic regions and which are also considered to be time-minimizers (Gudmundsson et al. 1991). In three passerine species (including wheatears on Helgoland), time-minimizing was found to be the strategy during autumn migration (Lindström and Alerstam 1992; Weber et al. 1999; Schmaljohann and Dierschke 2004), but evidence for such behaviour is flimsy in spring (Maitav and Izhaki 1994).

In contrast to males, *leucorhoa* females departed with about the same level of fuel stores (0.55–0.83), regardless of refuelling rate and stopover length. According to the optimal migration theory, such behaviour should resemble energy-minimization. However, as mentioned above, a fuel load of 0.6 would roughly cover the costs for a non-stop flight to Iceland. Thus, the females can by-pass stopover sites in Norway and Scotland as well, and also fit the pattern of time-minimizers that face ecological barriers along their migration route (Gudmundsson et al. 1991). Compared to males, the migration strategy of females seems to differ with respect to an obligatory stop-

Table 4 Outcome (wins-losses from the point of view of the attacking bird) of all intraspecific aggressive interactions among wheatears (draws are not considered)

Attacking bird	Attacked bird					
	<i>leucorhoa</i> male	<i>leucorhoa</i> female	<i>oenanthe</i> male	<i>oenanthe</i> female	Unidentified male	Unidentified female
<i>leucorhoa</i> male	64-4	90-1	6-0	7-0	9-1	2-0
<i>leucorhoa</i> female	28-1	52-0	9-1	9-0	3-1	2-0
<i>oenanthe</i> male	8-0	13-0	7-0	8-0	2-0	2-0
<i>oenanthe</i> female	2-0	3-0	1-0	2-0	–	1-0
Unidentified male	19-0	41-1	15-0	7-0	3-0	4-0
Unidentified female	–	1-0	1-0	–	–	–

Fig. 5 Index of selectivity D (Jacobs 1974) for male and female wheatears directing aggressive encounters against females in relation to the proportion of females present at the study site. Positive values indicate that birds attack females disproportionately to males; negative values stand for birds preferring to attack males.

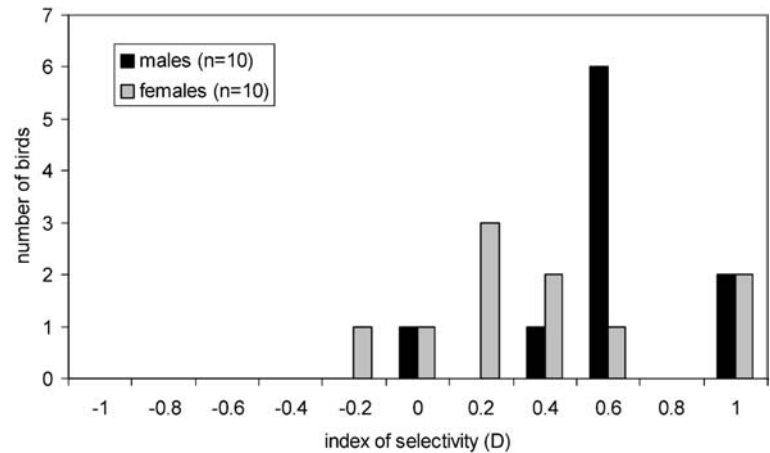


Table 5 Results of Spearman rank correlations of dominance index against size (wing length), fuel load and prior residency (number of days present before). Significant results are printed in **bold type**. No significant correlations remained after Bonferroni correction

Date	Size			Fuel load			Prior residency		
	<i>n</i>	R_S	<i>P</i>	<i>n</i>	R_S	<i>P</i>	<i>n</i>	R_S	<i>P</i>
26 April	9	0.64	0.062	6	-0.06	0.913	9	-0.05	0.892
27 April	12	0.28	0.380	10	0.40	0.255	12	-0.40	0.201
28 April	11	0.37	0.260	10	-0.09	0.801			
29 April	9	0.57	0.108	9	0.42	0.262	9	-0.42	0.259
30 April	14	0.43	0.123	11	-0.01	0.979	14	0.15	0.610
1 May	12	0.00	0.996	10	0.37	0.296			
2 May	10	0.21	0.563	10	0.65	0.043	10	0.00	1.000
3 May	10	-0.16	0.664	9	0.37	0.327	10	-0.25	0.481
4 May	12	-0.54	0.069	10	0.22	0.542	12	0.43	0.168
5 May	11	-0.37	0.260	9	0.72	0.028			
6 May	9	-0.53	0.144	9	-0.21	0.596	9	0.63	0.066
7 May	8	0.38	0.358	7	0.51	0.243	8	-0.52	0.184
8 May	10	-0.04	0.905	9	-0.16	0.680	10	0.51	0.135
9 May	8	0.05	0.213	8	0.26	0.543	8	-0.58	0.128
10 May	11	0.02	0.946	7	-0.02	0.969	11	0.18	0.602
18 May	6	0.09	0.868	5	0.41	0.493	6	-0.66	0.150
19 May	8	0.25	0.545	7	0.19	0.691	8	0.09	0.841

Table 6 Arrival fuel load (AFL), total fuel deposition rate (FDR_{tot}), departure fuel load (DFL) and stopover lengths of subordinate (dominance index <1) and dominant wheatears (dominance index 1–2) staying at least one night on Helgoland

	Subordinate birds			Dominant birds			<i>Z</i>	<i>P</i>
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD		
AFL	25	0.121	0.139	33	0.092	0.106	-0.762	0.446
FDR_{tot}	14	0.101	0.049	25	0.139	0.043	-2.348	0.019
DFL	15	0.470	0.252	26	0.562	0.311	-0.839	0.311
Stopover length	26	3.42 days	2.93 days	33	2.82 days	1.74 days	-0.267	0.790

over in Iceland. Perhaps a non-stop flight to Greenland is not possible or too dangerous for females, and stopovers in Iceland may provide safety. Perhaps this strategy involves an arrival in Greenland with reserves sufficient for successful breeding, which have to be stored in Iceland beforehand. Although both males and females seem to maximize their speed of migration, males are more pronounced in this. They seem to incorporate non-stop flights to Greenland in their strategy if they meet superb refuelling conditions and, compared to females, appear to take more risks with respect to wind drift during long flights or starvation when arriving in poor body condition. In line with speculations on waders (Gudmundsson et al. 1991), wheatears may experience worse refuelling conditions as

they move further north in spring. Therefore, it makes sense to gain the reserves necessary for the flight to Greenland further south and to by-pass all the other stopover sites en route.

The more strict time-minimization with a higher degree of risk-taking undoubtedly fits with the hypothesis of earlier male migration owing to a higher speed. That all *leucorhoa* wheatears are time-optimizing migrants is further illustrated by immediate departures of individuals that are not settled. Regarding their DFL, those birds can afford to move on to the German coastline (50 km) or even Norway (450 km), probably expecting better refuelling conditions than on Helgoland, where they perhaps failed to gain access to high-quality feeding patches.

Fig. 6 Relationship between total fuel deposition rate and the dominance index (calculated from intraspecific aggressions) for wheatears staying at least 1 day beyond the day of arrival. There is no significant correlation ($R_S=0.281$, $P=0.079$, $n=40$).

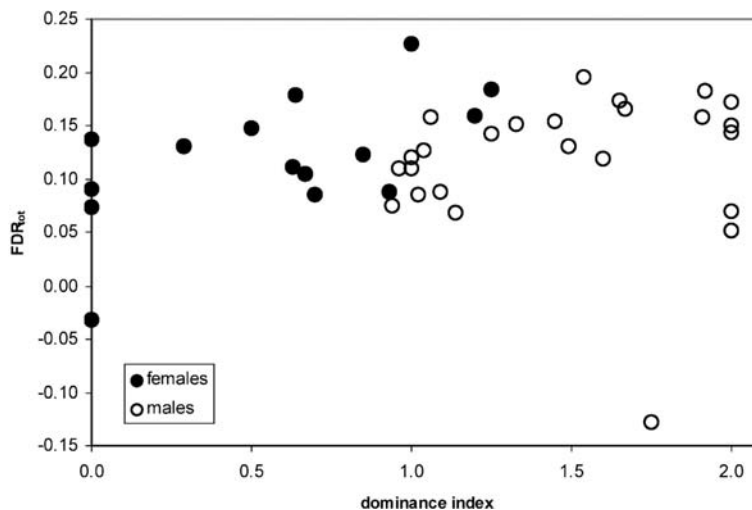


Table 7 Index of wing pointedness (I_5) in male and female wheatears during spring migration (1999–2000) on Helgoland (Volker Dierschke, unpublished work). The index was calculated as $I_5=(WL-P_8-P_5)/WL$ with wing length (WL) and the length of

primaries 5 and 8 (numbered in descending sequence) following Hedenström and Pettersson (1986). The smaller the I_5 , the more pointed is the wing. Differences between sexes were tested with two-tailed Kolmogorov-Smirnov two-sample tests

Subspecies	<i>n</i> males	<i>n</i> females	I_5 males	I_5 females	<i>P</i>
<i>Oenanthe o. oenanthe</i>	93	85	0.9105	0.9122	0.184
<i>O. o. leucorhoa</i>	31	65	0.9015	0.9063	0.188

Departures in connection with the expectation of better conditions elsewhere fit well the time-minimization in optimal migration theory (Alerstam and Lindström 1990; Lindström et al. 2002).

When food was supplied ad libitum, the refuelling pattern only slightly differed between dominant and subordinate individuals. Although the fuel load at arrival and at departure was the same, the average refuelling rate was higher in dominant birds. However, this result was not maintained when FDR_{tot} was compared with the more precise dominance index, and in addition, FDR_{tot} did not differ between territorial and non-territorial birds. The observed higher doses of food taken during visits at a bowl in non-territorial birds suggest that those birds compensated for the restricted access to the resource with a more efficient exploitation. A similar pattern was found among dominant and subordinate rufous hummingbirds (*Selasphorus rufus*) during autumn migration stopover, with low-ranking females supposed to achieve the same FDR as high-ranking males by robbing nectar from male's territories (Carpenter et al. 1993). Subordinate red-eyed vireos (*Vireo olivaceus*) also increased meal size when dominant individuals were removed in a laboratory experiment, and confirmed that social rank of migrants affects the access to resources (Moore et al. 2003). During autumn migration, a field experiment with bluethroats (*Luscinia svecica*) quite similar to the present study found a positive correlation of FDR and dominance, with dominance being explained by body size rather than by fuel stores or prior residency (Lindström et al. 1990). In unmanipulated habitats without ad-libitum food, aggression rate among American redstarts at an autumn stopover

site was density-dependent, leading to the displacement of low-ranking juveniles from favourable habitats and relating FDR to social rank there as well (Woodrey 2000). A negative correlation between FDR and bird density was found or assumed in this and in other studies (Moore and Yong 1991; Schaub and Jenni 2000; Kelly et al. 2002), and territoriality may be a way to escape competition and secure profitable patches (Rappole and Warner 1976). On Helgoland, wheatears usually establish territories at profitable patches of food (wrack beds with larvae of Coelopidae; Delingat and Dierschke 2000; Dierschke et al. 2003) where they can achieve refuelling rates as high as in this experiment (according to recaptures up to 0.08 in spring and 0.16 in autumn; Volker Dierschke, unpublished data).

Although male wheatears were more often territorial and on average attained a higher social rank than females, this did not result in higher refuelling rates. Thus, there is no evidence for competition between the sexes leading to delayed migration of females. This is in contrast to the assumption of Spina and Pilastro (1999), who regard differential spring migration of sexes as a strategy to reduce competition at stopover sites before the crossing of ecological barriers. They base their assumption on the fact that males and females do not differ in residual fat loads after crossing the Sahara desert and the Mediterranean Sea, despite the lower flying efficiency of females, which would require more energy for the same flight distance. With wheatears, however, we cannot adhere to this hypothesis, because the sexes do not differ in wing morphology in either subspecies (Table 7). We therefore suggest that competition between the sexes at stopover

sites may be species-specific, because in line with our results on wheatears, no difference between the sexes regarding stopover behaviour and refuelling rate was found during spring migration in American redstarts (Morris and Glasgow 2001) and blackcaps (*Sylvia atricapilla*) (Maitav and Izhaki 1994), whereas male Wilson's warblers (*Wilsonia pusilla*) refuelled at a higher rate than females (Yong et al. 1998). In the case of wheatears, it seems that different migration, risk-taking and refuelling strategies contribute to the differential timing of the sexes during spring migration. As it is unknown whether male wheatears winter further north than females or start from the wintering grounds earlier, we cannot exclude that these factors are also involved.

Acknowledgements Assistance during the field work was provided by R. Morgenstern and A. Walter. Technical support was obtained from R. Nagel. We are much indebted to F. Bairlein for initiating the study. He, N. Anthes, L. Jenni and an anonymous referee commented on the manuscript. The study was financially supported by the "Freunde und Förderer der Inselstation der Vogelwarte Helgoland e.V." and by the Deutsche Forschungsgemeinschaft (BA 816/15-1). The experiments comply with the current laws of Germany and Schleswig-Holstein.

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