For centuries, the seasonal arrival and departure of bird species to and from their breeding grounds remained a mystery. Although these events were described by early observers such as the wall and floor painters of ancient Egypt, Aristotle and the Emperor Friedrich von Hohenstaufen (who recognised that, in the northern hemisphere, birds moved south in autumn and north in spring), very little information was available about particular origins or destinations, although there were some intriguing clues. One example concerns a female White Stork Ciconia ciconia that was observed and later shot at its nest in Mecklenburg, northeast Germany, on 21st May 1822; embedded in the bird was an 80-cm long spear of the type used by tribes in central Africa (plate 48; Kinzelbach 2005). This was the first evidence that migrating White Storks winter in tropical Africa.

The study of bird migration by ringing

Our knowledge of bird migration improved dramatically with the development of bird ringing, first practised by the Danish school teacher Hans Christian Cornelius Mortensen in 1899 (Jespersen & Tåning 1950; Bairlein 2001). For the first time, birds were ringed in a concerted effort to unravel the mystery of their movements, although bird ringing had occasionally been used for that purpose in earlier times (Bairlein 1999). After Mortensen, systematic ringing for the study of bird migration was first introduced by Johannes Thienemann in 1903, at the newly founded (in 1901) ‘Vogelwarte Rossitten’ on the Courish Spit, on the east shore of the Baltic (Stresemann 1951). Although ringing was much criticised by animal welfare protestors at that time, its development for the study of migration continued, and with great success. Also in 1903, bird ringing began...
at the Hungarian Centre for Ornithology. In 1909, Hugo Weigold started ringing birds on the island of Helgoland, Germany, while H. F. Witherby and A. Landsborough Thomson first introduced ringing in Great Britain that same year. It was also in 1909 that the first birds were ringed in the USA, but systematic ringing in North America started only in 1920, with the collaboration of the US Fish and Wildlife Service and the Dominion Wildlife Service of Canada. Organised ringing began in Switzerland in 1911, in Sweden in 1912, in The Netherlands and France in 1914, and in Finland in 1916. Subsequently, bird ringing gradually developed as a routine technique used by avian scientists worldwide and many countries founded ‘Ringing Centres’.

Since migrating birds ignore political boundaries, international collaboration in the study of bird migration was essential. Consequently, in 1963, the national Ringing Centres in Europe founded the ‘European Union for Bird Ringing’ (EURING); they agreed on a common code to computerise ringing and recovery data, and to gather recovery data in a centralised database. The EURING database was established and maintained at the Dutch Ringing Centre in Heteren until 2005, when it was moved to the BTO in Thetford, Norfolk.

Currently, the EURING database contains details of some 2.3 million recoveries (Chris du Feu pers. comm.), an extraordinary resource for the analysis of bird movements (for details see www.euring.org). Such an effort would not have been possible without the many enthusiastic volunteer ringers whose spare-time activities are so important for avian science. These volunteers are trained to extremely high levels, the training being co-ordinated by national ringing centres, and participate in targeted scientific projects. This degree of collaboration between professional and amateur ornithologists is unique among biological sciences worldwide.

For many decades, the major interest in and objective of bird ringing was to understand the migration routes and non-breeding distribution of birds. As early as 1910, Thienemann published the first 35 recoveries of ringed White Storks, while, in 1929, von Lucanus compiled several hundred recoveries of 127 species and identified the major migration routes of European birds. The first ‘Migration Atlas’ was published by Ernst Schüz and Hugo Weigold in 1931, and contained 262 maps showing some 9,200 recoveries of 151 species. After about 100 years of bird ringing, various migration atlases have now been published, either nationally (Yamashina Institute for Ornithology 1996; Fransson & Pettersson 2001; Wernham et al. 2002; Bakken et al. 2003 & 2006; Bønløkke et al. 2006) or internationally (Zink 1973–1985; McClure 1974; Zink & Bairlein 1995); these and the many papers which have analysed recoveries of single species or species groups have unveiled many of the former mysteries of bird movements (Bairlein 2001).

New techniques

In recent years, new techniques have supplemented bird ringing and even widened its scope for establishing migratory routes (Bairlein 2003). One of the most widely used of the new methodologies for tracking the routes of individual migrants is that of satellite telemetry, and numerous studies have been conducted. This enables a much more detailed spatial and temporal resolution of avian migrations and helps to identify migratory routes, stopover sites and wintering grounds, especially of birds for which comparatively few recoveries are available or could be obtained, such as larger or rare species. The technique has so far been applied only to comparatively large species (e.g. storks (Ciconiidae), cranes (Gruidae), geese (Anatidae), raptors), owing to the weight of the transmitters, but miniaturisation of transmitters and improved receiver sensitivity is likely to enable application to smaller species. Geolocation (GLS) and Global Positioning System (GPS) are two other new tools to track migrating birds on a worldwide scale (von Hünerbein et al. 2000; Weimerskirch & Wilson 2000; Gauthier-Clerc & Le Maho 2001; Wilson 2001). Geolocation is based on real-time measurement of ambient light intensity to determine geographic co-ordinates, while GPS receives data from satellites for calculating a bird’s position. Initially, these techniques required an archival tag on the bird to collect the data and subsequent recapture of the bird and recovery of the logger. However, recent developments to link GLS and GPS to satellite transmitters allow the stored data to be downloaded without recapture. Biotelemetry and bio-logging have become challenging new tools in the study of bird movements and bird behaviour (for reviews see Cooke et al. 2004, Ropert-Coudert & Wilson 2005).

In addition to electronic wizardry, recently established chemical and molecular markers may be used to establish the origin of migrants and to delineate bird migration routes (Webster et al. 2002). The earth’s surface varies in its chemical composition. Through diet, birds carry a signature of that chemical composition in their tissues. Stable isotopes are found to function as natural markers and provide new insight into the location histories of highly mobile animals by delineating the origin of birds feeding in areas where diets differ in isotope composition (e.g. Hobson & Wassenaar 1997, Alisauskas et al. 1998, Bensch et al. 1999, Hobson 1999, Chamberlain et al. 2000, Rubenstein et al. 2002, Hobson 2003, Lott et al. 2003, Bearhop et al. 2003, Yohannes et al. 2007). Similarly, trace-element composition of plumage can be used to identify the origins of migrating birds (e.g. Parrish et al. 1983, Szép et al. 2003).

Innate migratory behaviour

In recent decades much has also been revealed about the endogenous control of avian migrations (for reviews see Alerstam 1990, Gwinner 1990, Berthold 1996, 2001, Bairlein et al. 2002, Berthold et al. 2003). For their first outbound migration, young migrants appear to be equipped with an innate knowledge about timing, distance, direction and energetic demands. They are capable of finding their way by using external means of orientation – the sun, the stars, or the earth’s magnetic field (e.g. Wiltschko & Wiltschko 2002, 2003). The vast quantities of data gathered during a century of modern bird migration research might suggest that there is not much left to be explained. However, there is still much to be explored with respect to migration routes and

Fig. 1. A complex set of factors is involved in shaping an innate migration template into realised migration. The order of the factors does not imply a hierarchy of relevance.
The distribution of migrants, migration systems, winter ecology of migrants, the integration of migration in the annual cycle of a migratory species, and life-history aspects of migration (Bairlein 2003; Piersma et al. 2005). The remainder of this paper will focus on a case study with Northern Wheatears Oenanthe oenanthe, which illustrates that bird migration research is still a dynamic subject.

The factors affecting migration – a case study with Northern Wheatears

In order to understand migration and to reveal different migration strategies, we need to learn more about the external factors which affect migration and which mould an innate template into actual migration patterns (fig. 1).

Recent theories predict that, in order to optimise their migration, birds should minimise either the time spent on migration or their total energy expenditure, and that predation risk is a further criterion to be considered (Alerstam & Lindström 1990; Alerstam & Hedenström 1998). While migrating, birds spend about 90% of the entire migration period at stopovers in order to store or to replenish fuel for the next flight (Hedenström & Alerstam 1997); the flight itself is of only minor importance in terms of time. Consequently, understanding stopovers and how birds adjust stopover decisions with respect to their migration strategy is crucial to an understanding of how migrating birds organise their journey.

For migratory birds, the timing of their arrival on the breeding grounds (in relation to their competitors) is an important factor affecting breeding success (e.g. Currie et al. 2000, Smith & Moore 2005). If birds are under time pressure, the rate of fuel deposition and the bird’s departure fuel load are the two major factors affecting departure decisions (Alerstam & Lindström 1990). Birds maximising the speed of migration (i.e. minimising the time spent on migration) should leave a stopover site quickly if food is not easily available – in theory at the point when fuel deposition rate is too low for the bird to reach the expected average speed of migration for the whole journey (Alerstam & Lindström 1990). However, 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 species are restricted in their choice of stopover sites, either because suitable habitats are scarce or distributed patchily, or because ecological barriers like oceans or deserts hinder resting and/or refuelling. Thus, prior to embarking on a flight across an ecological barrier, birds have to prepare for a long-distance flight by intense fuelling. For successful fuelling, birds rely on an appropriate supply of food (in terms of quality as well as quantity; Bairlein 2002). During a migratory stopover, a bird does not necessarily find the kind of habitat which fits all its requirements. Consequently, after landing, a bird has to establish whether conditions at a site are sufficient for refuelling, and it must evaluate the pros and cons of staying there or continuing in the hope of finding better habitat elsewhere. If a bird does not find adequate conditions for refuelling and/or surviving at a given site, it should leave quickly and this decision is particularly important for birds facing an ecological barrier. Successful migration also involves predator avoidance and the ability to interpret weather conditions at take-off, but studies examining these complex inter-relationships are scarce.

In order to investigate the effects of imminent long-distance flights on stopover behaviour and departure decisions, researchers at the Institute of Avian Research are studying the Northern Wheatear. This nocturnal, long-distance migrant has a nearly circumpolar distribution and a fascinating migration system (fig. 2). On migration it occurs in a variety of
lowland habitats including meadows, arable land, beaches and other habitats with sparse vegetation (Cramp 1988; Glutz von Blotzheim & Bauer 1988). In the northern breeding range, two subspecies are distinguished, both of which overwinter in Africa. Nominate *oenanthe* breeds in Great Britain and in an area ranging from continental Europe via Siberia as far east as Alaska (Cramp 1988). ‘Greenland Wheatear’ *O. o. leucorhoa* breeds in Iceland, Greenland and eastern Canada and is one of the few passerine migrants regularly covering distances of more than 1,000 km over sea.

During both autumn and spring migration, the two subspecies occur together at stopover sites in northern and western Europe, including Helgoland, where *oenanthe* of Scandinavian origin mingle with *leucorhoa* breeding in Greenland and Iceland (Dierschke & Delingat 2003). Whereas Scandinavian birds face sea crossings of only 50–150 km when heading northeast 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 (c. 1,000 km) or their breeding areas (up to 2,500 km). Because such long flights require sufficient preparations, one hypothesis is that *leucorhoa* adjust their stopover behaviour more carefully for intense fuel deposition than do *oenanthe* before their (relatively) short-distance flights. Furthermore, *leucorhoa* would be expected to be more selective in terms of weather conditions at departure because strong headwinds and orientation errors would have a much greater impact on long-distance flights than short-distance ones.

As a bird of open landscapes, Northern Wheatear is a convenient study species that can be easily trapped using baited spring traps (plate 49) and many individuals can be identified to subspecies in the hand (Svensson 1992). Once colour-ringed, they are easy to observe at stopover sites owing to their habitat choice and visibility. Moreover, they can be attracted to remote-controlled baited balances placed in their habitats (plate 50) so that data on refuelling can be gathered without retrapping the birds. Helgoland is a small island of some 150 ha in the southeastern North Sea (54°11'N 07°55'E), 53 km off the mainland coasts of Schleswig-Holstein and Lower Saxony and 43 km from the nearest Wadden Sea island of Wangerooge (also part of Germany), which offers various stopover habitats for Northern Wheatears. Apart from the village and some small bushy areas, most of the island is open habitat and Northern Wheatears generally occur in two main habitat types: sandy beaches with beds of rotting brown alga, 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 for
food (Delingat & Dierschke 2000). These circumstances and the general habits of Northern Wheatears make the entire set-up unique for examining the stopover behaviour and decisions of a migrant species.

**Phenology**

On Helgoland, Northern Wheatears occur from late March to early June, peak spring migration being in early May, and from late July to early November, peak autumn migration being between late August and mid September (Dierschke & Delingat 2003; Dierschke et al. 2005). Compared with nominate *oenanthe*, *leucorhoa* migrate earlier in spring and later in autumn. In spring, the median dates of trapped birds are 2nd May for *leucorhoa* and 7th May for *oenanthe*; in autumn, the comparative dates are 11th September and 31st August respectively. In spring, males migrate earlier than females in both subspecies, although significantly so only in *leucorhoa*, for which the median date is 27th April for males and 4th May for females. During the early part of autumn migration, including the first peak in late August/early September, *oenanthe* occurs almost exclusively, while from mid September onwards *leucorhoa* is more prominent and outnumbers *oenanthe* in the latter part of the autumn.

**Habitat use**

As described above, two different habitats are available to migrant Northern Wheatears on Helgoland: beach and grassland. In terms of their suitability for stopover wheatears, they differ in various respects. In spring, the two habitats were used equally but in autumn an increasing proportion of wheatears in beach habitats was attributed to declining food supplies in grassland habitats compared with wrack beds on beaches with their abundant kelp flies (Delingat & Dierschke 2000). The proportion of wheatears found in grassland was significantly correlated with the number of invertebrates collected in net sweeps; and the latter measure declined during autumn migration. Conversely, the proportion of wheatears observed in beach habitats increased with estimated abundance of kelp fly larvae. In spring, pecking rates tended to be higher in grassland (6.4 pecks/two-minute period in grassland compared with 4.4 on the beach), but were significantly higher on the beach in autumn (9.8 on beaches versus 6.5 in grassland; Delingat & Dierschke 2000). The density (birds/ha) of wheatears was generally much higher in beach habitats.

Individually colour-ringed birds revealed different patterns in utilisation of the two habitats. Grassland birds were transient and explorative and most individuals departed on the day of arrival; they were characterised by high mobility on the island, having significantly larger dispersal distances than beach birds. In contrast, a higher proportion of beach birds stayed for at least one night and remained rather stationary, often exhibiting territorial behaviour, which was rare in grassland birds. Territories on beaches contained patches of wrack (up to 250 m²) and these were defended against conspecifics and other passerines. On beaches, 34% of the wheatears showed aggressive encounters, but only 3% did so in grassland. Wheatears do not seem to settle in grassland; instead they switch to the more profitable beaches if they remain on the island. A greater proportion of Northern Wheatears stayed in the beach habitats and stopovers were longer on beaches than in grassland (Dierschke 2003). These data clearly reveal the role of habitat quality in stopover decisions.

**Length of stopover and body condition**

Food availability at stopover sites and the resulting gain in body mass per day (fuel deposition rate) are expected to play a major role in optimal behaviour decisions. Time-minimising migrants aim to feed as quickly as they can and move on rapidly, and would thus be expected to show a positive correlation between fuel deposition rate and departure fuel loads; while energy-minimising migrants will remain at a stopover site for as long as it takes to reach their optimum fuel load for the next leg of the journey, regardless of fuel deposition rate (Alerstam & Lindström 1990).

In spring, the two subspecies of Northern Wheatear on Helgoland differ in the respective proportion of birds staying on the island, and their length of stopover. In *oenanthe*, 9% of males and 14% of females did not depart on the day of ringing, while in *leucorhoa* 40% of males and 30% of females stayed on the island for at least one day. However, a greater proportion of early migrating *oenanthe* stayed compared with late migrating *oenanthe* (Dierschke & Delingat 2001). For birds which stayed on the island, the length of stopover did not differ significantly between the subspecies, although many
oenanthe stayed for only one day, while most of the long-stayers were leucorhoa.

At first capture, most oenanthe showed low to moderate fat scores (scores 1–4 on a scale of 0–9; Kaiser 1993), whereas 15% of leucorhoa were very fat and scored 5–7, although the average fat scores did not differ significantly between subspecies (Dierschke & Delingat 2001). Moreover, the breast muscle score (Bairlein 1994) did not differ between subspecies. However, standardised body mass (adjusted for size differences, since leucorhoa is on average larger than oenanthe) was significantly higher in leucorhoa (26.8 ± 5.7 g, n=138) than in oenanthe (24.4 ± 2.1 g, n=210). When foraging in beach habitats, wheatears gained mass by 1.7 g per day in spring (fig. 3) and 1.8 g per day in autumn, which is close to the maximum rate of mass increase in a passerine of that size (Lindström 1991). Since leucorhoa stay longer, the difference in body mass between the two subspecies at departure is much larger than on the day of ringing.

Fuel deposition rate and departure fuel load
Changes in body mass during stopovers are generally difficult to measure using capture and recapture efforts so, to examine the relationship between food availability, fuel deposition rate and departure fuel load, supplementary food (bowls with mealworms) was provided. These bowls were attached to digital scales and the body mass of colour-ringed birds visiting these feeders could be read from a distance to the nearest 0.1 g, using binoculars or a telescope. During the experiment, the scales were observed daily throughout most daylight hours.

During their stay, wheatears used this unlimited food supply for fuel deposition. The relationship between fuel deposition rate and departure fuel load in spring differed between the two subspecies, and tended to differ also between males and females in leucorhoa (Delingat et al. 2006; fig. 4). For male leucorhoa, the relationship between fuel deposition rate and departure fuel load is strongly positive (and almost statistically significant), so this group can be considered time-minimisers (Alerstam & Lindström 1990). Female leucorhoa tended to show a weaker relationship between fuel deposition rate and departure fuel load, reflecting a compromise between time- and energy-minimising; while oenanthe leave the island at a particular departure fuel load, irrespective of fuel deposition rate, an energy-minimising...
strategy. But female *leucorhoa* leave the island with a higher fuel load than *oenanthe*, which reflects the difference in onward migration distance.

The two subspecies are able to accumulate fuel at the same rate (fuel deposition rate; Delingat *et al*. 2006) but show significant differences in their departure fuel loads. Most *leucorhoa* left the island with a much higher fuel load compared with their arrival, but male *oenanthe* (there are few data for females) increased their stores only slightly (Dierschke *et al*. 2005; fig. 5). The rate of refuelling for the whole stay was similar in both male (0.133 g/day) and female (0.135 g/day) *leucorhoa*, but lower in male *oenanthe* (0.083 g/day). (Note that fuel deposition rate as given here is a relative measure of body mass gain, calculated by dividing body mass gain by lean body mass. Lean body mass is the estimated body mass without visible fat – see Delingat *et al*. 2006.) In *leucorhoa* with a stopover length of more than two days, departure fuel load ranged from 0.497 to 1.102 in males (mean 0.856) and from 0.554 to 0.828 in females (mean 0.695) (note that departure fuel load is also a relative measure: a fuel load of 0.5 means that the bird’s weight is 50% above lean body mass). Departure fuel load was not correlated with wing length (body size) nor with a dominance index which reflects the wins and losses in intraspecific aggressive interactions observed at the mealworm bowls (Dierschke *et al*. 2005). Departure fuel load in female *leucorhoa* was lower than for males, but nonetheless sufficient to enable them to bypass stopover sites en route. Thus, time selection seems to be more pronounced in males and may be the reason why males migrate earlier. However, females are not able to reach Greenland without additional refuelling elsewhere, which supports the idea that female *leucorhoa* adopt a compromise strategy of time- and energy-minimising. Intraspecific aggressive interactions between colour-ringed birds were predominantly won by the initiator, by males and by larger birds; fuel load and subspecies did not affect the outcome. Although, compared with 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 compensated by 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 males and females (of course, this result may be species-specific).

**Time allocation**

In order to identify factors which influence time budgets, and thus possibly limit the refuelling of passerine migrants, the time allocation of Northern Wheatears on Helgoland was examined (Dierschke *et al*. 2003). Full-day observations revealed that Northern Wheatears on stopover spent 51–67% of the daylight period foraging. Large parts of the day were also spent resting or being vigilant, whereas flying, preening and aggressive behaviour were of minor importance. The density of wheatears did not influence the time devoted to foraging and aggressive behaviour, and the time spent resting/being vigilant was not correlated with

![Fig. 5. Arrival fuel load (white) and departure fuel load (grey) of subspecies and sex classes of Northern Wheatear *Oenanthe oenanthe* on Helgoland in spring for birds staying at least two days (after Dierschke *et al*. 2005). Departure fuel load is a relative measure – see text, above left.](image)
predation risk (measured by an index of fly-over raptors). Several observations showed that refuelling on beach habitats, which presented the most favourable feeding conditions and allowed high rates of body mass gain, was metabolically limited. The total time devoted to foraging was independent of day length, and supplementary food (mealworms) was completely ignored, indicating that reduced foraging effort would not improve net energy gain. In the poorer grassland habitat, in contrast, there was a marked response to supplementary food. Although this suggests that refuelling is limited by the amount of food available and the costs of obtaining it, foraging times were the same as on the beach. In grassland, the behaviour pattern of birds refuelling was probably distorted by a high proportion of transient and explorative individuals.

Predation risk and stopover

Experiments testing predictions of optimal migration theory have so far concentrated on time and energy as the elements that birds strive to minimise during migration. Taking advantage of the great variation in numbers of migrating raptors over Helgoland, a field experiment looking at predation risk as a possible factor in stopover decisions of migrating Northern Wheatears was carried out (Schmaljohann & Dierschke 2005). Wheatears show time-consuming antipredator behaviour: they either stop feeding when detecting birds of prey and try to hide behind or under stones, or they ‘freeze’ by staying motionless. Freezing usually lasts 1–7 minutes, but can last up to 33 minutes after a raptor flight. Predation risk was assessed by recording all raptors posing a threat to passerines. The daily threat from raptors fluctuated between 0 and 4.7 raptor flights per hour, with a maximum of 53 flights per day. Eurasian Sparrowhawk Accipiter nisus was the most abundant species, accounting for 75% of all flights.

The results showed that predation risk influenced the stopover decision. Birds experiencing more danger showed lower rates of refuelling (fig. 6), indicating that danger indirectly affected the stopover pattern via the effect on fuel deposition rate – time-minimisers avoid stopover sites with low fuel deposition rate when better refuelling conditions may be expected elsewhere (Schmaljohann & Dierschke 2005). Lighter birds were more likely to be predated than heavy birds (Dierschke 2003), indicating that the role of fuel load with respect to predation (in theory, heavy birds should be less able to escape from predators as they are less manoeuvrable) is less important than exposure to predators (in theory, birds in poor condition are more vulnerable to predators because they are forced to spend more time foraging and less time being vigilant).

In addition to this field experiment, a laboratory experiment was carried out (Dierschke & Walter in prep.). Northern Wheatears were trapped under licence and, in the laboratory, were exposed to different degrees of predation danger using a Sparrowhawk model, and either unlimited or restricted (5 g mealworms) food supply, during which time their diurnal and nocturnal activity was recorded. Whether wheatears were active or inactive at night, resembling ‘departing’ or ‘staying’, was dependent on fuel deposition rate, fuel stores, and predation risk. The proportion of ‘departing’ birds was significantly higher among those wheatears exposed to the Sparrowhawk model than those in the other groups. Birds with unlimited food were recorded ‘departing’ to a lesser degree than those with restricted food availability; while ‘departing’ birds had higher evening fuel loads and lower fuel deposition rates than ‘staying’.
birds. Moreover, diurnal activity was significantly higher in birds with low food supply than in those with unlimited food. These data suggest that migrating Northern Wheatears try to leave a stopover site with inappropriate fuelling conditions, even during the daytime, despite the fact that they are normally nocturnal migrants.

Weather and departure
As well as being influenced by stopover-site characteristics, the decision to embark on migratory flight is affected by weather: strong headwinds or drift will increase fuel consumption, while overcast conditions may compromise orientation. During spring migration, wind conditions did not seem to play a major role in the departure decisions of Northern Wheatears on Helgoland (Dierschke & Delingat 2001; Dierschke 2006). However, when a comparison was made between birds staying or departing, cloud cover was significantly greater for the former group (for both subspecies) and the majority of stays coincided with a nearly completely overcast sky. Visibility seems to be an important factor in the decision to depart, which is in line with previous results that visual cues are important in the orientation of migrating birds in general (Åkesson & Bäckman 1999). This was further illustrated when combining tailwind conditions and cloud cover. The percentage of departing leucorhoa was considerably lower with a completely overcast sky. When both weather variables were unfavourable, only a few leucorhoa left the island. By contrast, most oenanthe departed irrespective of weather conditions. Only when both weather variables were favourable were no differences between subspecies observed in the percentage of departing birds.

These results suggest that factors which are probably important in the decision to depart or stay differed between subspecies. In leucorhoa, few birds departed with bad or deteriorating weather conditions (wind and cloud), whereas departures of oenanthe seemed to be little affected by those factors; this may be attributed to the differences in onward migration flight. In summary, almost all oenanthe departed quickly, irrespective of refuelling and weather conditions, whereas many (but not all) leucorhoa seemed to prepare for a long-distance flight and carefully adjusted departure to weather conditions.

Departure direction
A release experiment was conducted to study the departure direction of Northern Wheatears from Helgoland (Dierschke & Delingat 2003). Wheatears trapped in spring during the day were caged until the evening (food and water were provided in captivity). One hour before sunset, the cages were exposed to the natural sky. When the sky was completely dark, the birds were equipped with a 0.16-g activated green lightstick, taped to the two outermost tail feathers. The birds were then released and their departure direction observed and measured to the nearest 5° with a compass. Cloud cover, wind force and wind direction at release were recorded.

Both subspecies showed the same proportion of birds departing immediately after release but differed significantly in their departure direction. Most of the Scandinavian oenanthe departed northwards, while Greenland/Icelandic leucorhoa headed predominantly north-
west (fig. 7). Departure was affected by the weather – many more birds departed with a clear sky and departure was then faster than on evenings with cloud cover.

These data reveal that the southern North Sea is at the northeastern edge of the flyway of *leucorhoa* and one of the last areas where they switch their northerly migration, which starts in western Africa, towards the northwest to reach their breeding grounds. A few may even continue to southern Norway before they switch direction, but (as ringing recoveries reveal) most *leucorhoa* change their spring migration direction at lower latitudes (Zink 1973; Wernham *et al.* 2002).

**European patterns of Northern Wheatear migration**

In order to look at spring migration patterns of Northern Wheatears on a wider scale, departure fuel loads at eight stopover sites across Europe were recorded, and related to flight distance and optimality models (Delingat *et al.* 2006). Mean fuel loads of wheatears at various stopover sites in western Europe were generally rather low, with variability being highest in the North Sea (Wilhelmshaven, northern Germany, and Fair Isle, as well as Helgoland; fig. 8). Results showed that *leucorhoa* carried higher fuel loads than *oenanthe*; differences were moderate when migrating over land but more pronounced when approaching the sea crossing at Helgoland and on Fair Isle. Individual *leucorhoa* on Helgoland were recorded with fuel loads of more than 90% of lean body mass without supplementary feeding. Flight range estimates for *oenanthe* showed that most birds trapped during migration were probably in sufficient condition for a ‘night-long’ flight. Mean fuel loads (see definition on p. 75) were 0.05, which would be sufficient for a 7-hour flight. Fuel loads below 0.11 were shown by 75% of all *oenanthe* and, consequently, they could fly less than c. 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 1,200 km in 28 hours. In other words, most birds on migration over the European continent deposit sufficient fuel to fly at least a few hours each night. Very few birds, especially in southern Europe, deposited sufficient fuel stores to enable them 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 significant barrier has to be crossed.

The data on *leucorhoa* 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 stores.
loads, exceeding by far those that were observed for *oenanthae*. Regarding the importance of arrival date and condition at the breeding grounds for migrating passerines, it seems that selection acts on migratory behaviour to favour a ‘numerous-stops-and-flights strategy’ on migration over continental Europe (Delingat et al. 2006).

**Conclusion and perspectives**

Since their introduction to bird migration research by Alerstam & Lindström (1990), models of optimal bird migration have been tested by very few field studies (Carpenter et al. 1983; Lindström & Alerstam 1992; Fransson 1998a,b). The ongoing study on Northern Wheatears summarised here is the first of sufficient complexity to deal concurrently with various factors that might be involved in the organisation of migration. It is also the first that relies largely on colour-ringed birds and their individually assigned behaviour rather than looking in general at non-marked individuals.

Some of the key findings of this study can be summarised briefly:

- Compared with Scandinavian-bound *oenanthae*, Greenland-/Iceland-bound *leucorhoa* migrate earlier in spring and later in autumn.
- Habitat quality of stopover sites is important; wheatears did not settle in grassland, but used the more profitable beaches, where stopovers were longer.
- A greater proportion of *leucorhoa* than *oenanthae* stayed on the island for at least one day.
- Male *leucorhoa* showed a strong positive relationship between fuel deposition rate and departure fuel load and can be considered time-minimisers; female *leucorhoa* tended to show a compromise between time- and energy-minimising; while *oenanthae* are energy-minimisers.
- Competition during stopover was not responsible for the differential timing of migration of males and females.
- Predation risk influenced stopover decisions and birds experiencing more danger showed lower rates of refuelling.
- Few *leucorhoa* departed in bad or deteriorating weather conditions (wind and cloud), whereas departures of *oenanthae* seemed to be little affected by those factors.

This study confirmed model predictions for time- and energy-minimised migration, but it also showed that the effect of weather on stopover and departure decisions should not be underestimated and might lead to shorter or longer stopovers under favourable or unfavourable weather conditions, respectively, than predicted by the current optimality models (e.g. Alerstam & Lindström 1990, Hedenström & Alerstam 1997, Alerstam & Hedenström 1998, Weber et al. 1999). Moreover, flight route and length of impending flight have to be taken into consideration when modelling optimal bird migration.

This study is the first that links manifold quantitative field and laboratory studies under controlled conditions, so providing a unique opportunity to investigate the interplay between internal (genetic) and external factors in the control of avian migration. This will also help to explain more about flexibility in migratory behaviour and the adaptability of this behaviour to a changing environment – for example, habitat changes on a local, regional and global scale, and climate change. Climate change is affecting bird migration (e.g. Walther et al. 2002, Hüppop & Hüppop 2003, Bairlein & Hüppop 2004, Thorup et al. 2007), although in a very complex manner, and as well as affecting the process of migration itself, this will have consequences for subsequent breeding and demography (e.g. Both et al. 2006a,b). Migration is an integral part of the annual life-cycle and the life-history of a migrant species, and future research should emphasise the relationship between migratory performance and reproductive performance, and vice versa (Bairlein 2003; Drent et al. 2006). These studies would greatly benefit from improved miniaturisation and availability of remote data loggers and receiver platforms so that many birds could be tagged and tracked, and the connectivity between migration and breeding performances evaluated through data based upon individual animals.

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