Morphometrics and stable isotopes differentiate populations of Northern Wheatears (*Oenanthe oenanthe*)

Julia Delingat[1], Keith A. Hobson[2], Volker Dierschke[1], Heiko Schmaljohann[1], Franz Bairlein[1]

1) Institute of Avian Research
An der Vogelwarte 21
26386 Wilhelmshaven
Germany

2) Environment Canada
11 Innovation Blvd., Saskatoon,
Saskatchewan,
Canada S7N 0H3

Corresponding author:
Julia Delingat
jdelingat@gmx.de

Abstract

Linking events of breeding, wintering and stopover areas has important ecological and conservation implications for migratory species. To find a tool to connect these different events in a long-distance migrating songbird, the Northern Wheatear *Oenanthe oenanthe*, we applied a discriminant analysis based on morphometrics and analysed stable isotope values ($\delta^{13}C$, $\delta^{15}N$, δD) in feathers. Morphometric differences were additionally analysed with respect to wing shape as an adaptation to migration routes. Discriminant analysis separated 100% a group of long-winged migrants passing the German offshore island of Helgoland from Icelandic and Norwegian breeding birds, as well as from Northern Wheatears passing the Baltic Sea coast on migration. This clear assignment suggests a Greenlandic origin of these long-winged Northern Wheatears. The most likely Greenlandic origin was further supported by depleted δD values in feathers of these birds grown at the breeding grounds. We found a relatively high proportion of presumed Greenlandic birds on Helgoland and especially on Fair Isle (Scotland) during spring migration. Morphometric differences were based mainly on wing morphology and could be successfully connected with migration routes. Presumed Greenlandic Northern Wheatears showed more pointed wings than birds from other European breeding areas. Such wings might be natural selection's solution for the long obligatory non-stop-flights during the Atlantic crossings.

Keywords: Northern Wheatear; population differentiation; stable isotopes; morphometrics; wing shape

Zusammenfassung

Differenzierung von Populationen des Steinschmätzers (*Oenanthe oenanthe*) mittels Morphometrie und Stabilen Isotopen

Für ziehende Tierarten hat der Zusammenhang von Ereignissen in Brut-, Winter- und Rastgebieten wichtige Konsequenzen für ökologische Aspekte und den Artenschutzes. Um im Falle eines typischen Langstreckenziehers, des Steinschmätzers (*Oenanthe oenanthe*), ein Werkzeug zu finden, um Ereignisse in

den verschiedenen Aufenthaltsgebieten verbinden und verschiedene Populationen ansprechen zu können, haben wir eine Diskriminanzanalyse aufgrund von morphometrischen Daten durchgeführt und Stabile Isotope ($\delta^{13}C$, $\delta^{15}N$, δD) aus Federn analysiert. Morphometrische Unterschiede wurden zusätzlich in Hinsicht auf Adaption der Flügelform aufgrund verschiedener Zugrouten untersucht. An Hand der Diskriminanzanalyse ließ sich eine Gruppe von besonders langflügeligen Durchziehern auf Helgoland vollständig sowohl von Isländischen und Norwegischen Steinschmätzern unterscheiden, als auch von Steinschmätzern, die auf dem Zug an der baltischen Ostseeküste erscheinen. Diese klare Abgrenzung lässt einen Grönländischen Ursprung dieser langflügeligen Steinschmätzer vermuten. Eine Vermutung, die weiterhin durch deutlich abgereicherte δD Werte in Federn, die im Brutgebiet gewachsen waren, unterstützt wird. Wir fanden während des Frühjahrszuges einen relativ hohen Anteil an vermutlich Grönländischen Vögeln auf Helgoland und besonders auf Fair Isle (Schottland). Morphometrische Unterschiede basierten hauptsächlich auf Unterschieden in der Flügelform und konnten mit den unterschiedlich Anforderungen während des Zuges in Verbindung gesetzt werden. Steinschmätzer mit vermutlich Grönländischen Ursprung zeigten spitzere Flügel als Vögel von anderen Europäischen Brutgebieten. Diese Flügel scheinen das Ergebnis natürlicher Selektion innerhalb dieser Population zu sein, die besonders lange nonstop Flüge zur Überquerung des Nordost-Atlantiks bewältigen muss.

Introduction

The establishment of migratory connectivity or the linking of breeding, wintering and stopover sites in migrating birds is an important component of conservation and essential to understanding population regulation. This area of investigation traditionally depended on ring recoveries since the beginning of the last century (e.g. Alerstam 1990; Andersson *et al.* 2001; Bairlein 2001; Fransson 1995). The use of satellite tracking methods are, so far, restricted to larger birds (e.g. Fuller *et al.* 1998; Hake *et al.* 2001; Martell *et al.* 2001) and therefore, hardly applicable for passerines, while geolocators now have reached a size applicable for songbird migration studies (Stutchbury et al. 2009). Within the last two decades new methods have become available including genetic markers (e.g. Haig *et al.* 1997; Wenink and Baker 1996;) and stable isotope compositions to reveal migratory connectivity (reviewed by Hobson and Wassenaar 2008). The stable isotope approach is based on the fact that the stable isotope composition of a consumer reflects its diet and that for certain elements stable isotope values in foodwebs show geographical variation (Hobson and Wassenaar 2008). Since many migrating birds like the Northern Wheatear (*oenanthe oenanthe*) moult at least part of their feathers at the breeding grounds, the analysis of these feathers collected during migration or wintering could give valuable information on the breeding origin of the sampled birds. Previous studies have shown that both δD and $\delta^{13}C$ values in bird feathers varied over a latitudinal gradient in North America (Chamberlain et al. 1997, Hobson and Wassenaar 1997). For δD, it is evident that such patterns found in bird feathers vary with the values for the geographic distribution of δD in precipitation both in North America and Europe and thus may serve as useful tool to track the approximate origins of migratory birds on these and other continents (Kelly *et al.* 2002; Marquiss *et al.* 2008; Rubenstein *et al.* 2002).

Beside these recent techniques, traditional analysis of morphometric parameters can be used as a good predictor for migration distance (Leisler and Winkler 2003). Morphometric data have uncovered evolutionary traits of adaptation, which can be used to assign single birds to their breeding area. A well known example is the evolution of wing morphometry: For example long-distance migrating birds developed more pointed wings than closely related sedentary species (e.g. Alerstam 1990; Kipp 1958; Kipp 1959; Lockwood *et al.* 1998; Mönkkönen 1995). For different bird populations, wing morphology has also proven useful in studies of migratory connectivity, providing geographical segregation of morphotypes (Jenni and Jenni-Eiermann 1987; Ramos and Warner 1980; Tellería and Carbonell 1999; Tellería *et al.* 2001).

A combination of ring recoveries, stable isotope and trace element analyses, molecular markers and morphometric data often reveals a satisfying resolution to explain migratory movements of species, subspecies or even single populations (Bensch *et al.* 1999; Boulet *et al.* 2006; Boulet and Norris 2006; Gómez-Díaz and González-Solís 2007; Mazerolle *et al.* 2005). We, therefore, combined stable isotope analyses with morphometric data to analyse the pattern of migratory connectivity of Northern Wheatears. The Northern Wheatear is a long-distance migratory passerine with an almost circumpolar distribution (Cramp 1988) that winters mainly in Africa South of the Sahara.

One focus of our study was to clarify the origin of Northern Wheatears passing the German offshore island Helgoland with a special focus on a group of very long-winged Northern Wheatears passing the island every spring (Dierschke and Delingat 2003). Secondly, we applied a discriminant analysis to investigate potential separation of Northern Wheatears from Icelandic, Scandinavian, Northeast European and presumably Greenlandic breeding sites and to subsequently assign Northern Wheatears from different stopover sites in Europe to these geographic breeding ranges. We expected that differences in wing morphology between these breeding populations should show some adaptation to specific migration routes. For Northern Wheatears from Greenland and Iceland we hypothesize wing morphometry to be adaptive to long sustained flights and thus expect more pointed wings than in continental populations.

We expected geographical variation in δD of Northern Wheatear feathers with a resolution related to latitude with high-latitude populations showing more depleted feather δD values (Bowen et al. 2005) and less variability in $\delta^{13}C$ and $\delta^{15}N$ values of Northern Wheatear feathers with the possible exceptions of differential influence of access of birds to marine-influenced foodwebs in coastal populations (Hobson 1999, Yerkes et al. 2008).

Study species and methods

The Northern Wheatear has been sub-classified among eight “races“ (Portenko 1954 in Panov 2005). For the Palaearctic breeding range there are currently four recognized races: *O. o. oenanthe*, *O. o. libanotica*, *O. o. leucorhoa* and *O. o. seebohmi* (Cramp 1988, Conder 1989; Panov 2005) that can be distinguished partly by plumage coloration and morphometric differences such as wing length, but overlap in these traits (Svensson 1992). In this study we focused on two subspecies: 1) the nominate form *O. o. oenanthe* breeding from Northwest Europe through Siberia, Alaska and Northwest Canada and as far South as Spain and the Balearic Islands (Conder 1989), and 2) the Greenlandic subspecies *O. o. leucorhoa* breeding from Northeast Canada and Baffin Island eastwards through Greenland, Iceland and Jan Mayen Island (Godfrey 1986). While *O. o. leucorhoa* winters in West Africa from Senegal to Mali, *O. o. oenanthe* has a broader winter distribution from Arabia and East Africa to West Africa South of the Sahara (Cramp 1988). Both subspecies meet at European stopover sites during migration (Dierschke and Delingat 2001; Taylor et al. 1999).

The Northern Wheatear shows a pronounced sexual dimorphism with females having shorter wings than males (Svensson, 1992). This complicates a simple assignment of migrants to their breeding grounds based on wing lengths when a bird's sex is unknowm (as for most juveniles during autumn migration). We therefore determined sex genetically in some first-year birds that were sampled on their first autumn migration. For genetic sexing we extracted DNA from either blood or feathers and followed roughly the protocol from Fridolfsson and Ellegren (1999).

Data collection

Morphometric data

Northern Wheatears were trapped at several breeding and stopover sites in Europe (Table 1). Morphometric measurements for all birds presented in this study were taken by the authors JD, VD or HS and measurements between these ringers were calibrated. We measured wing length (max. wing chord method 3, Svensson 1992) and the 7 distal-most primary feathers following Svensson (1992), excluding the first vestigial feather (called P2-P8 hereafter). Feathers were numbered from distal to proximal. At Ventotene, Wilhelmshaven, Gibraltar and Fair Isle, we measured additionally P9 and P10. We also measured tarsus (method B with bent tarsus, Svensson 1992), bill to skull and tail length in all birds. For tail measurements, we used the same approach as for primary length measurements with a small pin fixed at zero on the ruler. We inserted the pin between the two inner tail feathers. The tail feathers were straightened out at the ruler and the bird's body was held in an angle to the ruler so that a maximum tail length could be measured.

We aimed to define four geographic groups of Northern Wheatears based on the following discrimination traits:

a) Presumed Greenlandic birds which consisted of Northern Wheatears passing Helgoland during spring migration in the years of 1999 and 2002. We regularly found Northern Wheatears passing Helgoland with wing length exceeding those of average Icelandic birds by far (Iceland males: mean wing = 103.5 mm, n = 29; females: mean wing = 100.0 mm, n = 26; this study) and assume that these very long-winged birds originate from Greenland following data from Salomonsen (1934) and Ottoson et al. (1990). To find an objective way to group these "long-winged" Northern Wheatears at Helgoland and to separate these birds in a discriminant analysis from birds of other North European breeding areas, we used a hierarchical cluster analysis for all migrants from Helgoland and for each sex separately. Variables used for the cluster analysis (wing, P2-P8, tarsus, tail and bill) were z-transformed. Squared Euclidian distance was used as a distance measurement and the "Ward method" as a clustering algorithm (Backhaus et al. 1990). Testing other algorithms such as complete-linkage and average-linkage resulted in identical or very similar clusters. In both sexes we found two clusters containing two sub clusters each. We chose the sub cluster including birds with longest wings (males: 104.5-109.5mm, mean 106.6, n = 18; females: 101.5-107; mean = 103.8; n = 19) as the suspected Greenlandic cluster (hereafter "presumed Greenland"). This group of presumed Greenlandic birds was compared with the three following groups of North European Northern Wheatears in a discriminant analysis.

b) Icelandic birds trapped at the end of the breeding season in Iceland,

c) Scandinavian birds trapped at the end of the breeding season in North Norway,

d) Birds passing the Baltic Sea coast at the Biological station Rybachy, Russia, during autumn migration (hereafter "Baltic Sea coast"); these birds were analysed as representatives for Northeast European populations which pass this area and partly mix with Fennoscandian birds.

The group of presumed Greenlandic and Icelandic birds represents Northern Wheatears of the subspecies *O. o. leucorhoa* while birds from Norway and the Baltic Sea Coast belong to the nominate form *O. o. oenanthe* (Cramp 1988).

Morphometric data within each group were normally distributed and homogeneity of covariance matrices was confirmed by a Box *M* test. Groups were weighed according to sample size. To compare relative importance of different variables we calculated mean discriminant coefficients following Backhaus et al. (1990).

A discriminant analysis with four groups leads to three discriminant functions, each of which helped to discriminate between the four groups. After establishing these three discriminant functions for each sex separately we used the discriminant functions to assign birds that were trapped during migration to one of the four groups, which we presumed reflected their breeding origin. We also calculated for each case the likelihood to belong to either of the groups. When assigning birds to geographical regions of origin, we accounted only for such birds that could be assigned to any of the four groups by a likelihood of more than 70 %.

To further unravel morphometric differences between our four geographic regions, as revealed by the discriminant analyses, we investigated Northern

Wheatear wing shape. In order to tackle the problem of allometry and to consider wing-shape parameters independently of different wing size, which is undoubtedly pronounced in Northern Wheatears, we used wing shape indices developed from a size-constrained component analyses developed for 244 bird species by Lockwood et al. (1998). In this study the authors used size-constrained component analyses to derive two characteristic components of wing morphometry, each independent of isometric size. Precisely, these characteristic wing shape components are C2 (nominated after Lockwood et al. 1998), which is an index for wing pointedness, with smaller C2 values denoting more pointed wings. The second characteristic trait, C3, reflects wing convexity, with higher values indicating more convex wings.

Both C2 and C3 indices were based on measurements of primary feather length P2-P9. To compare wing shape indices of different populations of Northern Wheatears, we used the above-described discriminant analyses based on morphometric data to assign birds to any of the four groups: Iceland, Norway, Baltic Sea coast and presumed Greenland and subsequently calculated C2 and C3 directly from the formulae given in Lockwood et al. (1998) for each bird within each group. We applied nonparametric Kruskal-Wallis tests for comparisons between groups and Nemenyi test (Sachs 1984) for subsequent pairwise comparisons.

Stable isotope analyses

Northern Wheatears undergo a complete post-breeding moult at the breeding area (Jenni and Winkler 1994; Larson and Hobson 2009) and so tail feathers collected at any stage in the annual cycle were expected to reflect the isotope composition at the breeding grounds. Here we focus on the second outermost tail feather to detect putative isotope differences of geographically distinct breeding populations.

We analysed tail feathers collected from Northern Wheatears at Iceland and Fair Isle during the breeding season and at the Baltic Sea coast during autumn migration and at Helgoland during both autumn and spring migration (Table 1). At Helogland we intended to sample tail feathers of Northern Wheatears with wings longer than mean wings of Icelandic birds (males: > 103.5 mm, females > 100mm) to see whether these long-winged birds differed from Icelandic breeding birds in their isotope composition. Depending on season and year the amount of such long winged birds varies between 6-25 % of females and 3-18% of males caught per sampling season. In detail, the analysed feathers were sampled from females with wing length of 103-107 mm and males with wing length of 105-108 mm.

From the stopover site at the Baltic Sea Coast, we chose feathers from long-winged females (wings: 97.5-100 mm), which can be barely distinguished from Icelandic birds by wing length. We assumed an eastern origin of these females, which may have longer wings than Scandinavian females (Glutz and Bauer 1988).

Stable isotope analysis was carried out at the Stable Isotope Hydrology and Ecology Lab, National Water Research Institute Canada, using methods described elsewhere (Wassenaar and Hobson, 2003; Wassenaar, 2008). All values are expressed in the typical delta notation in units per thousand (‰) deviations from international standards. International standards were Vienna standard mean ocean water (SMOW for δD), Vienna Peedee belemnite (VPDB, for ^{13}C) and atmospheric N_2 (AIR for ^{15}N). All δD values coreresponded to nonexchangeable H (Wassenaar and Hobson 2006). We compared groups by Kruskal Wallis and subsequent pairwise Nemenyi test (Sachs, 1984) to find differences in stable isotope values between groups.

To judge the most likely origin of the long-winged Helgoland migrants, we compared our measured feather δD values with those expected for feathers grown in

Iceland, Greenland and North Scandinavia based on precipitation data. We obtained monthly precipitation δD values from Greenland (hypothetical location of 70.8°N 22.6°W), Iceland (weighted average for 65.53°N 17°W and 63.43°N and 20.28°W according to sample size) and North Scandinavia (hypothetical location at 69°N 24°E) available from Bowen (2009) at http://wateriso.eas.purdue.edu/waterisotopes/pages/information/oipc_info.html. After averaging mean precipitation δD for May through August for each location we applied the feather vs. precipitation regression from Bowen et al. (2005) (growing season data from Europe) and Clark et al. (2006) to calculate expected feather δD values, based on European and North American datasets, respectively.

Statistical analyses were carried out with SPSS 15.0 (SPSS 2006) unless specified otherwise.

Results

Morphometric data

Discriminant analyses comparing breeding birds from Norway, Iceland, presumed Greenland and migrants from the Baltic Sea coast allows us to classify 96% of all males and 87% of all females correctly (Fig.1). For both sexes, all three discriminant functions contributed significantly to the discrimination between the four groups (Table 2). For both males and females over 90% of the variance was explained by the first two discriminant functions.

Discriminant Function 1, which explained most of the variance between groups (68% and 65%, for males and females respectively), formed two groups: Norway/Baltic Sea coast and Iceland/presumed Greenland, and thus mainly distinguished subspecies (Table 2, Fig. 1). High eigenvalues, high correlations of discriminant values with group membership and low values for Wilk´s Lambda (λ) were found (Table 2). In females, mean discriminant coefficients showed that P7 (mean coefficient = 0.856) was most important for the discrimination followed by P4 (0.624) and wing length (0.514). P5 (0.115) was of least importance for the discrimination. The first two discriminant functions in females were:

$$F1 = 0.157 \cdot \text{wing} + 0.089 \cdot \text{P2} + 0.028 \cdot \text{P3} + 0.178 \cdot \text{P4} + 0.069 \cdot \text{P5} - 0.233 \cdot \text{P6} + 0.360 \cdot \text{P7} - 0.095 \cdot \text{P8} + 0.375 \cdot \text{tarsus} - 0.119 \cdot \text{tail} + 0.511 \cdot \text{bill}$$

$$F2 = -0.376 \cdot \text{wing} + 0.231 \cdot \text{P2} - 0.116 \cdot \text{P3} + 0.798 \cdot \text{P4} - 0.182 \cdot \text{P5} + 0.354 \cdot \text{P6} - 0.971 \cdot \text{P7} + 0.176 \cdot \text{P8} + 0.099 \cdot \text{tarsus} - 0.237 \cdot \text{tail} + 1.253 \cdot \text{bill}$$

In males, P6 contributed the most to the discrimination between groups with a mean discriminant coefficient of 0.726, followed by wing length (0.701) and P4 (0.489). Bill length was of least importance with a coefficient of 0.190. In males the first two functions were as follows:

$$F1 = 0.245 \cdot \text{wing} + 0.207 \cdot \text{P2} - 0.102 \cdot \text{P3} + 0.099 \cdot \text{P4} - 0.181 \cdot \text{P5} + 0.462 \cdot \text{P6} + 0.251 \cdot \text{P7} - 0.265 \cdot \text{P8} + 0.414 \cdot \text{tarsus} - 0.117 \cdot \text{tail} + 0.018 \cdot \text{bill}$$

$$F2 = -0.585 \cdot \text{wing} + 0.125 \cdot \text{P2} + 0.293 \cdot \text{P3} + 0.857 \cdot \text{P4} + 0.238 \cdot \text{P5} - 0.608 \cdot \text{P6} - 0.455 \cdot \text{P7} + 0.072 \cdot \text{P8} + 0.497 \cdot \text{tarsus} - 0.168 \cdot \text{tail} + 0.908 \cdot \text{bill}$$

To further illustrate the morphometric differences in wing morphology of the populations the different feather lengths for both sexes are listed in Table 3.

In both sexes, 100% of the presumed Greenlandic birds were classified correctly and were not admixed with Icelandic birds or birds of any other origin. In males, the Norwegian group and migrants from the Baltic Sea coast were more difficult to distinguish. But they barely mixed with Icelandic and not at all with presumed Greenlandic birds. In females, migrants from the Baltic Sea Coast were to a small degree admixed with both Icelandic and Norwegian birds (Fig.1).

We used the discriminant function for both males and females to assign birds on spring migration at different stopover sites (Gibraltar, Ventotene, Wilhelmshaven, Helgoland and Fair Isle) to either of the four groups (Iceland, Norway, presumed Greenland and Baltic Sea) with a correct assignment probability of more than 70%. From South to North we found a clear difference in population composition at the stopover sites in Gibraltar and Ventotene (Italy; Fig. 2). While the few migrants passing Gibraltar seem to belong mainly to Icelandic and presumed Greenlandic populations (both subspecies *O. o. leucorhoa*), birds passing Ventotene were clearly of different origin, mainly belonging to northeastern European populations like those passing the Baltic Sea coast and to a lesser degree Scandinavia. There was one uncommon male bird in the Ventotene sample which was assigned to the Icelandic population with a correct assignment probability of 79 %.

Further North at the coastal stopover site of Wilhelmshaven we found birds of all four groups, but mostly belonging to the Norwegian and Baltic Sea group. There were several birds (39%) which could not be assigned to either group with more than 70% probability; these birds showed a similar (high) probability to belong either to the Baltic Sea or Norway group. At Helgoland, the proportion of presumed Greenlandic birds increased, while the proportion of Icelandic, Norwegian and Baltic Sea birds was similar to the coastal site at Wilhelmshaven. In migrants from Fair Isle, the proportion of presumed Greenlandic birds was highest. Most birds passing Fair Isle in mid-May were assigned to the assumed Greenlandic group, while few were assigned to the Icelandic group. There was one bird assigned to the Baltic Sea Coast.

We also measured two males and 8 females breeding at Fair Isle, which were assigned either to the Rybachy or to the Norwegian Group, none to the Icelandic /

Greenlandic populations. Morphometric data therefore supported the hypothesis that breeding birds from Shetland/ Fair Isle clearly belong to the nominate subspecies *O. o. oenanthe* versus the arctic subspecies *O. o. leucorhoa*.

Concerning wing shape we found very similar patterns in males and females. In both sexes, we found significant differences in C2 and in females also in C3 between the four groups, presumed Greenland, Iceland, Norway and Baltic Sea Coast (Kruskal Wallis Test: males C2: χ^2 = 18.342, p <0.001; males C3: χ^2 = 2,409, p = 0,492; females C2: χ^2 = 37.257, p <0.001; females C3: χ^2 = 14,506, p <0.01), graphically illustrated in Fig. 3. Results of pairwise comparisons and sample sizes are presented in Table 4.

In both sexes, the presumed Greenlandic birds had significantly more pointed wings (smaller C2) than all other groups, with an exception of Scandinavian males that showed no significant difference to the presumed Greenlandic males. In both sexes, the birds passing the Batic Sea coast showed the less pointed wings and in females they were significantly less pointed than Icelandic, Norwegian and presumed Greenlandic birds. In males birds from Norway, Iceland and the Baltic Sea did not differ significantly in their wing pointedness (Table 4 and Fig. 3).

Concerning wing convexity (C3) the populations showed less variety and differences in males were not significant, while in females the birds from the Baltic Sea Coast showed slightly more convex wings than the Norwegian birds (Table 4, Fig. 3).

Stable Isotopes

Boxplots of feather δD, $\delta^{13}C$ and $\delta^{15}N$ values for birds from two breeding sites (Iceland and Fair Isle) and two stopover sites (presumed Greenlandic birds from Helgoland and Rybachy) are shown in Fig. 4.

Presumed Greenlandic migrants from Helgoland differed clearly in their isotope values from Icelandic birds. For all three stable isotopes, we found significant differences between the four groups (Kruskal Wallis H-Test: **δD**: $\chi^2 = 25.74$, $p < 0.001$; **$\delta^{15}N$**: $\chi^2 = 9.57$, $p < 0.05$; **$\delta^{13}C$**: $\chi^2 = 15.27$, $p < 0.01$, n = 10 per group). The feather δD measurements of the presumed Greenlandic sample (mean: -120 ±21‰) was consistent with such a high latitude origin and was significantly different from all other samples which showed no further differentiation in feather δD (Fig. 4). Values of feather δD confirmed the expected more depleted values for both the hypothetical Greenlandic and North Scandinavian location compared with the Iceland population (Table 5). Comparing feather δD values of our Icelandic feathers with the expected feather δD we found slightly enriched values of -75 ‰ versus expected values of less than -82‰, while the depleted values of the presumed Greenlandic sample agreed with both the expected values for Greenland and North Scandinavia, when applying the regression after Bowen et al. 2005 (Table 5).

Although a Kruskal Wallis H-test showed significant differences between our four locations for feather $\delta^{15}N$, the pairwise Nemenyi test was unable to detect significant differences in feather $\delta^{15}N$ between pairs of locations, due to high variances in all except the presumed Greenland sample. $\delta^{13}C$ values were useful to separate the Icelandic samples from the Fair Isle birds and the Baltic Sea migrants (Fig. 4).

Discussion

For all three stable isotopes we expected some variance within populations due to a variety of biotic and abiotic factors. For example, the general enrichment of the light stable isotopes in marine food webs versus terrestrial or freshwater food webs is well established (Chisholm *et al.* 1982; Hobson *et al.* 1997; Hobson 1999, Mizutani 1990). Many birds at the breeding sites at Iceland and Fair Isle were trapped close to beaches were they potentially could feed on marine arthropods like those observed in Iceland or during migration at Helgoland, while they otherwise feed on terrestrial insects. For the presumed Greenlandic and the Baltic Sea sample, we do not know in what kind of habitats these birds fed during feather growth and thus cannot exclude any marine influence. As a consequence feather δ^{15}N values showed high variability in most populations and could not be used for a population differentiation in our case.

We found that variation in δ^{13}C values was less than in δ^{15}N and this isotope discriminated between Icelandic Northern Wheatears and long-winged females trapped on migration at the Baltic Sea coast and breeding birds from Fair Isle. These differences were mainly based on the high variance in the Icelandic samples, which might be connected with sampling areas around the freshwater lake Myvatn and marine coastal feeding sites at the Vestmaneya islands. Since long-winged females from northeastern European population might not be easily distinguished from Icelandic females by morphometric data, δ^{13}C might be the tool of choice for their differentiation in future.

Marine influences at the Vestmaneya islands may have resulted in the slightly higher than expected feather δD values for the Icelandic sample (-75‰ vs. -82.6‰-89.1‰, Table 5). Alternatively, our predicted values of May through August precipitation ignores any potential inputs to the foodweb from snowmelt which are typically depleted compared to precipitation. For the presumed Greenlandic sample, the expected feather δD values we calculated using the Bowen et al. (2005) isoscape were in excellent agreement between our measured values and those expected for that area. However, examination of the isoscape pattern from the rest of Europe cannot preclude putative origins from North Scandinavia to Northeast Europe. However, the extreme wing length of these birds speaks clearly against Scandinavian or Northeast European birds (Cramp 1988). Here, the combination of morphometric data and feather δD analyses offers us valuable information on the origin of migrating Northern Wheatears passing Helgoland and other stopover sites.

The morphometric data reveal considerable differences between the investigated populations and can be used to differentiate populations and to reliably assign most birds to one of the source areas by the presented discriminant analyses. The investigated morphometric differences between populations are mainly caused by a variation in wing shape, while tarsus and bill length was of minor importance. Compared to the other populations Greenlandic birds (which have to cover long non-stop flapping flights over water), show more pointed wings which presumably reduce energy expenditure during flight due to reduced induced drag and optimized wingtip vortices (e.g. Lockwood et al. 1998). The north Scandinavian and northeast European Populations that pass the Baltic Sea Coast have to fly approximately similar distances to their winter quarters but along less hazardous flyways with multiple opportunities for frequent stopovers. We found thus strong support for the general assumption that the evolution of wing morphology is adapted to migratory challenges (e. g. Copete *et al.* 1999, Fiedler 2005; Leisler and Winkler 2003; Lockwood *et al.* 1998; Marchetti *et al.* 1995; Mönkkönen 1995) and in our case not only to the overall migration distance, but also to the distance of the obligatory non-stop flight over the Northeast Atlantic. The selection pressure on wing shape evolution produced a very similar pattern for males and females with the main difference in female wings being less convex and thus providing less thrust during flapping flight but with lower wing weight and inertia (Lockwood et al. 1998).

Based on the evolution of these morphological traits we have nowadays the opportunity to differentiate populations by simple morphometric data like in the presented discriminant analysis. In our example, it was evident that regions lacking distinct geographical or ecological barriers like Scandinavia and the Baltic Sea coast area, which is connected with the eastern breeding range of the Northern Wheatear, presents a morphological gradient which partly hampered a clear differentiation of birds. As a consequence, a typical range of overlap in morphometric patterns might lead to low assignment probabilities in some birds or even wrong assignment, e.g. the one bird at Ventotene assigned to the Icelandic population and the one bird at Fair Isle assigned to the Baltic Sea Coast. Alternatively, such birds can be vagrants (e.g. Dymond 1991). Here, an additional analyses of feather stable isotopes e.g. of $\delta^{13}C$ should increase the probability of the right assignment in future.

Since we analysed only four geographic regions, our discriminant analysis could assign birds to only these origins, even if the birds in fact came from other areas like the British Isles or central Europe. Including morphometric data from other breeding sites might enable us to assign birds with a higher accuracy and should be the task of future studies.

Nevertheless, applying the presented discriminant function allows us to assign birds to a geographical area with a higher accuracy than previous studies which assigned migrating Northern Wheatears to subspecies by wing length only (Delingat *et al.* 2006; Dierschke and Delingat 2001; Dierschke *et al.* 2005; Schmaljohann and Dierschke 2005). Assigning birds by the discriminant functions, we found evidence that the populations migrating on the Southeast Baltic coast cross the Mediterranean along the Italian coastline, while the northwestern populations including Scandinavian birds, occur at the Strait of Gibraltar. Like in many other species of the European-African migration system a migratory divide resulting in western and eastern flyways around the Alps and the Mediterranean seems to exist for different Northern Wheatear populations (e.g. Berthold 1993; Erni *et al.* 2005). In the case of the Northern Wheatear, such a migratory divide can be expected somewhere in Fennoscandia, but note that even breeding birds from northernmost Norway (Bakken et al. 2006) seem to follow a route to SSW as do nominate birds from Helgoland (VD unpubl. data) according to ringing recoveries.

We also found new information on the potential for the affiliation of the Helgoland and Fair Isle migrants. Most of the migrants of the subspecies of *O. o. leucorhoa* which were trapped at these stopover sites during spring migration were not Icelandic Northern Wheatears as one might expect, but were assigned to the presumed Greenlandic population. The correct assignment of these birds was supported by the analyses of stable isotopes, that showed a clear difference between this group and Icelandic birds especially in δD values. At Fair Isle we did not measure birds over the complete migration period and therefore might have missed the Icelandic birds. In contrast, at Helgoland, birds were trapped and measured over the complete migration season in all study years and still showed a high proportion of presumed Greenlandic birds during spring migration. We therefore assume that because of the much larger Greenlandic source population, the likelihood of trapping Greenlandic birds on migration is higher than trapping Icelandic birds. Finally, for Greenlandic Northern Wheatears migrating from West Africa northward during spring, a direct route from Spain to the southern tip of Greenland would imply a non-stop flight of approximately 3000 km (Delingat et al. 2008). A detour along the European continental coastline, the North Sea and eventually Norway would shorten the obligatory non-stop flight over water and could thus save energy and time, which would be required to deposit enough fuel for such a non-stop flight (Alerstam 2001). This would explain why so many presumed Greenlandic Northern Wheatears can be trapped at stopover sites along the eastern North Sea. By this detour, Northern Wheatears would also avoid strong headwinds along the direct migration route over the North Atlantic, where westerly winds prevail (Snow 1953). We, therefore, believe that our assignment of migrants gives support to the hypothesis that Greenlandic birds follow an extended detour migration route to avoid the crossing of the Atlantic between the European and the American continents. The assignment of migrants supports the picture of Northern Wheatear migration in Europe based on ring recoveries (Bakken et al. 2006, Salomonsen 1967; Zink 1973) which shows first indications of a loop migration especially for the Greenlandic Northern Wheatear when choosing an easterly migration route during spring.

Our use of stable isotopes and morphometric data can now be used to shed more light on previous discussions on the origin of migrating Northern Wheatears previously based on wing length and plumage colouration only (Drost 1930, Handtge and Schmidt-König 1958, Salzmann 1930). Those previous studies already suspected that some migrating Northern Wheatears at the European coast originated from both Greenland and Iceland. Since our approach allows a quantification of migrants from different origins trapped during stopover it will provide more detailed insights into Northern Wheatear migratory connectivity ultimately linking breeding, wintering and stopover sites.

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Bird trapping and measurements comply with the current laws of the country in which they were performed.

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Table 1 Sampling locations for morphometric measurements and feather collection for stable isotope analyses at breeding areas and stopover sites

Location	**Coordinates**	**Status**	**Date**	**Sample size for morphometric analyses**	**Sample size for stable isotopes**
Iceland (Myvatn/Heimaey)	65° 32' N, 17° 0' W 63° 26' N, 20°17' W	breeding	23.7.01-14.8.01	$n_{males} = 29$ $n_{females} = 24$	n = 10
Scotland (Fair Isle)	59° 32' N, 1° 39' W	breeding	5.5.02-27.5.02	$n_{males} = 2$ $n_{females} = 8$	n = 10
Scotland (Fair Isle)	59° 32' N, 1° 39' W	migrating	5.5.02-27.5.02	$n_{males} = 10$ $n_{females} = 26$	
Norway (Gamvik)	71° 05' N, 28° 13' E	breeding	22.6.99-2.7.99	$n_{males} = 23$ $n_{females} = 19$	
Germany (Helgoland)	54° 11' N, 7° 55' E	migrating	complete spring migration 99-02	$n_{males} = 301$ $n_{females} = 280$	n =10
Germany (Wilhelmshaven)	53°58' N, 8°11' E	migrating	15.4.03-22.5.03 25.8.03-30.9.03	$n_{males} = 32$ $n_{females} = 18$	
Russia, Baltic Sea (Rybachy)	55°05' N, 20°44' E	migrating	28.8.00-14.9.00	$n_{males} = 23$ $n_{females} = 28$	n = 10
Italy (Ventotene)	40°47' N, 13°25' E	migrating	17.4.02-28.4.02	$n_{males} = 32$ $n_{females} = 38$	
Gibraltar	35°57' N, 5° 36' W	migrating	15.9.01-24.10.01 3.4.02-13.4.02	$n_{males} = 5$ $n_{females} = 1$	

Table 2: Results of discriminant analyses with morphometric data in males and females. For graphical illustration and sample size see Fig. 1.

		Eigen value	Percent of variance	Canonical correlation	Wilk´s Lambda	significance
males	Function 1	5.213	67.9	0.916	0.039	0.000
	Function 2	2.044	26.6	0.819	0.251	0.000
	Function 3	0.424	5.5	0.546	0.702	0.000
females	Function 1	3.932	64.6	0.893	0.050	0.000
	Function 2	1.608	26.4	0.785	0.248	0.000
	Function 3	0.544	8.9	0.594	0.684	0.000

Table 3: Mean feather length ± standard deviation for each primary feather (P2- P8) that was integrated in the discriminant analyses. Sample size for each sex of each population is given in brackets.

		presumed Greenland	**Iceland**	**Norway**	**Baltic Sea**
P2	males	79.0 ± 1.4 (18)	76.3 ± 2.2 (29)	71.7 ± 1.8 (23)	71.3 ± 1.7 (23)
	females	77.2 ± 1.4 (19)	73.4 ± 1.8 (24)	69.1 ±1.7 (19)	70.1 ± 2.6 (28)
P3	males	81.0 ± 1.2 (18)	78.3 ± 1.9 (29)	73.7 ± 1.7 (23)	73.5 ± 1.8 (23)

	females	79.1 ± 1.4 (19)	75.4 ± 1.8 (24)	70.7 ± 1.5 (19)	72.6 ± 2.2 (28)
P4	males	81.2 ± 1.2 (18)	78.6 ± 1.8 (29)	74.2 ± 1.6 (23)	74.1 ± 1.7 (23)
	females	79.1 ± 1.5 (19)	75.7 ± 2.0 (24)	71.2 ± 1.4 (19)	72.8 ± 2.0 (28)
P5	males	76.8 ± 1.1 (18)	74.7 ± 1.8 (29)	70.1 ± 1.8 (23)	70.4 ± 1.8 (23)
	females	74.8 ± 1.2 (19)	72.0 ± 2.1 (24)	67.3 ± 1.4 (19)	69.3 ± 1.9 (28)
P6	males	70.4 ± 1.3 (18)	69.7 ± 1.7 (29)	64.4 ± 1.4 (23)	65.6 ± 1.5 (23)
	females	69.3 ± 1.1 (19)	67.3 ± 1.9 (24)	62.5 ± 1.5 (19)	64.8 ± 2.0 (28)
P7	males	67.4 ± 1.2 (18)	67.1 ± 1.6 (29)	61.6 ± 1.6 (23)	62.9 ± 1.4 (23)
	females	66.4 ± 1.1 (19)	64.7 ± 1.5 (24)	59.6 ± 1.4 (19)	62.3 ± 1.9 (28)
P8	males	65.6 ± 1.0 (18)	65.0 ± 1.7 (29)	60.2 ± 1.5 (23)	61.1 ± 1.7 (23)
	females	64.3 ± 1.3 (19)	62.7 ± 1.5 (24)	58.2 ± 1.2 (19)	60.2 ± 2.0 (28)

Table 4: Summary of pairwise comparisons of wing shape indices between different groups of males (A) and females (B) after Nemenyi (1963) in Sachs (1984). Significance levels for differences between groups are indicated, non significant (ns) noted where groups did not differ. C2 indicates wing pointedness and C3 wing convexity after Lockwood et al. (1998). Under the diagonal results for C2 comparisons are given, above the diagonal results for C3.

A)

C3 C2	Presumed Greenland N = 7	Iceland N = 35	Norway N = 19	Baltic Sea N = 26
Presumed Greenland		ns	ns	ns
Iceland	**P<0.05**		ns	ns
Norway	ns	ns		ns
Baltic Sea	**P<0.001**	ns	ns	

B)

C3 C2	Presumed Greenland	Iceland N = 4	Norway N =23	Baltic Sea N = 25

	N = 13			
Presumed Greenland		ns	ns	ns
Iceland	**P<0.01**		ns	ns
Norway	**P<0.01**	ns		**P<0.05**
Baltic Sea	**P<0.001**	**P<0.05**	**P<0.05**	

Table 5 Comparison of expected feather δD based on precipitation data and empirical feather δD of this study. Mean precipitation δD from May to August were downloaded from Bowen (2009) for Iceland (weighted average for two locations according to our sample sizes and sampling locations) and two hypothetical locations on East Greenland and North Scandinavia. Feather δD for these three locations were calculated using regression of feather vs. precipitation δD following either Bowen et al. (2005) (growing season data for Europe) or Clark et al. (2006).

	Mean precipitation δD	Expected feather δD after Clark et al. 2006	Expected feather δD after Bowen et al. 2005	Mean feather δD in this study
Iceland	-64‰	-82.22‰	-89.12‰	-75‰
Greenland	-88‰	-103.34‰	-119.84‰	-120‰
North Scandinavia	-86‰	-101.58‰	-117.28‰	

Fig. 1 Results of discriminant analyses based on morphometric data for males and females. Each bird is mapped according to the calculated value for the first and second discriminant function. Equations for discriminant functions are given in the text

Fig. 2 Affiliation of migrating Northern Wheatears trapped at different stopover sites in Western Europe after applying the discriminant analyses based on morphometric data. The black arrow indicates the trapping location in Rybachy at the Baltic Sea Coast.

Fig. 3 Size constrained components of wing shape based on measurements of P2-P9 (Lockwood et al. 1998) for male and female Northern Wheatears from four different geographic regions. Decreasing C2 values indicate increasing wing pointedness. C3 increases with wing tip convexity

Fig. 4 Boxplots showing the 5%, 25%, 50%, 75 % and 75 % percentiles and outliers of stable isotope analyses of δD, $\delta^{15}N$ and δ^{13} C in tail feathers of Northern Wheatears. Sample size for each location is 10