Volker Dierschke · Julia Delingat

Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances

Abstract On the small North Sea island Helgoland (54°11′ N, 07°55′ E) we studied the stopover ecology of two subspecies of northern wheatear, *Oenanthe oenanthe*, during spring migration. Birds heading for Scandinavia (*O. o. oenanthe*) face only short flights across an ecological barrier (50–500 km) whereas those originating from Greenland and Iceland (*O. o. leucorhoa*) have to cover between 1,000 and 2,500 km in the impending flight. Colour-ringed individuals showed that 90% of Scandinavian birds left on the day of ringing while 40% (males) and 30% (females) of Greenland/Icelandic birds stayed at least 1 night. The birds who remained were thus mostly *O. o. leucorhoa*. They often established desirable feeding territories on the beach and had a high rate of body mass increase (1.7 g/day). However, subspecies did not differ in habitat choice and in foraging effort, but *O. o. leucorhoa* had a higher success rate in pecking. Departure decisions were analysed by comparing (a) conditions on the day of ringing between departing and staying birds and (b) for birds staying between the day of departure and the preceding day. The factors that were probably important in the decision to depart differed between subspecies. In *O. o. leucorhoa*, few birds departed with bad or deteriorating weather conditions (tailwind component, cloud cover), whereas departures of *O. o. oenanthe* seemed to be little affected by those factors. A few *O. o. oenanthe* stayed early in the spring migration season and/or had low fat reserves. Interference during foraging seemed to play a role because both subspecies tended to leave when the densities of northern wheatears were high. Other factors related to refuelling conditions (food supply, foraging effort, predation risk) failed to show differences between staying and departing individuals. In summary, almost all Scandinavian birds departed quickly and irrespective of refuelling and weather conditions, whereas many (but not all) Greenland/Icelandic birds seemed to prepare for a long-distance flight and carefully adjusted departure to weather conditions. The observed differences in stopover behaviour and departure decisions in the two subspecies of northern wheatear indicate that the distance to the next stopover site or to the goal area has to be considered when applying optimal migration models.

**Keywords** Northern wheatear · *Oenanthe oenanthe* · Stopover ecology · Ecological barrier

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Introduction

Migration of birds usually takes place in a number of successive flights which are interrupted by stopovers for resting and refuelling. Models dealing with optimality in bird migration predict that such stopovers should last until enough fuel is stored to reach the next stopover site if the birds are minimizing energy expenditure during migration (Alerstam and Lindström 1990). If birds are under time pressure, for example trying to arrive early to secure good breeding territories (Møller 1994), fuel deposition rate and departure fuel load are the major determinants in departure decisions (Alerstam and Lindström 1990). Birds maximizing the speed of migration (i.e. minimizing the time spent on migration) should leave a stopover site when the fuel deposition rate lowers the instantaneous speed of migration below the expected average of the whole journey (Alerstam and Lindström 1990). In addition to time and fuel, predation risk has to be considered as an important factor influencing stopover behaviour of migrants. Models of optimal migration are based on the assumption that suitable stopover sites are available all along the migration route and that a bird may make a stopover whenever it wants to. In reality, many bird species are quite restricted in such a choice either because suitable habitats are scarce or distributed

Fig. 1 Hypothetical migration routes of Greenland/Icelandic (subspecies *O. o. leucorhoa*) and Scandinavian (subspecies *O. o. oenanthe*) northern wheatears from Helgoland (*circle*) in spring. The shortest possible sea crossing of Scandinavian birds to northern Germany and Denmark is not shown. Map projection is equidistant azimuthal with Helgoland as the projection centre
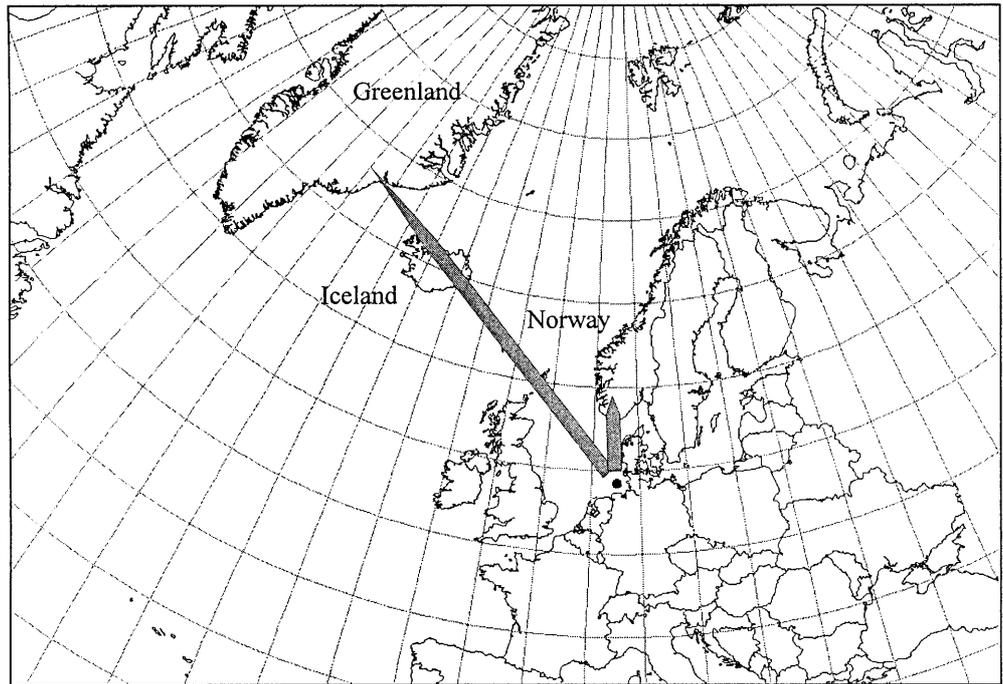
patchily (e.g. for many coastal waders: Piersma 1987) or because ecological barriers hinder resting and/or refuelling. To overcome such problems, birds have to conduct long-distance flights which require intense preparations in body condition and selection of favourable weather conditions at take-off (Safriel and Lavee 1988; Piersma and Jukema 1990; Clark and Butler 1999). The distance between stopover and destination sites has been considered with respect to optimality in the analysis of spring migration of three wader species (Gudmundsson et al. 1991) and in dynamic modelling (Weber et al. 1998).

To investigate the effects of imminent long-distance flights on stopover behaviour and departure decisions, we studied two subspecies of northern wheatear (*Oenanthe oenanthe*) during spring stopovers on a small offshore island in the North Sea. On Helgoland, northern wheatears of Scandinavian breeding origin (*O. o. oenanthe*) and those breeding in Greenland and Iceland (*O. o. leucorhoa*) occur simultaneously from mid March to early June, peaking from late April to late May (J. Delingat and V. Dierschke unpublished data). Whereas Scandinavian birds face sea crossings of only 50–150 km (when heading north-east towards Schleswig-Holstein or Denmark) or a maximum of 500 km (when flying to southern Norway), much longer flights are necessary for Greenland/Icelandic birds to reach stopover sites in Scotland (ca 1,000 km) or the breeding area (up to 2,500 km; Fig. 1). Several observations indicate that northern wheatears are capable of very long flights across the northern Atlantic (Snow 1953; Luttik and Wattel 1979). Because such long flights afford sufficient preparations, we hypothesize that birds of the subspecies *O. o. leucorhoa* adjust their stopover behaviour more carefully for intense fuel deposition than do Scandinavian birds before their short-distance flights. Furthermore, Green-land/Icelandic birds are expected to be more selective in weather conditions at departure because strong headwinds and orientational mistakes would have much more impact on long-versus short-distance flights. Because birds of the subspecies *O. o. leucorhoa* are reported from southern Norway in spring (Haftorn 1971), some of the Greenland/Icelandic birds on Helgoland may move to the north first and shift to a north-western direction after stopping over in Norway. Birds following such a strategy probably resemble Scandinavian birds, making differences between the two subspecies less obvious.

Study area

The small island of Helgoland (150 ha) is situated in the south-eastern North Sea (54°11′ N, 07°55′ E), 53 km off the mainland coasts of Schleswig-Holstein and Lower Saxony and 43 km off the Wadden Sea island Wangerooge. Apart from the village and some small bushy areas, most of the island is open habitat. Northern wheatears generally occur in two main types of habitat: sandy beaches with beds of rotting brown algae [with kelp flies (Coelopidae) and their larvae as the only but abundant food supply] and grassland habitats with interspersed open patches and boulders (with various ground-dwelling arthropods as food supply). For further details of these habitats see Delingat and Dierschke (2000).

Methods

During the spring migration seasons 1998, 1999 and 2000, northern wheatears were captured with spring traps baited by mealworms. Birds were sexed and aged according to Svensson (1992), measured [flattened wing length to the nearest 0.5 mm, length of

third outermost primary (P3) to the nearest 0.1 mm and many other measurements not included in this study], weighed to the nearest 0.1 g with Pesola or electric balances and ringed with individual combinations of one metal ring and three to four colour-rings. Fat score was estimated on a nine-class scale (Kaiser 1993) and breast muscle size was scored on a four-class scale (Bairlein 1994). Following Svensson (1992), females with wing lengths exceeding 97 mm ($n=82$) and males exceeding 102 mm ($n=50$) were treated as belonging to the subspecies *O. o. leucorhoa*, whereas females with wings shorter than 96 mm ($n=123$) and males below 99 mm ($n=129$) were assigned to the subspecies *O. o. oenanthe*. Birds in the range of overlap ($n=86$) were not considered in this study. Because of the large differences in body size, the body mass measured (BM_m) was standardized to the average length of P3 (74 mm) by standardized body mass $BM_{s,i}=BM_{m,i}+x(P3_{mean}-P3_i)$, with $x=0.401$ as the slope in the linear regression of body mass against P3 for all individuals with fat score 2 ($n=150$). The respective slopes of the two subspecies do not differ ($t=0.31$, $P>0.05$).

The island was searched for colour-ringed individuals daily. Birds not seen on days subsequent to the day of ringing were assumed to have left Helgoland on the day of ringing or during the following night and are called "departing birds" in this study. In contrast, "staying birds" were resighted on days following ringing and had therefore spent at least 1 night on Helgoland. The length of stay was calculated as the number of days between last sighting and ringing. Because many (but not all) northern wheatears present at the main study sites were trapped, and fluctuation in the number of birds on the island was strong (Delingat and Dierschke 2000), considering the day of ringing as the day of arrival appeared to be acceptable. For the 74 individuals treated as staying in this study, the resighting probability was 60% (for all birds pooled the number of days with observations divided by the number of days between ringing and last observation). The procedure of trapping, ringing and measuring was thought not to influence the length of stay, because birds were processed quickly and released after only 5–15 min close to the trapping site.

Foraging behaviour was observed in focal birds which were followed with a telescope for 2 min, during which time the number of hops, pecks, flights and aggressive encounters were recorded. In the case of aggressive interactions, the initiator and the victim were classified by species, sex and/or individual (in colour-ringed birds). Under good conditions, pecks were judged as successful (prey or swallowing visible) or unsuccessful. As only a few colour-ringed individuals could be observed in grassland habitats, observations assigned to subspecies are only available for beach habitats.

The decision of a bird whether or not to leave a stopover site might be influenced by a number of factors. To identify the important ones, we tried to quantify stopover conditions for every colour-ringed bird on the day of ringing and calculated average conditions for staying and departing birds, for the two subspecies separately. Because most parameters investigated were not distributed normally, they were analyzed separately, but some factors could be included in a logistic regression analysis.

Because the food supply was very difficult to quantify on a daily base, we took several parameters of foraging behaviour as indicators of food availability (number of pecks and successful pecks per minute), of effort in foraging (number of hops per peck or per successful peck, success rate of pecks) and of interference (number of aggressive encounters per minute). A more global measurement of interference is the bird density, expressed as the number of northern wheatears counted on the island.

Predation risk was estimated according to the total number of raptors observed per day on the whole island according to the ornithological log of Vogelwarte Helgoland. Only raptors posing a threat for passerines (sparrowhawk *Accipiter nisus*, kestrel *Falco tinnunculus*, merlin *F. columbarius*, hobby *F. subbuteo* and peregrine *F. peregrinus*) were considered. For a more precise estimate, we counted the number of raptor flights across or close to our study sites, resulting in a rate of raptor flights per hour.

As many northern wheatears probably depart in the evening, we selected weather conditions at 2130 hours as relevant for departure decisions. Studies dealing with other passerines on Helgoland (Landes 1999; V. Dierschke and F. Bindrich unpublished data) have shown that wind and overcast conditions are the only important weather variables accounting for the number of birds (and perhaps for the percentage of the birds aloft) alighting on the island. Therefore, we compared the departure decisions with respect to the cloud cover (in $x/8$), the wind force (Beaufort) and the tailwind component (TWC). The latter was calculated as $TWC=cos(v)v$ with v as the angle between wind direction and tailwind and v as the wind velocity (m/s; Fransson 1998). Because the main departure directions are north for Scandinavian birds and north-west for Greenland/Icelandic birds (according to release experiments; V. Dierschke unpublished data), winds from the south and south-east were treated as tailwinds, respectively.

All these factors were compared between birds staying and those departing for each subspecies separately. Within the group of staying birds, another comparison was made between the conditions on the day of actual departure and the preceding day, to test whether improvements in flight conditions or deteriorations in stopover conditions could have influenced the departure. The latter analysis was restricted to the five factors with sufficiently large sample sizes

Results

### Differences in stopover behaviour

Length of stay

For Scandinavian birds, only 9% of males ($n=129$) and 14% of females ($n=123$) did not depart on the day of ringing, whereas in Greenland/Icelandic birds, 40% of males ($n=50$) and 30% of females ($n=82$) stayed on Helgoland for at least 1 night. The difference between subspecies is significant for both sexes (χ^2-tests: females $P=0.004$, males $P=0.001$). With Scandinavian birds, there was a clear seasonal trend in the likelihood to stay, with many birds remaining on the island during the early spring migration, but nearly all birds departing immediately from the second half of April onwards (Fig. 2). No such trend was shown by Greenland/Icelandic birds. Among birds not departing on the day of ringing, the length of stay did not differ significantly between subspecies (Mann-Whitney U-test: $P=0.149$), although
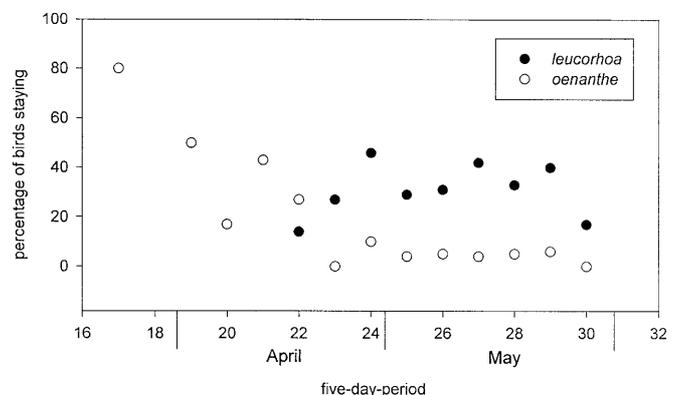
Fig. 2 Percentages of colour-ringed northern wheatears staying (not departing on the day of ringing) on Helgoland per 5-day period in spring. Sample sizes per symbol vary from 6 to 35 in *O. o. leucorhoa* (total $n=127$) and from 5 to 45 in *O. o. oenanthe* (total $n=219$)
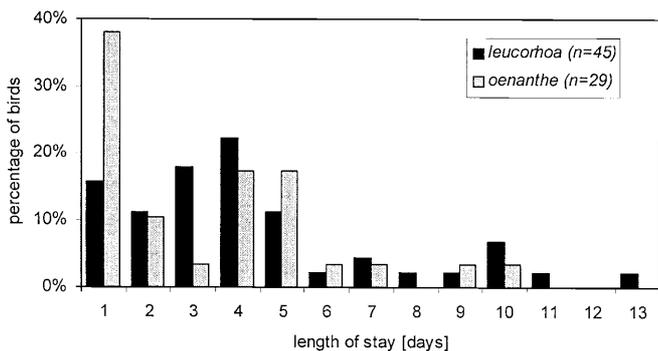
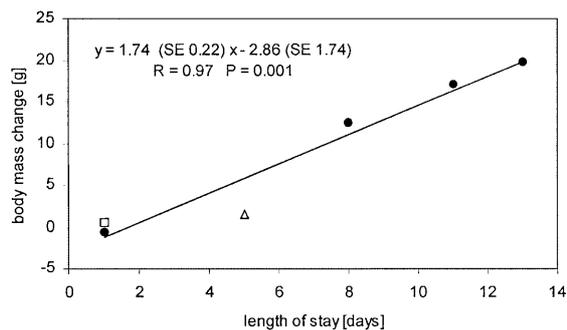**Fig. 3** Length of stay by northern wheatears on Helgoland in spring
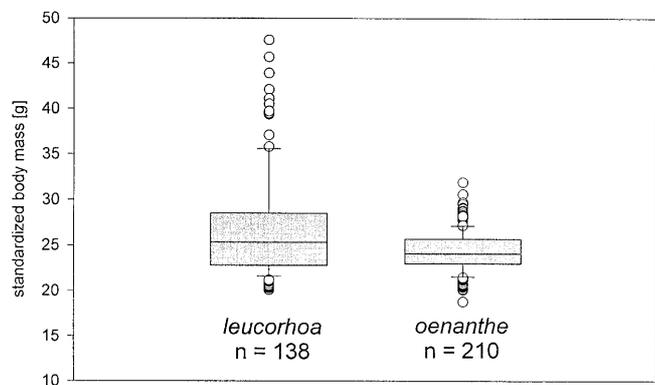
Fig. 4 Box plot of standardized body mass of northern wheatears on Helgoland at first trapping in spring. The 10, 25, 50, 75 and 90% percentiles are shown as are all outliners (*circles*)

many *O. o. oenanthe* stayed for only 1 day and most long-stayers belonged to *O. o. leucorhoa* (Fig. 3).

Body condition

At first capture, most Scandinavian birds showed fat scores of 1–4, whereas 15% of Greenland/Icelandic birds were scored 5–7 (Table 1). The average (±SD) fat scores (2.7±1.7 in *O. o. leucorhoa*, 2.3±1.1 in *O. o. oenanthe*) did not differ significantly (Mann-Whitney *U*-test: *P*=0.234). The breast muscle score was the same in both subspecies (average 2.0±0.6 in *O. o. leucorhoa* and 2.0±0.5 in *O. o. oenanthe*; Mann-Whitney *U*-test: *P*=0.786). The standardized body mass average of *O. o. leucorhoa* (26.8±5.7 g) was significantly higher than in *O. o. oenanthe* (24.4±2.1 g; *t*-test: *P*=0.001; Fig. 4). As many birds did not leave the island on the day of ringing, body condition has to be regarded in connection with the length of stay. When foraging in beach habitats, recaptured individuals increased body mass rapidly at a rate of 1.7 g day^{-1} (Fig. 5), a result produced mainly by Greenland/Icelandic birds. Remote weighing of two *O. o. leucorhoa* individuals gave a similar result (Dierschke et al. 2000). Since Greenland/Icelandic birds stay longer, the difference between the two subspecies in the body mass at departure is much larger than indicated by the body mass on the day of ringing.

Fig. 5 Increase of body mass in retrapped northern wheatears on Helgoland in spring. Each individual is only treated once (only at the last retrap in the case of several weighings) (*circles* subspecies *O. o. leucorhoa*, *squares* subspecies *O. o. oenanthe*; *triangles* subspecies unknown)

Table 1 Fat scores (after Kaiser 1993) of northern wheatears on Helgoland at first trapping in spring. Sample sizes exceed those in the rest of the study because birds that were not colour-ringed are included

Fat score	*O. o. leucorhoa* (n=142)	*O. o. oenanthe* (n=299)
0	9 (6.3%)	10 (3.3%)
1	27 (19.0%)	61 (20.4%)
2	40 (28.2%)	87 (29.1%)
3	26 (18.3%)	86 (28.8%)
4	19 (13.4%)	52 (17.4%)
5	8 (5.6%)	3 (1.0%)
6	11 (7.8%)	0
7	2 (1.4%)	0

Table 2 Percentages of northern wheatears trapped in grassland and beach habitats and staying (not departing on the day of ringing) on Helgoland in spring. Sample sizes are given in *parentheses*

	O. o. leucorhoa	*O. o. oenanthe*	*P* (χ2)
Percent trapped in beach habitats			
April	35% (57)	48% (83)	0.124
May	70% (80)	60% (188)	0.106
Percent birds staying			
Beach	44% (72)	19% (123)	
Grassland	23% (48)	6% (97)	

Habitat choice

In an earlier study, we showed that the two habitat types differ in quality for northern wheatears, leading to low percentages of staying birds in the poorer grassland habitats (Delingat and Dierschke 2000). In this study, percentages of both subspecies trapped in either grassland or beach habitats did not differ in either April or May (Table 2). In both subspecies, the percentage of staying birds was below average in grassland habitats, but higher in beach habitats (Table 2).

Table 3 Foraging-related parameters (mean±SD, sample sizes in *parentheses*) for subspecies of northern wheatears on Helgoland beach habitats in spring. *P* refers to Mann-Whitney *U*-tests (pecks/min, hops/peck) and χ^2-test (successful pecks)

	O. o. leucorhoa	O. o. oenanthe	P
Pecks/min	4.35±3.27 (77)	2.77±2.26 (13)	0.075
Hops/peck	2.82±3.07 (77)	3.11±2.38 (12)	0.407
Successful pecks	61.4% (607)	48.3% (58)	0.050

Foraging

The long-distance flights faced by Greenland/Icelandic birds stopping over on Helgoland suggest a foraging behaviour appropriate for deposition of large amounts of fuel. Compared to Scandinavian birds, individuals of the *O. o. leucorhoa* subspecies seemed to feed more intensively, as they tended to peck more often and used a lower effort of locomotion per peck (Table 3). However, the only significant difference found was in the percentage of successful pecks, which was higher in *O. o. leucorhoa*.

Territoriality

In beach habitats, the rate of aggressive encounters initiated by Scandinavian birds was 0.12/min (*n*=50 min of observation in seven birds) but twice as high in Greenland/Icelandic birds (0.24/min, *n*=314 min in twelve birds; Mann-Whitney *U*-test: *P*=0.007). Most aggressive encounters were directed against conspecifics, but other species (numbers usually fluctuating from zero to ten) were attacked as well (*O. o. leucorhoa*: observed attacks against conspecifics 40, white wagtail *Motacilla alba* 10, yellow wagtail *M. flava* 1, house sparrow *Passer domesticus* 1, starling *Sturnus vulgaris* 1; *O. o. oenanthe*: conspecifics 4, meadow pipit *Anthus pratensis* 1). The high rate of aggression in beach habitats coincided with the establishment of feeding territories lasting for several days in staying birds. Together, the higher aggression rate and the longer stays are indications that the Greenland/Icelandic birds were holders of territories. In grassland habitats, neither *O. o. leucorhoa* nor *O. o. oenanthe* focal birds showed any aggressive encounter (*O. o. leucorhoa*: *n*=36 min in five birds; *O. o. oenanthe*: *n*=42 min in five birds).

The decision of departure on the day of arrival

Whereas above we compared between subspecies, this section deals with differences within subspecies between individuals departing on the day of ringing and those staying at least 1 night.

Time of year

Greenland/Icelandic birds stayed or departed independently of season (Table 4). As shown above, Scandinavian birds tended to stay in the first part of spring migration season, but departed in almost all cases after mid April (Fig. 2). Therefore, season seems to play a role in the departure decision in the subspecies *O. o. oenanthe* (see also Table 4).

Body condition

In Greenland/Icelandic birds, neither body mass nor fat scores differed between staying and departing birds (Table 4). The few Scandinavian birds staying had lower visible fat reserves than those departing early, but this difference in body condition was not reflected in body mass (Table 4).

Foraging

Conditions of foraging in beach habitats on the day of ringing did not differ for staying and departing birds of either subspecies when regarding parameters reflecting food supply and effort to exploit it (Table 4). The foraging-related factor interference revealed a significant difference in Scandinavian birds, with a much higher rate of aggressive encounters occurring in departing birds (Table 4). A related indicator, the density (i.e. the number present on the island) of northern wheatears significantly differed between departing and staying individuals of both subspecies with more birds departing when the density was high (Table 4). Although no rates of energy intake could be calculated, in an earlier study, we found the general habitat quality to be better in beach than in grassland habitats (Delingat and Dierschke 2000). As shown above, percentages of staying birds were much higher in beach than in grassland habitats. Therefore, general habitat quality seems to be of importance in departure decisions of both subspecies.

Predation risk

The presence of raptors did not reveal differences between staying and departing birds of either subspecies, neither for the total number of raptors observed on the island nor the frequency of their flights across wheatear habitats (Table 4).

Weather

Wind velocity did not differ between staying and departing birds, and this result was the same for Greenland/Icelandic birds when including the wind direction (re-

Table 4 Factors possibly affecting departure decisions of northern wheatears on Helgoland in spring. Averages±SD are given for staying and departing individuals of both subspecies separately (sample sizes are given in *parentheses*). Differences between stay- ing and departing birds of either subspecies were testes with Mann-Whitney *U*-tests. Note that not all factors were available for each individual bird

	O. o. leucorhoa			*O. o. oenanthe*		
	Staying	Departing	*P*	Staying	Departing	*P*
Time						
Season (number of 5-day periods)	25.2±2.3 (45)	25.5±2.3 (87)	0.601	21.9±3.4 (29)	25.4±2.5 (223)	<0.001
Body condition						
Fat reserves (fat score)	2.9±1.6 (45)	2.5±1.7 (87)	0.178	1.7±1.1 (28)	2.4±1.1 (222)	0.002
Standardized body mass (g)	27.3±5.9 (45)	26.5±5.6 (83)	0.389	24.0±2.5 (27)	24.4±2.1 (216)	0.513
Foraging						
Food supply: pecks/min	3.7±1.1 (13)	4.1±1.3 (9)	0.647	3.8±1.9 (7)	3.6±0.7 (30)	0.243
Food supply: successful pecks/min	1.8±0.9 (12)	1.7±1.8 (9)	0.277	1.7±0.9 (7)	1.7±0.7 (30)	0.776
Effort: hops/peck	7.8±1.7 (13)	7.4±2.8 (9)	0.794	7.4±2.9 (7)	7.1±2.2 (30)	0.719
Effort: hops/ successful peck	13.7±6.8(12)	16.8±11.9 (9)	0.972	14.6±8.1 (7)	12.7±4.9 (30)	0.925
Effort: success rate of pecks (%)	46±14 (12)	43±20 (9)	0.972	69±70 (7)	47±11 (30)	0.925
Interference: aggressions/min	0.14±0.17 (13)	0.18±0.19 (9)	0.601	0.04±0.06 (7)	0.23±0.04 (30)	0.013
Interference: number of wheatears on island	36.2±21.1 (45)	45.2±26.2 (87)	0.038	24.4±18.9 (29)	45.8±29.5 (223)	<0.001
Predation risk						
Number of raptors on island	5.6±5.3 (45)	4.7±4.2 (87)	0.436	3.6±4.5 (29)	4.5±3.5 (223)	0.260
Raptor flights/h	0.33±0.50 (25)	0.38±0.40 (38)	0.249	0.22±0.18 (11)	0.40±0.44 (87)	0.374
Weather						
Flight: wind force (Beaufort)	4.22±1.33 (45)	3.97±1.31 (87)	0.305	3.76±1.75 (29)	4.22±1.21 (223)	0.170
Flight: tailwind component (m/s)	–0.55±6.38 (45)	–0.10±5.60 (87)	0.649	–0.43±3.56 (29)	–2.57±4.91 (223)	0.004
Orientation: cloud cover (*x*/8)	5.51±2.76 (45)	4.69±2.70 (87)	0.043	5.17±2.84 (29)	3.89±2.29 (223)	0.019

sulting in TWC) (Table 4, Fig. 6a). Scandinavian birds departed when headwinds were significantly stronger (a more negative TWC) compared to staying individuals (Table 4). For both subspecies, cloud cover was signifi- cantly larger for staying birds than for departing birds (Table 4) and the majority of stays coincided with a near- ly completely overcast sky (7–8/8; Fig. 6b). Thus visibil- ity appeared to be an important factor in the decision to depart. This was further illustrated when combining TWC and cloud cover (Table 5): the percentage of departing Greenland/Icelandic birds was considerably lower with a completely overcast sky, and when both weather variables were unfavourable, only a few *O. o. leucorhoa* departed. By contrast, most Scandinavian birds departed whatever the weather. Only when both weather variables were favourable were no differences between subspecies observed in the percentage of de- parting birds (Table 5).

The factors combined

A logistic regression with the dichotomous result "stay" or "depart" and containing the factors season, fat score, body mass, overcast, wind velocity, TWC, to- tal number of raptors and total number of northern wheatears was calculated for both subspecies separate- ly. For Scandinavian birds, the model was based on two significant parameters (season and fat; Table 6) and classifies 90.4% of all individuals (*n*=250) correctly. Thus, only two out of six parameters identified as im- portant in the single factor analyses were included in the model. For Greenland/Icelandic birds, the model gave a correct classification for 69.7% of the 132 birds and was based on three significant factors (TWC, num- ber of wheatears, number of raptors; Table 6), of which only one was significant when looking at the factors separately.

The decision to departure at the end of a stopover

For the birds staying at least 1 night, for some factors a comparison between the day of departure and the day before departure was made to investigate the role of improvements in flight conditions or deterioration in stopover conditions.

Foraging

Due to sample sizes, the number of northern wheatears present was the only factor allowing analysis. Whereas for most Scandinavian birds, no major changes occurred in conditions in the last 2 days of their stay, the majority of Greenland/Icelandic birds left with an increasing density of conspecifics (Table 7).

Predation risk

Although more northern wheatears departed after an increase rather than after a decrease in the number of raptors, the majority did not experience changing conditions in predation risk. No difference was found between the two subspecies (Table 7).
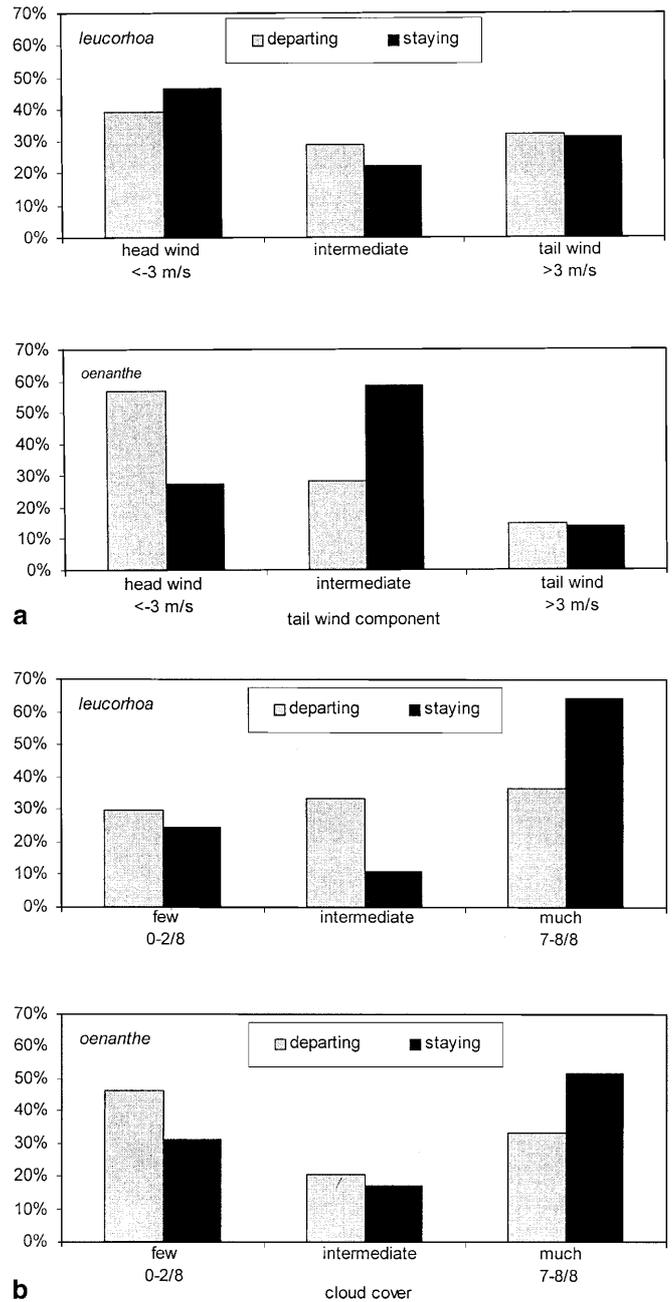
Weather

For both subspecies, wind force decreased during the 2 days before departure for most individuals (Table 7).

Table 5 Percentages of northern wheatears departing from Helgoland under different combinations of wind assistance [*bad* tailwind component (TWC)<−5m/s] and visibility of sky (*bad* cloud cover 7–8/8). Sample sizes are given in *parentheses*

	Wind assistance			
	Good	Bad	Good	Bad
	Visibility of sky			
	Good	Good	Bad	Bad
O. o. leucorhoa	79% (56)	73% (15)	57% (53)	25% (8)
O. o. oenanthe	90% (108)	95% (55)	81% (73)	94% (16)
P (Fisher's exact test)	0.060	0.034	0.005	0.001

Fig. 6 Effects of wind assistance (**a**) and cloud cover (**b**) on the departure of northern wheatears on Helgoland in spring

Table 6 Logistic regression models classifying northern wheatears as staying ("0") or departing ("1"). The factors wind force, overcast and body mass were not contained in any model

| | *O. o. leucorhoa* | | | *O. o. oenanthe* | | |
	Coefficient	SE	*P*	Coefficient	SE	*P*
Season (five-day-period)				0.404	0.079	0.001
Fat score				0.616	0.234	0.009
TWC	0.082	0.041	0.047			
Number of raptors	−0.113	0.050	0.024			
Number of northern wheatears	0.026	0.010	0.009			
Constant	0.205	0.412	0.618	−8.807	1.910	0.001
Model	χ^2=10.46	*df*=3	0.015	χ^2=42.18	*df*=2	0.001
Cases classified correctly		69.7%			90.4%	

Table 7 Differences in factors possibly affecting departure decisions of northern wheatears between the day of departure and the preceding day. The number of birds is given for each category. *P* refers to differences between subspecies (χ^2-tests)

	O. o. leucorhoa			*O. o. oenanthe*			*P*
	Deteriorating	Unchanged	Improving	Deteriorating	Unchanged	Improving	
Cloud cover	4 (9%)	27 (60%)	14 (31%)	7 (24%)	10 (34%)	12 (41%)	0.061
Wind force	13 (29%)	5 (11%)	27 (60%)	9 (31%)	3 (10%)	17 (59%)	0.979
TWC	15 (33%)	10 (22%)	20 (44%)	18 (62%)	5 (17%)	6 (21%)	0.043
Total number of raptors	16 (36%)	22 (49%)	7 (16%)	10 (34%)	12 (41%)	7 (24%)	0.635
Total number of wheatears	26 (58%)	9 (20%)	10 (22%)	7 (24%)	19 (66%)	3 (10%)	<0.001

When including wind direction, the majority of Scandinavian birds departed despite a decreasing TWC, whereas *O. o. leucorhoa* birds behaved indifferently, with only one-third of all individuals departing after deteriorating wind conditions (Table 7). Again, an overcast sky seemed to be more important than wind: only 9% of Greenland/Icelandic birds departed when cloud cover increased whereas the remaining 91% did so with unchanged or improving conditions (Table 7). The same trend was observed in the subspecies *O. o. oenanthe*, but a larger percentage departed after increasing cloud cover (Table 7).

Discussion

Stopover strategies of northern wheatear subspecies

The results of this study clearly demonstrate differences in the strategies of migration and stopover shown by two subspecies of northern wheatear with very different migration routes. Birds heading towards Scandinavia do not have to prepare for a long-distance flight. They depart soon after arrival and if staying, they feed less intensively than Greenland/Icelandic birds and do not defend feeding territories. Fat depots are sufficient to reach Scandinavian coastlines in one flight, and individuals staying on Helgoland are often those with poorer fat reserves. Since Scandinavian birds depart irrespective of the flight and orientation conditions, their priority seems to be early arrival in the breeding area, which enhances breeding success and recruitment of offspring, at least for males (Currie et al. 2000). The priority of early arrival for Scandinavian birds is further demonstrated by the fact that birds touching Helgoland early in the spring migratory season stayed beyond the day of ringing, whereas from mid April onwards, almost all birds departed immediately. The advantage of a more relaxed migration in March and early April might be to avoid the risk of death due to harsh weather further north (Møller 1994). However, that Scandinavian northern wheatears are time-minimizers as defined by the optimal migration model remains to be proven, because retraps showing a correlation between fuel deposition rate and departure fuel load (Alerstam and Lindström 1990) are lacking.

Greenland/Icelandic northern wheatears, in contrast, adjust their stopover behaviour to the demands of a long-distance flight. Foraging in *O. o. leucorhoa* birds is more intense than in *O. o. oenanthe* and territories at good food patches food seem to guarantee rapid fattening. Many birds were already fatter and heavier than Scandinavian birds at the first trapping, and observed lengths of stay and rates of mass gain suggest that most Greenland/Icelandic birds leave Helgoland with large fuel loads. Departures are timed with respect to weather and, especially, orientational conditions. Misorientation would have severer deflection consequences for birds on long- than on short-distance flights. However, whether birds can expect better conditions during the flight allowing them to correct orientation is not clear.

Another important criterion in departure conditions seems to be the foraging conditions. At high-quality habitats, birds stay for several days or more, whereas unfavourable sites, such as the grassland habitats in this study, are left more or less immediately (Delingat and Dierschke 2000). High densities of northern wheatears, which probably cause much interference, also lead to quick departures. Therefore, some *O. o. leucorhoa* birds seem to leave Helgoland with low amounts of fuel, which are not sufficient for reaching the breeding area in a non-stop flight. If flying a direct route, Scotland can be used as stopover site. However, assuming that *O. o. leucorhoa* birds winter in West Africa (Cramp 1988; Glutz von Blotzheim and Bauer 1988), at some point, those individuals in Helgoland have to shift their spring migratory direction from north-east to north-west. Some birds may continue on a north-easterly or northerly course and switch to the north-west in southern Norway, where good numbers of *O. o. leucorhoa* occur in spring (Haftorn 1971). Most Greenland/Icelandic northern wheatears may switch to north-westerly routes earlier and touch the British Isles (Cramp 1988) or cross the Atlantic in a direct flight from the Iberian Peninsula or even Morocco, as observed, in reverse, during the autumn migration (Snow 1953; Luttik and Wattel 1979; K. Thorup, personal communication).

Variation in departure body mass of Greenland/Icelandic birds could be due to different individual strategies in the timing of fuelling (Schaub and Jenni 2000a). Starting in West Africa, birds might keep fuel loads low and increase them only immediately before crossing a large ecological barrier, or they may slowly accumulate reserves during the journey. Those birds should leave Helgoland with low or intermediate levels of body mass,

but have to stopover again (probably in Scotland or Norway, see above) before the flight to Iceland or Greenland. Another strategy, as shown for sedge warblers, *Acrocephalus schoenobaenus*, during autumn migration (Bibby and Green 1981; Schaub and Jenni 2000b), would be to fuel up opportunistically wherever a high-quality feeding site is found and initiate a non-stop flight from that site without any further stopover before reaching the goal area. This strategy would fit for those Greenland/Icelandic Wheatears which stay for a long period and establish territories at the patches of rich food supply on Helgoland beaches. This may be a general strategy of *O. o. leucorhoa* birds in spring, but individuals unable to compete for territories do not experience a high-quality site and therefore depart with lower fuel loads.

Factors affecting departure decisions

Although a number of studies have considered a single or a few factors when analysing departures of migrant passerines, this study allows us to study the relationship of many variables with flight distance. The time-of-season factor was discussed above, and other passerine species behave similarly, staying longer early in the spring migratory season (Rabøl and Petersen 1973; Dinse 1991). The effect of body condition seemed to be low in northern wheatears at Helgoland, but in Scandinavian birds, a tendency to stay when fat reserves are low was noted, fitting into general results obtained elsewhere of a lower percentage of weaker birds departing compared to heavier birds (Petersen 1972; Rabøl and Hansen 1978; Cherry 1982; Moore and Kerlinger 1987; Sandberg et al. 1991). When discussing body condition, one must consider that the birds stopping over are perhaps not a random sample of those birds migrating across the North Sea. Although disproportionate landing of weak birds cannot be excluded in the case of northern wheatears, results from other Scandinavian species trapped on Helgoland show very slight, if any, differences in body condition between individuals stopping over and those departing early in the morning (i.e. departing without refuelling) or killed during migration at towers (lighthouse, telecommunication tower) at night (V. Dierschke and F. Bindrich unpublished data). Whether this is actually true for Greenland/Icelandic northern wheatears as well has not yet been established.

Indirect measurements of feeding conditions used in this study were probably too inaccurate to demonstrate the role of refuelling possibilities in departure decisions. Taking into account the general habitat quality, with high departure rates from the poor grassland habitat and a high tendency to stay in the favourable beach habitats (Delingat and Dierschke 2000), then the opportunity to refuel obviously affects the timing of departure. Food supply has been shown to influence departures of migrating birds in the field (Petersen 1972; Bibby and Green 1981) and in experiments (Biebach 1985; Gwinner et al. 1985; Thalau and Wiltschko 1987), and birds landing at unsuitable habitats after a migratory flight leave quickly (Cherry 1982; Bruderer and Jenni 1988; Moore et al. 1990; Jenni 1996; Morris et al. 1996). The results of this study also imply that density of conspecifics is a further habitat quality factor assessed by the birds. High densities cause interference during foraging and thereby limit the amount of food available to an individual. This effect is reinforced when some individuals defend territories and keep conspecifics away from profitable feeding patches. Our results with northern wheatears are in line with high percentages of departing robins, *Erithacus rubecula*, at high robin densities on a small Danish island in spring (Rabøl and Hansen 1978), and low rates of settling in autumn migrating pied flycatchers, *Ficedula hypoleuca*, in a Spanish stopover site when many conspecifics already held territories (Veiga 1986).

Predation risk and its effect on departure decisions of migrating passerines has not been previously studied in the field. The number of raptors was included in the logistic regression model for *O. o. leucorhoa*, but perhaps wheatears and raptors occurred simultaneously simply due to favourable migration conditions for both bird groups (numbers of both subspecies of northern wheatears were correlated with the number of raptors: *O. o. oenanthe* Kendall $\tau=0.27$, $P=0.001$, $n=252$; *O. o. leucorhoa* Kendall $\tau=0.15$, $P=0.018$, $n=132$). In our opinion, the avoidance of predation might be overruled by the necessity to refuel rapidly and optimize arrival time in the breeding area. As shown in turnstones (*Arenaria interpres*: Metcalfe and Furness 1984) and red-eyed vireos (*Vireo olivaceus*: Moore 1994), birds are less vigilant or cautious against predators when refuelling is an urgent demand; however, raptor-safe habitats are preferred by migrating bramblings, *Fringilla montifringilla*, despite a lower intake rate, when a choice was available (Lindström 1990). If intake rates on a daily scale impact on the departure decision in northern wheatears on Helgoland, then the presence of raptors could have an indirect effect. During raptor flights, wheatears often responded with phases of freezing of up to 30 min (V. Dierschke, unpublished data) and this loss of feeding time could considerably decrease the amount of energy ingested during the day when many raptors are present.

Wind conditions did not seem to play a major role in the departure decisions of northern wheatears on Helgoland. This might have been expected for Scandinavian birds with a short flight to the next possible stopover sites, because similar results have been found in other short-flight situations (Rabøl and Hansen 1978; Fransson 1998). On the other hand, autumn migrant passerines were found to depart for migratory flights after improving TWC (Åkesson and Hedenström 2000). Although included in the relevant logistic regression model, for Greenland/Icelandic birds we expected a more distinct effect of wind conditions on departures. For long oversea flights, taking advantage of tailwinds has been shown to be essential for other long-distance migrants crossing ecological barriers to reach their destinations (Piersma

and van de Sant 1992; Izhaki and Maitav 1998; Clark and Butler 1999). In addition, storms during oversea flights can cause substantial mortality, as suggested for many Neotropical migrants breeding in North America (Butler 2000). Perhaps, the *O. o. leucorhoa* birds moving towards Norway are less vulnerable to adverse wind conditions.

Given that visual cues are important in the orientation of migrating birds (Åkesson and Bäckman 1999) it was not surprising to find that overcast conditions were an important factor in the departure decisions of northern wheatears. A similar result was found for spring migrating robins on a Danish island (Rabøl and Hansen 1978). In contrast, in release experiments, northern wheatears departed from Greenland in late summer even when the sky was completely overcast (Ottosson et al. 1990), and a telemetry study in southern Sweden found no influence of visibility conditions on the departures of various passerines (Åkesson and Hedenström 2000). It is worth noting that on Helgoland, of the few remaining Scandinavian northern wheatears, many departed during completely overcast conditions.

In this study, birds with almost the same morphological features, stopping over in the same habitats with opportunities to use the same food supply and experiencing the same risk of predation and weather conditions behaved very differently in several respects. Because the migration route and the length of the impending flight are the only differences among the wheatears occurring on Helgoland, they have to be taken into consideration when modelling the optimality of bird migration.

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