ORIGINAL PAPER

The nature of the migration route shapes physiological traits and aerodynamic properties in a migratory songbird

**Anna-Marie Corman · Franz Bairlein ·
Heiko Schmaljohann**

Abstract Migration distance is supposed to represent an important selection pressure shaping physiological and morphological properties. Previous work has focussed on this effect, while the importance of ecological barriers in this context has been rarely considered. We studied two subspecies of a migratory songbird, the northern wheatear (*Oenanthe oenanthe oenanthe* and *O. o. leucorhoa* L.), on an island in the North Sea. The former subspecies reaches their Scandinavian breeding areas after a short sea crossing, whereas *leucorhoa* northern wheatears cross the North Atlantic towards Iceland, Greenland or Canada. Physiological traits (fuel deposition rate) and wings' aerodynamic properties (wing pointedness independent of body size), both affecting migration speed, were hypothesized to be more pronounced in *leucorhoa* than in *oenanthe* northern wheatears. Within subspecies, the physiological and aerodynamic properties were hypothesized to explain arrival date at the stopover site with "fast migrants" arriving early. Physiological and aerodynamic properties in *leucorhoa* northern wheatears lead to a faster and less costly migration, favouring a sea crossing, but in trade-off lower flight manoeuvrability than in *oenanthe* birds. Wings' aerodynamic properties affected the seasonal occurrence of *leucorhoa* females, whereas the physiological traits significantly influenced arrival date in *oenanthe* individuals. The less risky migration route in *oenanthe* birds with few short sea crossings may have favoured higher flight manoeuvrability for foraging

(less pointed wings), in trade-off an energetically more costly flight. Hence, not the migration distance itself, but the presence/absence of a sea barrier presents an important selection pressure in migratory land birds favouring low flight costs.

Introduction

As migration distance increases, its associated costs in terms of time, energy and safety should increase as well (Alerstam and Lindström 1990; Houston 1998; Lank et al. 2003), although there might be advantages in terms of time, energy and safety of undertaking detours and avoiding barriers during migration (Alterstam 2001). Indeed, migration distance was shown to affect endogenously controlled migratory traits: The longer the migration distance, the higher the migratory restlessness "Zugunruhe" (Berthold and Querner 1981, 1988; Maggini and Bairlein 2010; Bulte and Bairlein 2013), the fuel load (Fransson et al. 2001; Maggini and Bairlein 2010) and the aerodynamic properties of the bird (Marchetti et al. 1995; Fiedler 2005; Baldwin et al. 2010; Delingat et al. 2011; Förschler and Bairlein 2011). Hence, with an increasing migration distance, selection favours physiological and aerodynamic properties of a bird that enable fast and efficient flying (Fiedler 2005; Baldwin et al. 2010). Nevertheless, there are some species, e.g. the hoopoe (*Upupa epops*), with rounded wings and relatively low wing beat also crossing large distances during migration (Bächler et al. 2010).

In addition to the migration distance, the challenge of the migration route, i.e. whether an ecological barrier has to be crossed or not, plays an important role in the expression of migratory traits (Dierschke and Delingat 2001; Dierschke et al. 2005; Bulte and Bairlein 2013). Considering land birds crossing large bodies of water (Gill et al. 2009; Bairlein et al. 2012), we

A.-M. Corman · F. Bairlein · H. Schmaljohann (✉)
Institute of Avian Research "Vogelwarte Helgoland", An der Vogelwarte 21, 26386 Wilhelmshaven, Germany
e-mail: heiko.schmaljohann@ifv-vogelwarte.de

A.-M. Corman
Research and Technology Centre Westcoast, Hafentörn 1,
25761 Büsum, Germany

hypothesize that ecological barriers may act as a strong selection pressure forming populations well adapted for long non-stop flights in terms of their physiology and aerodynamics. In respect of bird's physiology, the fuel deposition rate is an important currency, as it indicates the overall migration speed of a bird (Alerstam and Lindström 1990). The higher the fuel deposition rate at a stopover site, the faster birds reach the necessary fuel load for their next migratory flight. High fuel deposition rates prior to a crossing of an ecological barrier are crucial to obtain the required large fuel loads, i.e. lipids, in relatively short time. Lipids are the main energy source for long sustained migratory flights, while carbohydrates fuel short flights (e.g. Jenni and Jenni-Eiermann 1998; Gerson and Guglielmo 2013). A high-fuel deposition rate reflects enhanced lipogenesis. By that, fattening migrants are confronted a trade-off between lipid anabolism and carbohydrate metabolism as there is competitive inhibition (Bairlein 1986, 1987). Moreover, a high-fuel deposition rate is associated not only with increased food intake but also with increased assimilation efficiency of the ingested fat (Bairlein 1985). Increased assimilation efficiency of fat is associated with increased intestine length (Klaassen and Biebach 1994), requires enhanced lipid transport systems across the intestine epithelium (Whittow 2000) as well as an increased delivery of bile acid to facilitate lipid digestion (Totzke et al. 1998). These are "costly" processes. As lipids are relevant for migratory flights, they are only enhanced during fattening and more so in long-distance migrants than in short-distance migrants. Bird's flight performance mostly depends on the aerodynamic properties of its wings and body (Rayner 1988; Norberg 1990; Mönkkönen 1995; Fiedler 2005; Pennycuick 2008). Within a species, flying with more pointed wingtips increases air speed and aspect ratio, but decreases drag, wing load and flight manoeuvrability than with rounder wingtips (Rayner 1988; Norberg 1990; Lockwood et al. 1998; Swaddle and Lockwood 2003; Bowlin and Wikelski 2008; Pennycuick 2008). A decrease in flight manoeuvrability is disadvantageous for foraging especially in aerial feeders or avoiding predators (Swaddle and Lockwood 2003; Baldwin et al. 2010). We hypothesize that individuals crossing a large ecological barrier during migration experience selection pressures forming their fuel deposition-related physiological traits and their aerodynamic properties to allow for faster and more efficient flying than others of the same species not crossing this barrier.

To test this, we studied northern wheatears (*Oenanthe oenanthe*, wheatear hereafter) stopping over on Helgoland, an island in the North Sea. Two subspecies of northern wheatears with different breeding destinations co-occur there during spring migration (Dierschke and Delingat 2001; Dierschke et al. 2005). Nominate wheatears (*O. o. oenanthe*, oenanthe wheatear hereafter) face a sea crossing of 50 to 100 km before continuing migration over land into their Scandinavia breeding range (Schmaljohann et al. 2011). Birds of the *leucorhoa* subspecies (*leucorhoa* wheatear hereafter) travel at least

800 km at a stretch each across the North Sea and the North Atlantic to their breeding areas on Iceland, Greenland or in eastern Canada (Schmaljohann and Naef-Daenzer 2011; Bairlein et al. 2012). Thus, the length of the sea barrier crossing is the significant difference between both subspecies, while the overall migration distances are similar. We therefore hypothesize a stronger selection pressure on *leucorhoa* wheatears than on *oenanthe* wheatears towards fast and low-cost migration due to the long sea crossing. Specifically, we suppose that *leucorhoa* wheatears have higher fuel deposition rates (Dierschke et al. 2005; Henningsson and Alerstam 2005; Delingat et al. 2006; Maggini 2009; Maggini and Bairlein 2010) and aerodynamic properties (Leisler and Winkler 2003; Fiedler 2005; Delingat et al. 2011; Förschler and Bairlein 2011) yielding a faster and more efficient migration than *oenanthe* wheatears. The latter may have retained lower general physiological costs (see above) in trade-off lower fuel deposition rates and a better manoeuvrability for foraging or predator avoidance in trade-off with slightly lower air speeds and higher costs for migratory flights than *leucorhoa* wheatears.

Within populations, we expect that the quality of the physiological traits and aerodynamic properties explain to a certain extent individual arrival date. As both subspecies breed allopatrically, we assessed the effect of these traits on arrival date at the stopover site, where both subspecies co-occur regularly. At breeding grounds, individual variation in the arrival date is explained by individual variation in differing migratory traits such as endogenous onset of spring migration (Maggini and Bairlein 2012), environmental cues like photoperiod (Gwinner 1996), temperature (Singh et al. 2011), quality of winter and stopover habitats (Marra et al. 1998; Saino et al. 2004), weather conditions encountered en route (Erni et al. 2002; Schaub et al. 2004; Liechti 2006; Newton 2007; Shamoun-Baranes et al. 2010) or distances to go (Bearhop et al. 2005; Langin et al. 2009; Conklin et al. 2010; Maggini et al. 2013). As we could not consider these traits in our study, we hypothesize that individuals with generally high fuel deposition rates and favourable aerodynamic properties yielding a fast and efficient flight arrive earlier at a stopover site than individuals with less well pronounced traits. Within the subspecies, we hypothesize that stronger selection acts on males than on females to maximize males' speed of migration increasing their earlier arrival in comparison with females (Conder 1956; Brook 1979; Buchmann 2001; Morbey and Ydenberg 2001; Maggini and Bairlein 2012).

Materials and methods

Study

Wheatears were caught using spring traps baited with mealworms (*Tenebrio molitor*) at Helgoland (54°11′N, 07°55′E;

Germany) in spring 31 March to 8 June 1998, 9 April to 3 June1999, 25 March to 26 May 2000, 14 April to 26 May 2001, 17 April to 9 June 2002, 6 April to 23 May 2008, 15 April to 20 May 2009 and 22 March to 27 May 2010. Birds trapped between 1998 and 2002 were only considered in respect of species' seasonal appearance (Fig. 1). Birds were sexed and assigned to either subspecies according to Svensson (1992). In males, we distinguished between second calendar year birds and older birds, but not in females (Svensson 1992; Jenni and Winkler 1994). Body mass was taken at capture.

Fuel deposition rate

Fuel deposition rate was determined by an indoor cage experiment carried out in 2010 from 22 March to 26 May. Birds had no access to environmental cues, such as light and temperature, during the experiment. On day of capture, wheatears were put in separate common bird cages. All birds were released into the wild at the morning of their fourth day in lab (Fig. 2). Indoor temperature was constant throughout the whole study (8 am: 19.37±0.29 °C; mean± SD, linear regression, $n=66$, $F_{1,64}=1.4$, $p=0.235$; 9 pm: 19.42±0.30 °C; mean±SD, linear regression, $n=66$, $F_{1,64}=2.9$, $p=0.092$) under a constant daylight regime (13 L/11 D). Food (mealworms) and water were offered ad libitum during daytime from 8 am to 9 pm. At night, no food or water were provided. Wheatears were weighed to the nearest 0.1 g with a digital balance (WEDO Dig 2000, Germany) at 8 am and at 9 pm every day. Day of capture was treated as adaptation phase, as birds were captured at different times during the day. First data considered for analyses of physiological traits (see below) was first morning body mass (Fig. 2). Fuel deposition rate per day was estimated similarly to Lindström and Alerstam (1992), but we considered morning and not evening body mass to overcome the problem of undigested food influencing birds' body mass (Fig. 2). We examined the average daily fuel deposition rate, i.e. the spontaneous reaction to food and water ad libitum, over a period of 2 days:

$$\text{fuel deposition rate} \left[\text{day}^{-1}\right] = \left(\text{body mass}_{i \text{ 3rd morning}}[\text{g}] - \text{body mass}_{i \text{ 1st morning}}[\text{g}]\right) \times \text{lean body mass}_i^{-1}[\text{g}] \times \Delta\text{time}^{-1}[\text{day}] \quad (1)$$

Lean body mass$_i$ was estimated according to Schmaljohann et al. (2011) as:

$$\text{lean body mass}_i[\text{g}] = 0.29\left[\text{mm}^{-1}\right] \times \text{wing length}_i[\text{mm}]\text{-}6.85[\text{g}]. \quad (2)$$

Temperature, location of the cages and number of individuals staying simultaneously in the lab did not influence the fuel deposition rate (one-way ANOVA: all p values>0.2, $n=82$).

Fuel deposition rate was also expressed as mass increase per gram of mealworms taken as:
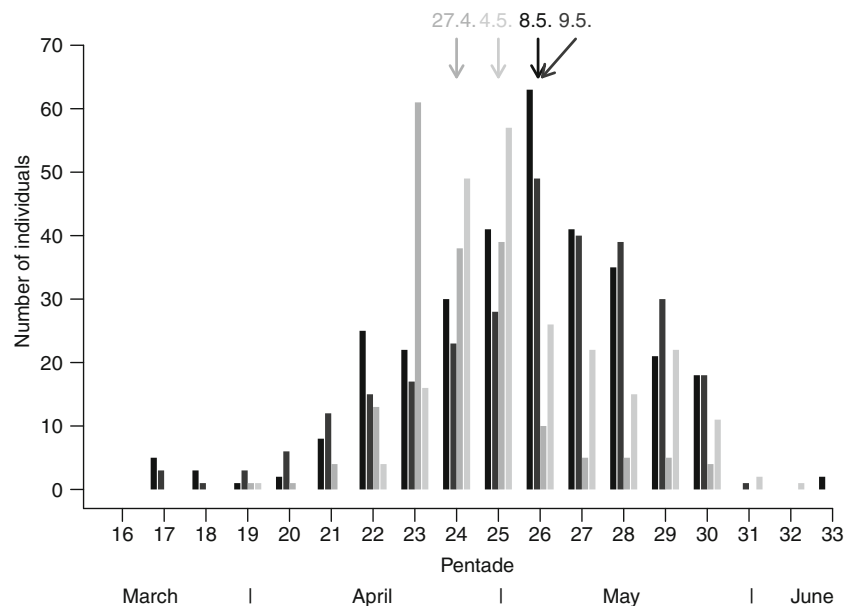

Fig. 1 Number of caught northern wheatears on Helgoland during spring migration of the years 1998 to 2002 and 2008 to 2010. Given are sums of pentads for male ($N=317$, *black*) and female ($N=285$, *dark grey*) *oenanthe* northern wheatears and male ($N=186$, *middle grey*) and female ($N=226$, *light grey*) *leucorhoa* northern wheatears. The *arrows* indicate the median arrival dates of the four different groups

$$\text{fuel deposition rate per gram fed mealworms}_i\,[\text{day}^{-1}\text{g}^{-1}] = \text{fuel deposition rate}_i\,[\text{day}^{-1}] \times \text{mass of fed mealworms}_i^{-1}[\text{g}] \quad (3)$$

whereas fuel deposition rate and mass of fed mealworms were the mean values of the corresponding two days (Fig. 2). Mass of fed mealworms was the difference between the offered mass of mealworms at 8 am and 9 pm per day. The nocturnal fuel loss rate per night was determined as:

$$\text{nocturnal fuel loss rate}_i\,[\text{night}^{-1}] = (\text{body mass}_{i\,\text{evening}}[\text{g}]\text{-body mass}_{i\,\text{next mornig}}[\text{g}]) \times \text{ lean body mass}_i^{-1}[\text{g}] \times \Delta\text{time}^{-1}[\text{night}] \quad (4)$$

We used the individual means of the second and third night (Fig. 2) in the "Results" section.

Morphological data

We measured the primaries 9 to 1 (descendent) and the outermost secondary to estimate the wing pointedness index which is independent of wing length following Lockwood et al. (1998). Between 1998 and 2002, only primaries 9 to 2 were measured. The wing pointedness index could not be calculated for these birds. The advantage of this wing pointedness index is its independency of body size and hence wing length (Lockwood et al. 1998). Some birds from 2008 to 2010 could not be used due to missing and worn feathers. Wing span and aspect ratio, both according to Pennycuick (1999), and wing load were only determined during spring 2010.

$$\text{Aspect ratio} = \text{wing span}^2\,[\text{cm}] \times \text{ wing area}^{-1}[\text{cm}^2] \quad (5)$$
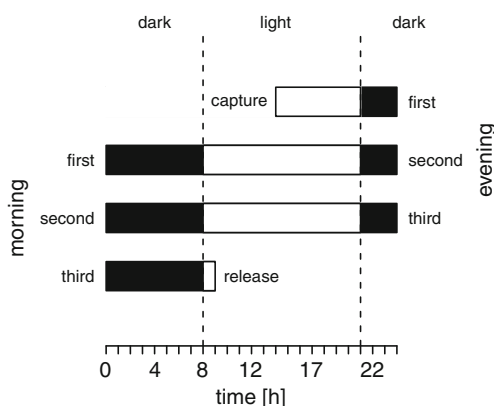

Fig. 2 Set-up of feeding experiment. After capture, birds were hold in standard bird cages with ad libitum food and water during the light phase. No food and water were provided during the nights (dark periods). Temperature (8 am: 19.37±0.29 °C, n=66 and 9 pm: 19.42±0.30 °C, n=66) and daylight regime (13 L/11 D) were constant throughout the experiment. Day of capture was treated as adaptation phase, as birds were captured at different times during the day. First data considered for analyses of physiological traits was first morning body mass. Birds were released into the wild after the third morning

Birds' wing load was estimated according to Lockwood et al. (1998):

$$\text{Wing load}\,[\text{g cm}^{-2}] = \text{body mass }[\text{g}] \times \text{ wing area}^{-1}[\text{cm}^2] \quad (6)$$

Wing area was estimated according to Bowlin and Wikelski (2008); for details see Supporting information. For estimating wing load, we used body mass at capture.

Statistics

Fuel deposition rate per gram fed mealworms showed five extremely low values in three males (one *oenanthe*, two *leucorhoa*) and two females (both *leucorhoa*). They fed only few mealworms throughout the experiment (within 48 h: 8, 3.1, 0.9, 1.2, 3.5 g) in comparison to the others (31.0±9.2 g; mean±SD, n=82). Their fuel deposition rate per gram fed mealworms had lower values (-0.10 ± 0.02 g^{-1} day^{-1}; mean± SD) than of the remaining birds (0.06±0.05 g^{-1} day^{-1}; mean± SD, n=82; Wilcoxon signed-rank test, W=409, p=0.0002). The basal metabolic rate of wheatears at 19 °C (see above) is about 50 kJ day^{-1} (Schmaljohann et al. 2012b; Maggini and Bairlein 2013). According to Rychlik and Jancewicz (2002), the energetic values of mealworms are 10.5 kJ g^{-1}. Thus, wheatears require 4.8 g of mealworms to cover their daily basal metabolic rate at 19 °C. As these five wheatears fed less than this amount, it seems that they did not habituate as well as the others or were ill. Therefore, we excluded these five birds from all of our fuel deposition rate analyses.

Statistics were calculated using the statistical software R 2.15.2 (R Development Core Team 2012). We performed a principal component analysis with 77 birds (45 *oenanthe* and 32 *leucorhoa* wheatears; excluding 5 individuals not identified on subspecies level, see sample size above) of which fuel deposition rate, mass of fed mealworms, nocturnal fuel loss rate, fuel deposition rate per gram fed mealworms, wing pointedness index, aspect ratio and wing load were available using the "prcomp" function from the R-package "stats" (Table 1). Variables were shifted to be zero centered and scaled to have unit variance prior the analysis. We performed a Horn's parallel analysis for this principal component analysis to adjust for finite sample bias in the retention of

Table 1 Results of the principal component (PC) analysis

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Standard deviation	1.7946	1.2127	0.9298	0.8447	0.61738	0.5318	0.25867
Proportion of variance	0.4601	0.2101	0.1235	0.1019	0.05445	0.0404	0.00956
Cumulative proportion	0.4601	0.6701	0.7936	0.8956	0.95004	0.9904	1.0000

components by using the function "paran" from the R-package "paran" with 50,000 iterations and centile set to 95 (Horn 1965; Glorfeld 1995; Dinno 2009): first principal component (PC1): adjusted eigenvalue=2.596, unadjusted eigenvalue=3.220, estimated bias=0.624; second principal component (PC2): adjusted eigenvalue=1.102, unadjusted eigenvalue=1.471, estimated bias=0.369. As adjusted eigenvalues >1 indicate the dimensions to retain, we considered only the first two principal components to assess to what extent they possibly explain the seasonal occurrence of wheatears. Shapiro–Wilk normality tests were non-significant for both PC1 ($W=$ 0.9808; $p=0.297$) and PC2 ($W=0.9925$; $p=0.934$), indicating their use for parametric tests. PC1 contains the physiological traits (Fig. 3). An increasing PC1-value is equivalent with an increase in fuel deposition rate, mass of fed mealworms, nocturnal fuel loss rate and fuel deposition rate per gram fed mealworms. PC2 includes wing pointedness index, aspect ratio and wing load. An increase in PC2 indicates an increasingly faster and more efficient flight style (Fig. 3). We assessed whether physiological traits (*PC1*) and aerodynamic (*PC2*) traits explain the seasonal occurrence (*date*) differently for the two subspecies (*subsp*) considering the following model:

$$Date_i = \beta_0 + \beta_1 PC1_{i,1} + \beta_2 PC2_{i,2} + \beta_3 subsp_{i,3} + \beta_4 (PC1:subsp)_{i,4} + \beta_5 (PC2:subsp)_{i,5} + \varepsilon_i \qquad (7)$$

If subspecies had a significant effect on seasonal occurrence, models were run separately for subspecies. Automated model selection was carried out with the "dredge" function from the R-package "MuMIn". Model averaging was performed for all models with a $\Delta AIC_c <4$ using the "model.avg" function form the R-package "MuMIn" and according 95 % confidence intervals are given. Analysis of the residuals did not show any violation of the normality assumption.

If not otherwise stated, means are reported with standard deviation (mean±SD), and all significances are two-tailed.
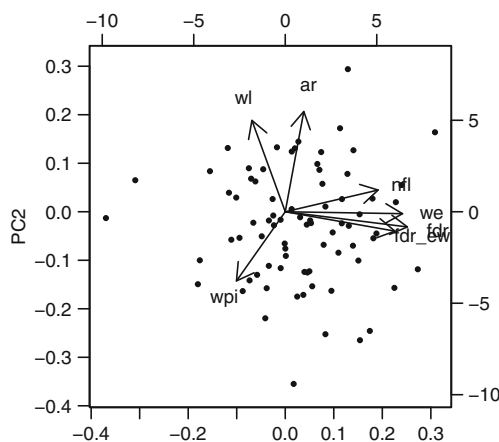

Fig. 3 Plot of loadings (*left and bottom axes*) and principal component scores (*right and top axes*) of the first two principal components (PC). The cosine of the angle between the lines indicates the approximate correlation between the variables they present. The closer the angle is to 0 or 180, the higher the correlation. PC1 includes all physiological traits, i.e. fuel deposition rate (*fdr*), mass of fed mealworms (*we*), nocturnal fuel loss rate (*nfl*) and fuel deposition rate per gram fed mealworms (*fdr_ew*), and explains 46 % of the variance in the data. PC2 includes all aerodynamic traits, i.e. wing pointedness index (*wpi*), aspect ratio (*ar*) and wing load (*wl*), and explains 21 % of the variance in the data. A decreasing "wingpoint.index" means that the wing gets more pointed creating higher air speed and less drag

Results

A total of 1,253 wheatears were caught, with 602 individuals belonging to the subspecies *oenanthe* (males: $n=317$, females: $n=285$) and 413 individuals to *leucorhoa* (males: $n=186$, females: $n=226$). One *leucorhoa* wheatear could not be sexed. A total of 238 birds could not be assigned to either subspecies (males: $n=161$, females: $n=77$).

Physiological traits

In *oenanthe* wheatears, there were no sex differences in the absolute values of the physiological traits (fuel deposition rate, mass of fed mealworms, nocturnal fuel loss rate and fuel deposition rate per gram fed mealworms; Wilcoxon signed-rank tests: p values >0.154; Fig. 4). Male *leucorhoa* wheatears fed a higher amount of mealworms (20.3±4.4 g day^{-1}, $n=19$) than females (16.4±3.3 g day^{-1}, $n=17$; Wilcoxon signed-rank test: $W=239$, $p=0.013$). The other traits did not
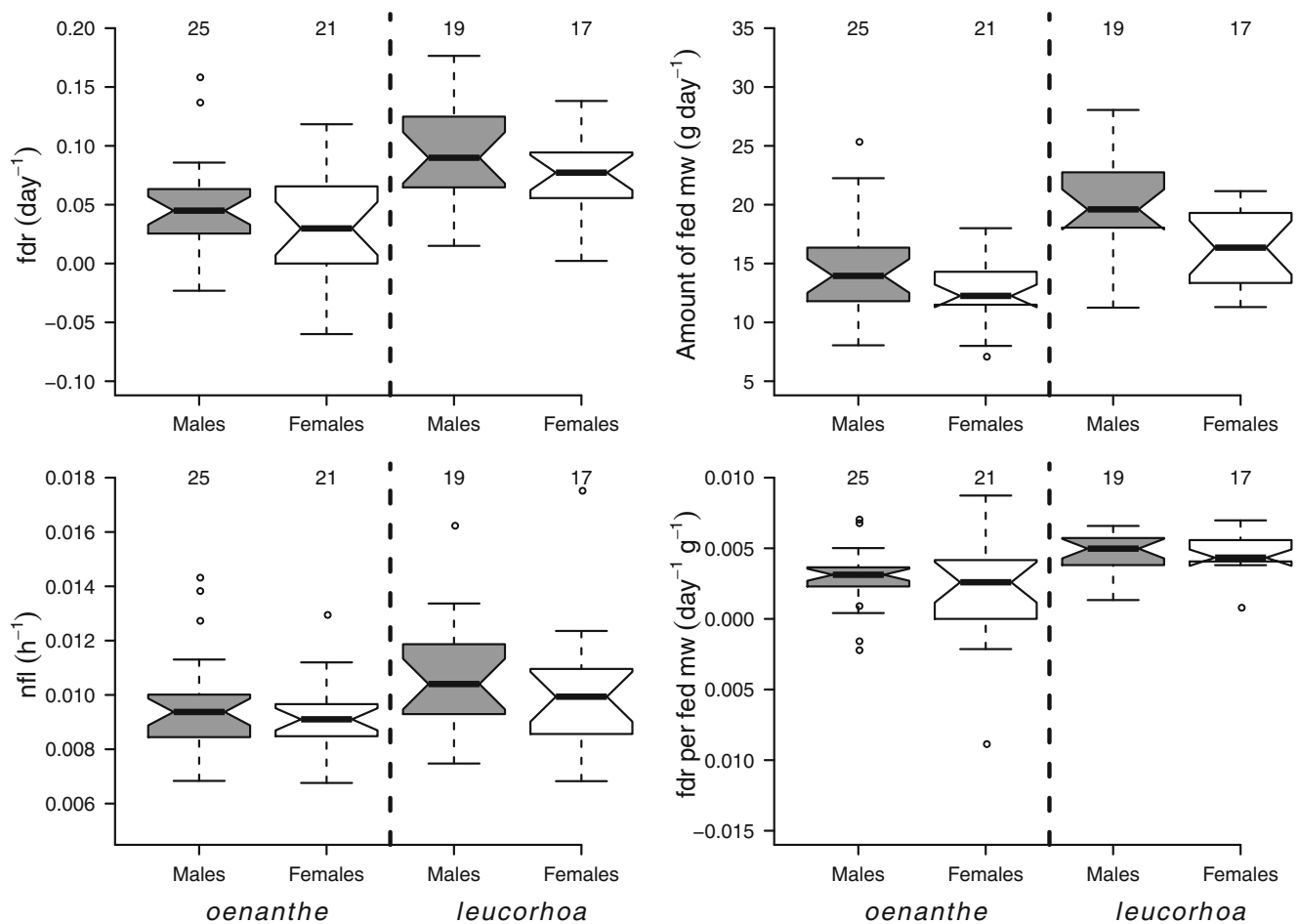
Fig. 4 Subspecies and sex differences in the physiological traits. Fuel deposition rate (*fdr*), amount of fed mealworms (*mw*), nocturnal body mass loss (*nfl*) and fdr per gram fed mealworms for *oenanthe* and *leucorhoa* northern wheatears for both sexes (males, *grey*; females, *white*). Significant differences between the groups are indicated by the non-overlapping notches. *Boxes* show the 5, 25, 50, 75 and 95 % percentiles as well as outliers (*dots*). Sample sizes are given *above the boxes*. See "Results" for statistical details

differ between the sexes (all Wilcoxon signed-rank tests: $p > 0.18$; Fig. 4).

Both sexes of *oenanthe* wheatears (males: 0.05 ± 0.04 day^{-1}, $n=25$; females: 0.03 ± 0.04 day^{-1}, $n=21$) had significantly lower fuel deposition rates than their corresponding *leucorhoa* sexes (males: 0.10 ± 0.05 day^{-1}, $n=19$; females: 0.08 ± 0.03 day^{-1}, $n=17$; Wilcoxon signed-rank tests: p values <0.007; Fig. 4). The same was true for the amount of fed mealworms (*oenanthe*: males, 14.5 ± 4.3 g, $n=25$; females, 12.6 ± 3.1 g, $n=21$; *leucorhoa*: males, 20.3 ± 4.4 g, $n=19$; females, 16.4 ± 3.3 g, $n=17$; Wilcoxon signed-rank tests: p values <0.002). The nocturnal fuel loss did not differ within sexes of the two subspecies (Wilcoxon signed-rank test: p values >0.06). Fuel deposition rate per gram fed mealworms was higher in *leucorhoa* wheatears than in *oenanthe* wheatears (males: *leucorhoa*, 0.005 ± 0.001 day^{-1} g^{-1}, $n=19$; *oenanthe*, 0.003 ± 0.002 day^{-1} g^{-1}, $n=25$; females: *leucorhoa*, 0.004 ± 0.002 day^{-1} g^{-1}, $n=17$; *oenanthe*, 0.002 ± 0.004 day^{-1} g^{-1}, $n=21$; females Wilcoxon signed-rank tests: p values <0.012; Fig. 4).

Aerodynamic traits of the wing

In *oenanthe* wheatears, there was no sex-specific difference in any aerodynamic property (Wilcoxon signed-rank tests: p values >0.11; Fig. 5).

Leucorhoa males (0.06 ± 0.09, $n=83$) had a lower wing pointedness index, i.e. more pointed wings, than their females (0.12 ± 0.12, $n=83$; Wilcoxon signed-rank test: $W=2,645$, $p=0.01$) and a higher aspect ratio (males: 6.9 ± 0.24, $n=55$, females: 6.7 ± 0.27, $n=42$; Wilcoxon signed-rank test: $W=1,482$, $p=0.018$). There was no sex-specific difference in the wing load of *leucorhoa* wheatears (Wilcoxon signed-rank test: $W=1,367$, $p=0.12$; Fig. 5).

Both sexes of *oenanthe* wheatears (males: 0.19 ± 0.12, $n=104$; females: 0.19 ± 0.14, $n=69$) had a higher wing pointedness index, i.e. less pointed wings, than *leucorhoa* wheatears (males: 0.06 ± 0.09, $n=83$; Wilcoxon signed-rank test: $W=7,013$, $p<0.0001$; and females: 0.11 ± 0.12, $n=83$; Wilcoxon signed-rank test: $W=3,939$, $p<0.0001$). *Oenanthe* males (6.67 ± 0.30, $n=40$) had significantly lower aspect ratios than
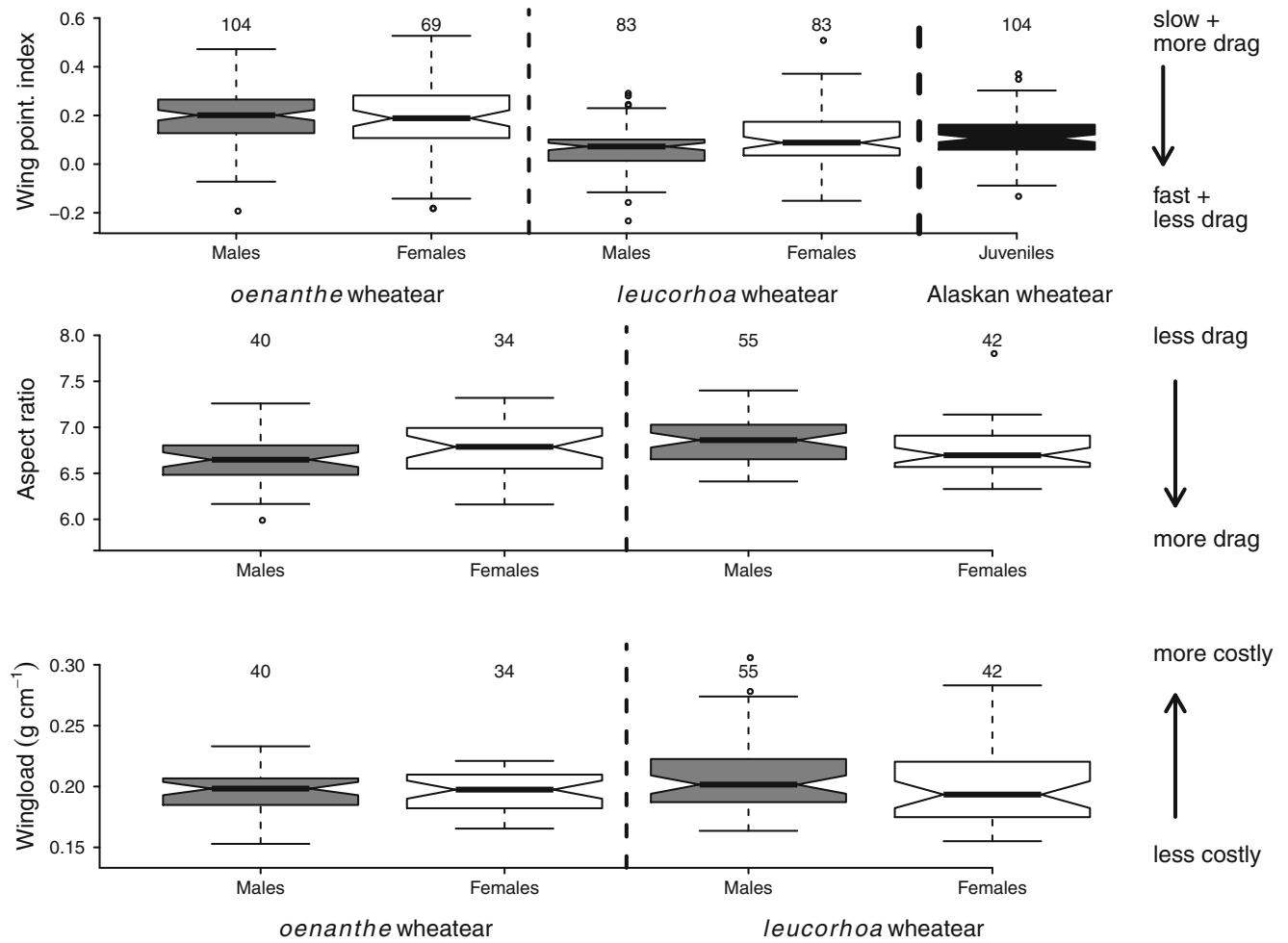
Fig. 5 Subspecies and sex differences in the aerodynamic traits. Wing pointedness index (wingpoint.index) after Lockwood et al. (1998), aspect ratio and wing load for *oenanthe* and *leucorhoa* northern wheatears for both sexes (males, *grey*; females, *white*). Wing pointedness is also shown for juvenile Alaskan northern wheatears (*dark grey*), data from Schmaljohann et al. (2013). Significant differences between the groups are indicated by the non-overlapping notches. Be aware that aspect ratio is a function of wing length and that wing length was used to distinguish between subspecies. *Boxes* show the 5, 25, 50, 75 and 95 % percentiles, as well as outliers (*dots*). Sample sizes are given *above the boxes*. See "Results" for statistical details

Table 2 Comparison of candidate models to investigate the effect of PC1, PC2, subspecies (subsp) and the corresponding interactions on spring arrival date in northern wheatears. Model's coefficients and presence of factors are given. Degrees of freedom (df), second-order Akaike's information criterion values (AICc), AICc differences (Δ_i) and AICc weights (ω_i)

Model	PC1	PC2	subsp	PC1:subsp	PC2:susbp	df	AICc	Δ_i AICc	ω_i
(1)	−0.079		+	+		5	649.9	0	0.493
(2)	−0.111	−1.531	+	+		6	651.2	1.31	0.256
(3)	−0.163	−4.030	+	+	+	7	651.5	1.60	0.222
(4)	−5.584		+			4	656.8	6.96	0.015
(5)	−5.487	−4.159	+		+	6	658.2	8.33	0.008
(6)	−5.718	−1.129	+			5	658.6	8.74	0.006
(7)	−2.659					3	669.5	19.62	0
(8)	−2.659	0.521				4	671.6	21.75	0
(9)			+			3	671.9	22.06	0
(10)						2	672.5	22.65	0
(11)		−4.026	+		+	5	672.7	22.89	0
(12)		−0.083	+			4	674.1	24.28	0
(13)		0.521				3	674.6	24.73	0

Table 3 Model averaged estimates of parameters included in models (1), (2) and (3) as shown in Table 2, their adjusted standard errors (SE) and 95 % confidence intervals (CIs). 95 % CIs excluding zero are given in italics

Parameter	Estimate±SE	95 % CI
PC1	−0.11±2.22	−4.45 to 4.23
Subsp	*−14.66±4.83*	*−24.12 to −5.20*
PC1:subsp	*−8.07±2.69*	*−13.34 to −2.80*
PC2	−2.69±2.35	−7.29 to 1.91
PC2:subsp (oen)	4.38±3.15	−1.80 to 10.57

Table 5 Model averaged estimates of parameters included in models (1), (2) and (3) as shown in Table 4, their adjusted standard errors (SE) and 95 % confidence intervals (CIs). 95 % CI excluding zero is given in italics

Parameter	Estimate±SE	95 % CI
PC1	*−8.06±1.75*	*−11.95 to −4.62*
Sex	4.96±5.60	−6.02 to 15.93
PC2	−0.35±2.43	−4.40 to 5.11

leucorhoa males (6.85±0.24, *n*=55; Wilcoxon signed-rank test, *W*=676, *p*=0.001), while females of both subspecies did not differ in their aspect ratios (*oenanthe*: 6.78±0.28, *n*=34; *leucorhoa*: 6.75±0.27, *n*=42; Wilcoxon signed-rank test, *W*=1,779, *p*=0.503). There were no differences in the wing load between both subspecies for the corresponding sexes (Wilcoxon signed-rank tests: *p*>0.09; Fig. 5).

Effect of physiology and aerodynamics on arrival date

Both sexes of *oenanthe* wheatears were present on Helgoland in all study years from mid-March until beginning of June (Fig. 1). Median arrival dates of male (8 May) and female (9 May) *oenanthe* wheatears did not differ significantly (Wilcoxon signed-rank test: *W*=40,080, *p*=0.21), whereas male *leucorhoa* wheatears arrived significantly earlier (27 April) than their females (4 May; Wilcoxon signed-rank test: *W*=11,468, *p*<0.0001). In both subspecies, males older than second calendar year (median arrival date: *oenanthe*, 2 May, *n*=71 and *leucorhoa*, 24 April; *n*=27) arrived significantly earlier than younger individuals (*oenanthe*, 9 May; *n*=246

and *leucorhoa*, 27 April; *n*=158; Wilcoxon signed-rank tests: *p* values <0.009). Male *leucorhoa* wheatears arrived significantly earlier than male *oenanthe* wheatears (Wilcoxon signed-rank test: *W*=40,730, *p*<0.0001), but there was no significant difference between the females (Wilcoxon signed-rank test: *W*=35,097, *p*=0.08; Fig. 1).

The subspecies and the interaction PC1/subspecies had a significant influence on arrival date of wheatears on Helgoland in spring (Tables 2 and 3). Both subspecies were therefore analysed separately. In *oenanthe* wheatears, PC1 was the most important parameter affecting arrival date (Tables 4 and 5). The higher the values of the included properties (fuel deposition rate, mass of fed mealworms, nocturnal fuel loss rate and fuel deposition rate per gram fed mealworms; Fig. 3), the earlier *oenanthe* wheatears arrived on Helgoland (Table 5). Sex and PC2 did not significantly influence *oenanthe* wheatears arrival date at the stopover site (see also Fig. 1). In contrast, PC2 summarizing the aerodynamic properties (wing pointedness index, aspect ratio and wing load; Fig. 3) affected the seasonal occurrence of *leucorhoa* wheatears on Helgoland (Tables 6 and 7). Here, individuals being more suited for fast and efficient flying arrived earlier at the stopover site than others. Furthermore, sex had a significant effect on arrival date with males arriving prior to their females (see above; Fig. 1 and Table 7).

Table 4 Comparison of candidate models to investigate the effect of PC1, PC2, sex and the corresponding interactions on spring arrival date in *oenanthe* northern wheatears on Helgoland. Model's coefficients and presence of factors are given. Degrees of freedom (*df*), second-order Akaike's information criterion values (AIC$_c$), AIC$_c$ differences (Δ_i) and AIC$_c$ weights (ω_i)

Model	PC1	PC2	Sex	PC1:sex	PC2:sex	df	AIC$_c$	Δ_i AIC$_c$	ω_i
(1)	−8.124					3	392.0	0	0.464
(2)	−7.908		+			4	393.5	1.53	0.216
(3)	−8.066	0.353				4	394.4	2.39	0.140
(4)	−7.591		+	+		5	396.0	4.00	0.063
(5)	−7.855	0.324	+			5	396.0	4.05	0.061
(6)	−7.963	−2.150	+		+	6	397.4	5.41	0.031
(7)	−7.541	0.319	+	+		6	398.6	6.65	0.017
(8)	−7.929	−2.138	+	+	+	7	400.2	8.22	0.008
(9)						2	409.1	17.15	0
(10)			+			3	409.7	17.74	0
(11)		2.749				3	410.4	18.45	0
(12)		2.596	+			4	411.2	19.22	0
(13)		0.717	+		+	5	413.2	21.24	0

Table 6 Comparison of candidate models to investigate the effect of PC1, PC2, sex and the corresponding interactions on spring arrival date in *leucorhoa* northern wheatears on Helgoland. Model's coefficients and presence of factors are given. Degrees of freedom (*df*), second-order Akaike's information criterion values (AIC$_c$), AIC$_c$ differences (Δ_i) and AIC$_c$ weights (ω_i)

Model	PC1	PC2	Sex	PC1:sex	PC2:sex	*df*	AIC$_c$	Δ_i AIC$_c$	ω_i
(1)		−3.990	+			4	243.4	0	0.450
(2)	1.078	−3.961	+			5	245.6	2.19	0.151
(3)		−4.788	+		+	5	246.0	2.63	0.121
(4)	2.521	−4.499	+	+		6	246.4	2.97	0.102
(5)			+			3	248.0	4.62	0.045
(6)	1.285	−5.153	+		+	6	248.2	4.82	0.040
(7)		−4.026	+			3	248.7	5.30	0.032
(8)	2.678	−5.550	+	+	+	7	249.3	5.92	0.023
(9)	1.178		+			4	250.0	6.63	0.016
(10)	−0.162	−4.030				4	251.3	7.91	0.009
(11)						2	252.1	8.74	0.006
(12)	1.851		+	+		5	252.5	9.06	0.005
(13)	−0.079					2	254.6	11.18	0.002

Discussion

Between-subspecies comparisons revealed that *leucorhoa* wheatears had a higher fuel deposition rate and more pointed wings than *oenanthe* wheatears. As the main difference between the subspecies is the nature of the ecological barriers to be crossed, the differences between both subspecies are most likely a result of the different selection pressures related to the crossing of the sea barrier. In male *leucorhoa* wheatears, the aerodynamic properties would allow a faster airspeed and lower flight costs then in their female counterparts. Physiological traits of early *oenanthe* wheatears also enabled fast migration, which might be the reason for their relatively early arrival at the stopover site in comparison to late individuals. Their aerodynamic properties did not seem to influence arrival date. In contrast, the aerodynamic properties correlated with the seasonal occurrence of *leucorhoa* wheatears at the stopover site, with individuals possessing features for faster airspeeds and lower flight costs arriving earlier.

Seasonal occurrence

As in other trans-Sahara migrants, male *leucorhoa* wheatears preceded their females (Spina et al. 1994) and older males arrived

Table 7 Model averaged estimates of parameters included in models (1), (2), (3) and (4) as shown in Table 6, their adjusted standard errors (SE) and 95 % confidence intervals (CIs). 95 % CIs excluding zero are given in italics

Parameter	Estimate±SE	95 % CI
PC2	*−4.165±1.757*	*−7.608 to −0.721*
Sex	*10.693±4.306*	*2.254 to 19.132*
PC1	1.660±1.785	− 1.839 to 5.160
PC2:sex	1.269±3.234	− 5.056 to 7.593
PC1:sex	−4.354±3.234	− 10.692 to 1.984

prior to younger males. The lacking protandry of *oenanthe* wheatears might be explained by a seasonally decreased trapping effort (Fig. 1) because observational data demonstrated a proportional increase in females with season (Dierschke et al. 2005, 2011). Considering data from 2010 with a seasonally constant trapping effort, male *oenanthe* wheatears arrived prior to their females (median arrival date: males, 28 April 2010, *n*=40; females, 8 May 2010, *n*=34; Wilcoxon signed-rank test: $W=481$, $p=0.031$) as observed at European breeding grounds (Conder 1956; Brook 1979; Buchmann 2001).

The seasonal decline of PC1 in *oenanthe* wheatears supports our hypothesis that migrants arrive earlier the higher their fuel deposition rate, i.e. the higher their speed of migration (Table 3). Alternatively, early birds may need more fuel reserves, as they may encounter more frequent cold spells (Gunnarsson et al. 2006). The aerodynamic properties of the wing did not affect the arrival date of *oenanthe* wheatears. In contrast, Maggini et al. (2013) found that *oenanthe* wheatears with more pointed wings arrived later in season than individuals with less pointed wings on a Mediterranean Island during spring. Based on stable-hydrogen isotope ratios, they argued that earlier birds might breed in "close" vicinity of their study area, whereas late individuals breed further north. *Oenanthe* wheatears described in Maggini et al. (2013) most likely breed in central and northern Europe, including the Baltic Sea area (Delingat et al. 2011). *Oenanthe* wheatears passing Helgoland breed in western Scandinavia, with only few individuals from the Baltic Sea region (Delingat et al. 2011; Dierschke et al. 2011). As Scandinavia is not characterized by a gradient in the stable-hydrogen isotope ratios (Bowen and Revenaugh 2003; Bowen 2008, 2010), they would not reveal the potential breeding areas of the *oenanthe* wheatears passing Helgoland.

Contrasting *oenanthe* wheatears, arrival date was significantly influenced by the aerodynamic traits in *leucorhoa* birds, with early individuals being more efficient and faster flyers than late ones. Male *leucorhoa* wheatears had more

pointed wings and a higher aspect ratio than their females (Fig. 5). This could contribute to explain *leucorhoa* wheatear's protandry on Helgoland (Hedenström and Pettersson 1987; Fig. 1) in addition to the endogenously controlled protandry (Maggini and Bairlein 2012). If males with a high migration speed arrive early in the breeding area, they will have a higher probability of occupying more favourable territories than "late migrants" (Kokko 1999). This would support the rank advantage hypothesis (indirect selection for protandry) (Morbey and Ydenberg 2001, but see also Kokko et al. 2006). This is likely to be true for wheatears, as early arriving individuals have generally higher reproduction success than late birds (Currie et al. 2000; Buchmann 2001), but this difference might also depend on other factors than territory quality (Currie et al. 2000; Arlt and Pärt 2008; Arlt et al. 2008).

Differences between subspecies

Both sexes of *leucorhoa* wheatears showed a significantly higher fuel deposition rate, probably caused by the higher amount of fed mealworms, than their corresponding sexes of *oenanthe* wheatears. Additionally, fuel deposition rate per gram fed mealworms was higher in *leucorhoa* wheatears (Fig. 4). The most parsimonious explanation seems to be that *leucorhoa* wheatears possess a physiological adaptation, i.e. enhanced lipogenesis, to accumulate body mass more efficiently than *oenanthe* wheatears which corresponds with the observed endogenously control of this migratory traits in wheatears (Maggini and Bairlein 2010; Bulte and Bairlein 2013). The costly processes for obtaining a high-fuel deposition rate are enhanced during fattening and seemingly more so in *leucorhoa* than in *oenanthe* wheatears.

While crossing a sea barrier, the aerodynamic properties of the wing increasing the success of such flights should be favoured by selection. Here, we demonstrate that *leucorhoa* wheatears had wings better adapted for fast and efficient flying, i.e. more pointed wings and higher aspect ratios, than *oenanthe* wheatears (Fig. 5). However, as both subspecies were distinguished by wing length and as aspect ratio is a function of wing length, the difference between the subspecies in this trait cannot be given much biological significance. In *oenanthe* wheatears, the almost entirely overland migration route might have favoured a higher manoeuvrability to potentially increase foraging success and predator avoidance, in trade-off an energetically more costly and slower flight style. This hypothesis is reinforced by Alaskan *oenanthe* wheatears having more pointed wings than European *oenanthe* wheatears (Wilcoxon signed-rank test: $W = 12,638$, $p < 0.0001$) but less pointed wings than *leucorhoa* wheatears (Wilcoxon signed-rank tests: $W = 7,165$, $p = 0.016$; data from Schmaljohann et al. (2013); Fig. 5). Hence, the general assumption that migration distance is the driving force forming wing shape in migrants (Mönkkönen 1995; Marchetti et al. 1995; Fitzpatrick 1998; Lockwood et al. 1998; Fiedler 2005; Förschler and Bairlein 2011) does not fully apply to wheatears. Alaskan *oenanthe* wheatears migrate a far longer distance than *leucorhoa* wheatears (14,500 versus 5,000–7,500 km), but do not encounter any significant sea barrier (Schmaljohann et al. 2012b). We, therefore, conclude that not the migration distance itself, but more importantly the nature of the migration route (presence of ecological barriers) sets the important selection pressure being responsible for species' expression in the appropriate physiological traits and aerodynamic properties.

Bird's overall migration speed is a combination of its appropriate physiological traits (Alerstam and Lindström 1990), its aerodynamic properties (Pennycuick 2008), its nocturnal departure time (Schmaljohann et al. 2013) and the experienced environmental conditions en route (Liechti 2006). Light-level geolocator studies have shown that the total migration speed was highest in *leucorhoa* wheatears (290 km day^{-1}), slightly slower in Alaskan *oenanthe* wheatears (260 km day^{-1}) and lowest in *oenanthe* wheatears from western Germany (130 km day^{-1}, Bairlein et al. 2012; Schmaljohann et al. 2012a, b). The differences in these total migration speeds are in agreement with our hypotheses, as *leucorhoa* wheatears' physiological and aerodynamic properties jointly enable a higher migration speed and probably even more important lower flight costs than in *oenanthe* wheatears.

References

Alerstam T, Lindström K (1990) Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner E (ed) Bird migration: physiology and ecophysiology. Springer, Berlin, pp 331–351

Alterstam T (2001) Detours in bird migration. J Theor Biol 209:319–331

Arlt D, Pärt T (2008) Post-breeding information gathering and breeding territory shifts in northern wheatears. J Anim Ecol 77:211–219

Arlt D, Forslund P, Jeppsson T, Pärt T (2008) Habitat-specific population growth of a farmland bird. PLoS ONE 3:e3006

Bächler E, Hahn S, Schaub M, Arlettaz R, Jenni L, Fox JW, Afanasyev V, Liechti F (2010) Year-round tracking of small trans-Saharan migrants using light-level geolocators. PLoS ONE 3:e9566

Bairlein F (1985) Efficiency of food utilization during fat deposition in the long-distance migratory garden warbler *Sylvia borin*. Oecologia 68:118–125

Bairlein F (1986) Spontaneous, approximately semimonthly rhythmic variations of body weight in the migratory garden warbler (*Sylvia borin*, Boddaert). J Comp Physiol B 156:859–865

Bairlein F (1987) Nutritional requirements for maintenance of body weight and fat deposition in the long-distance migratory garden warbler, *Sylvia borin* (Boddaert). Comp Biochem Physiol 86:A:337–A:347

Bairlein F, Norris DR, Nagel R, Bulte M, Voigt CC, Fox JW et al (2012) Cross-hemisphere migration of a 25-gram songbird. Biol Lett 8:505–507

Baldwin MW, Winkler H, Organ CL, Helm B (2010) Wing pointedness associated with migratory distance in common-garden and comparative studies of stonechats (*Saxicola torquata*). J Evol Biol 23:1050–1063

Bearhop S, Fiedler W, Furness RW, Votier SC, Waldron S, Newton J et al (2005) Assortative mating as a mechanism for rapid evolution of a migratory divide. Science 310:502–504

Berthold P, Querner U (1981) Genetic basis of migratory behavior in European warblers. Science 212:77–79

Berthold P, Querner U (1988) Was Zugunruhe wirklich ist - eine quantitative Bestimmung mit Hilfe von Video-Aufnahmen bei Infrarotbeleuchtung. J Ornithol 129:372–375

Bowen GJ (2008) Spatial analysis of the intra-annual variation of precipitation isotope ratios and its climatological corollaries. J Geophys Res 113:D05113

Bowen GJ (2010) Isoscapes: spatial pattern in isotopic biogeochemistry. Annu Rev Earth Pl Sc 38:161–187

Bowen GJ, Revenaugh J (2003) Interpolating the isotopic composition of modern meteoric precipitation. Water Resour Res 39:1299

Bowlin MS, Wikelski M (2008) Pointed wings, low wingloading and calm air reduce migratory flight costs in songbirds. PLoS ONE 3:e2154

Brook MDL (1979) Differences in the quality of territories held by wheatears (*Oenanthe oenanthe*). J Anim Ecol 48:21–32

Buchmann M (2001) Die Brutbiologie des Steinschmatzers (*Oenanthe oenanthe*) auf intensiv genutzten Flächen in Rheinland-Pfalz. Vogelwarte 41:1–17

Bulte M, Bairlein F (2013) Endogenous control of migratory behavior in Alaskan northern wheatears *Oenanthe oenanthe*. J Ornithol 154:567–570

Conder PJ (1956) The territory of the wheatear *Oenanthe oenanthe*. Ibis 98:453–459

Conklin J, Battley PF, Potter MA, Fox JW (2010) Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. Nat Commun 1:67

Currie D, Thompson DBA, Burke T (2000) Patterns of territory settlement and consequences for breeding success in the wheatear *Oenanthe oenanthe*. Ibis 142:389–398

Delingat J, Dierschke V, Schmaljohann H, Mendel B, Bairlein F (2006) Daily stopovers as optimal migration strategy in a long-distance migrating passerine: the northern wheatear. Ardea 94:593–605

Delingat J, Hobson K, Dierschke V, Schmaljohann H, Bairlein F (2011) Population differentiation of northern wheatears by means of morphometric data and stable isotopes. J Ornithol 152:383–395

Dierschke V, Delingat J (2001) Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behav Ecol Sociobiol 50:535–545

Dierschke V, Mendel B, Schmaljohann H (2005) Differential timing of spring migration in northern wheatears *Oenanthe oenanthe*: hurried males or weak females? Behav Ecol Sociobiol 57:470–480

Dierschke J, Dierschke V, Hüppop K, Hüppop O, Jachmann KF (2011) Die Vogelwelt der Insel Helgoland. OAG Helgoland, Helgoland

Dinno A (2009) Exploring the sensitivity of Horn's parallel analysis to the distributional form of random data. Multivariate Behav Res 44:362–388

Erni B, Liechti F, Bruderer B (2002) Stopover strategies in passerine bird migration: a simulation study. J Theor Biol 219:479–493

Fiedler W (2005) Ecomorphology of the external flight apparatus of blackcaps (*Sylvia atricapilla*) with different migration behaviour. Ann NY Acad Sci 1046:253–263

Fitzpatrick S (1998) Intraspecific variation in wing length and male plumage coloration with migratory behaviour in continental and Island populations. J Avian Biol 29:248

Förschler MI, Bairlein F (2011) Morphological shifts of the external flight apparatus across the range of a passerine (northern wheatear) with diverging migratory behaviour. PLoS ONE 6:e18732

Fransson T, Jakobsson S, Johansson P, Kullberg C, Lind J, Vallin A (2001) Magnetic cues trigger extensive refuelling. Nature 414:35–36

Gerson AR, Guglielmo CG (2013) Energetics and metabolite profiles during early flight in American robins (*Turdus migratorius*). J Comp Physiol B 183:983–991

Gill RE, Tibbitts TL, Douglas DC, Handel CM, Mulcahy DM, Gottschalck JC et al (2009) Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? Proc R Soc Lond B 276:447–457

Glorfeld LW (1995) An improvement on Horn's parallel analysis methodology for selecting the correct number of factors to retain. Educ Psychol Meas 55:377–393

Gunnarsson TG, Gill JA, Atkinson PW, GéLinaud G, Potts PM, Croger RE, Gudmundsson GA, Appleton GF, Sutherland WJ (2006) Population-scale drivers of individual arrival times in migratory birds. J Anim Ecol 75:1119–1127

Gwinner E (1996) Circadian and circannual programmes in avian migration. J Exp Biol 199:39–48

Hedenström A, Pettersson J (1987) Migration routes and wintering areas of willow warblers *Phylloscopus trochilus* (L.) ringed in Fennoscandia. Ornis Fennica 64:137–143

Henningsson SS, Alerstam T (2005) Barrier and distances as determinants for the evolution of bird migration links: the arctic shorebird system. Proc R Soc Lond B 272:2251–2258

Horn JL (1965) A rationale and a test for the number of factors in factor analysis. Psychometrika 30:179–185

Houston AI (1998) Models of optimal avian migration: state, time and predation. J Avian Biol 29:395–404

Jenni L, Jenni-Eiermann S (1998) Fuel supply and metaboli constraints in migrating birds. J Avian Biol 29:521–528

Jenni L, Winkler R (1994) Moult and ageing of European passerines. Academic Press, London

Klaassen M, Biebach H (1994) Energetics of fattening and starvation in the long-distance migratory garden warbler, *Sylvia borin*, during the migratory phase. J Comp Physiol B 164:362–371

Kokko H (1999) Competition for early arrival in birds. J Anim Ecol 68:940–950

Kokko H, Gunnarsson TG, Morrell LJ, Gill JA (2006) Why do female migratory birds arrive later than males? J Anim Ecol 75:1293–1303

Langin KM, Marra PP, Nemeth Z, Moore FR, Kyser KT, Ratcliffe LM (2009) Breeding latitude and timing of spring migration in songbirds crossing the Gulf of Mexico. J Avian Biol 40:309–316

Lank DB, Butler RW, Ireland J, Ydenberg RC (2003) Effects of predation danger on migration strategies of sandpipers. Oikos 103:303–319

Leisler B, Winkler H (2003) Morphological consequences of migration in passerines. In: Berthold PG (ed) Avian Migration. Springer, Berlin, pp 175–186

Liechti F (2006) Birds: blowin' by the wind? J Ornithol 147:202–211

Lindström A, Alerstam T (1992) Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. Am Nat 140:477–491

Lockwood R, Swaddle JP, Rayner JMV (1998) Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. J Avian Biol 29:273–292

Maggini I (2009) Migratory strategies in the northern wheatear (*Oenanthe oenanthe*). Institute of Avian Research "Vogelwarte Helgoland"

Maggini I, Bairlein F (2010) Endogenous rhythms of seasonal migratory body mass changes and nocturnal restlessness in different populations of northern wheatear *Oenanthe oenanthe*. J Biol Rhythm 25: 268–276

Maggini I, Bairlein F (2012) Innate sex differences in the timing of spring migration in a songbird. PLoS ONE 7:e31271

Maggini I, Bairlein F (2013) Metabolic response to changes in temperature in northern wheatears from an arctic and a temperate populations. J Avian Biol. doi:10.1007/s10336–012–0896–1

Maggini I, Spina F, Voigt CC, Ferri A, Bairlein F (2013) Differential migration and body condition in northern wheatears (*Oenanthe oenanthe*) at a Mediterranean spring stopover site. J Ornithol 154: 321–328

Marchetti K, Price T, Richman A (1995) Correlates of wing morphology with foraging behaviour and migration in the genus *Phylloscopus*. J Avian Biol 26:177–181

Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886

Mönkkönen M (1995) Do migrant birds have more pointed wings? A comparative study. Evol Ecol 9:520–528

Morbey YE, Ydenberg RC (2001) Protandrous arrival timing to breeding areas: a review. Ecol Lett 4:663–673

Newton I (2007) Weather-related mass-mortality events in migrants. Ibis 149:453–467

Norberg UM (1990) Vertebrate flight: mechanics, physiology, morphology, ecology and evolution. Springer, Heidelberg

Pennycuick CJ (1999) Measuring bird' wings for flight performance calculations. Boundary Layer, Bristol

Pennycuick CJ (2008) Modelling the flying bird. Elsevier, Amsterdam

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.r-project.org/

Rayner JMV (1988) Form and function in avian flight. In: Johnston RF (ed) Current ornithology. Plenum, New York, pp 1–66

Rychlik L, Jancewicz E (2002) Prey size, prey nutrition, and food handling by shrews of different body sizes. Behav Ecol 13:216–223

Saino N, Szép T, Romano M, Rubolini D, Spina F, Møller AP (2004) Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. Ecol Lett 7:21–25

Schaub M, Liechti F, Jenni L (2004) Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. Anim Behav 67:229–237

Schmaljohann H, Naef-Daenzer B (2011) Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird. J Anim Ecol 80:1115–1122

Schmaljohann H, Becker PJJ, Karaardic H, Liechti F, Naef-Daenzer B, Grande C (2011) Nocturnal exploratory flights, departure time, and direction in a migratory songbird. J Ornithol 152:439–452

Schmaljohann H, Buchmann M, Fox JW, Bairlein F (2012a) Tracking migration routes and the annual cycle of a trans-Sahara songbird migrant. Behav Ecol Sociobiol 66:915–922

Schmaljohann H, Fox JW, Bairlein F (2012b) Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. Anim Behav 84:623–640

Schmaljohann H, Korner-Nievergelt F, Naef-Daenzer B, Nagel R, Maggini I, Bulte M et al (2013) Stopover optimization in a long-distance migrant: the role of fuel load, temperature and nocturnal take-off time in Alaskan northern wheatears (*Oenanthe oenanthe*). Front Zool 10:26

Shamoun-Baranes J, Leyrer J, van Loon E, Bocher P, Robin F, Meunier F et al (2010) Stochastic atmospheric assistance and the use of emergency staging sites by migrants. Proc R Soc Lond B 277:1505–1511

Singh J, Budki P, Rani S, Kumar V (2011) Temperature alters the photoperiodically controlled phenologies linked with migration and reproduction in a night-migratory songbird. Proc R Soc Lond B 279:509–515

Spina F, Massi A, Montemaggiori A (1994) Back from Africa: who's running ahead? Aspects of differential migration of sex and age classes in Palearctic-African spring migrants. Ostrich 65:137–150

Svensson L (1992) Identification guide to European passerines. BTO, Stockholm

Swaddle JP, Lockwood R (2003) Wingtip shape and flight performance in the European starling *Sturnus vulgaris*. Ibis 145:457–464

Totzke U, Hübinger A, Bairlein F (1998) Glucose utilization rate and pancreatic hormone response to oral glucose loads are influenced by the migratory condition and fasting in the garden warbler (*Sylvia borin*). J Endocrinol 158:191–196

Whittow GC (2000) Avian physiology. Academic, San Diego