

Differential migration and body condition in Northern Wheatears (*Oenanthe oenanthe*) at a Mediterranean spring stopover site

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Abstract In many species of migratory birds, individuals of different populations, sexes and age classes migrate at different times and manage their energy reserves according to their specific migratory strategies. In this study, we analyzed the migratory patterns related to geographic provenance, sex and age in the Northern Wheatear *Oenanthe oenanthe*, a long-distance migratory passerine, during one spring season on the island of Ventotene (Italy), a Mediterranean stopover site. Individuals of different sex and age did not differ significantly in their average date of passage, but birds with longer and more pointed wings passed through later in the season than birds with shorter wings. Morphometric measurements combined with isotopic analysis revealed that late-arriving birds probably belonged to more distant breeding populations and this later date of passage probably mirrors the delayed arrival observed at their northern breeding grounds. Adult birds arrived in better condition than second-year birds, possibly as a result of better energy management. Birds passing through later in the season were also in better condition, which might be explained by their wing morphology

favoring endurance flights and thus improving energetic efficiency when crossing the Mediterranean. Birds which migrate longer distances might also carry larger fuel loads to safely complete their journey. This intra-specific study shows that the birds' organization of their migration schedule is population-specific in correspondence to the temporal requirements which depend on the different environmental conditions on the breeding grounds.

Keywords Differential migration · *Oenanthe oenanthe* · Barrier crossing · Body condition · Migration timing · Mediterranean

Zusammenfassung

Differentielles Zugverhalten und Körperkondition beim Steinschmätzer (*Oenanthe oenanthe*) an einen Rastplatz im Mittelmeer im Frühjahr

Bei vielen Zugvögeln ziehen verschiedene Populationen, Männchen und Weibchen und/oder verschiedene Altersgruppen zu verschiedenen Zeiten und gestalten ihre Energiereserven entsprechend ihrer spezifischen Zugstrategie. Wir betrachteten die Zugmuster des Steinschmätzer *Oenanthe oenanthe*, eines Langstreckenziehers, in Beziehung zur Lage des Brutgebietes, zu Geschlecht und Alter während einer Frühjahrssaison auf der italienischen Mittelmeerinsel Ventotene. Die Geschlechter und Altersgruppen unterschieden sich nicht in ihren mittleren Durchzugszeiten, doch zogen Vögel mit längeren und spitzeren Flügeln signifikant später durch als Vögel mit kürzeren Flügeln. Morphometrische Messungen in Kombination mit Isotopenanalysen zeigen, dass die spät durchziehenden Vögel wahrscheinlich zu weiter entfernten Brutpopulationen gehörten, korrespondierend zu deren späterer Ankunft in

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den nördlichen Brutgebieten. Altvögel kamen auf Ventotene in besserer Kondition an als Vögel in ihrem zweiten Kalenderjahr, möglicherweise eine Folge davon, dass Altvögel mit ihrer Energie besser haushalten. Auch waren später in der Saison durchziehende Vögel in besserer Kondition. Dies könnte eine Folge ihrer Flügelmorphologie sein, die lange Flüge begünstigt und so die Energiebilanz beim Flug über das Mittelmeer verbessert. Auch könnten die weiter ziehenden Vögel mehr Energiereserven für erfolgreichen Zug an sich benötigen. Diese intra-spezifische Studie zeigt, dass der Zugablauf populationspezifisch ist, korrespondierend mit den zeitlichen Anforderungen, die von den unterschiedlichen Umweltbedingungen im Brutgebiet bestimmt sind.

Introduction

In migratory birds, differences in timing and migratory routes often result from specific needs both at the individual and population level (Newton 2008). Birds need to adjust their migratory journeys in balance of two important criteria: arrival at their destination to initiate breeding at the optimal time, and high likelihood of completing their migration successfully. In long-distance migrants with broad breeding ranges and wintering areas, conditions may vary geographically and seasonally. This may require some adjustments of their migration strategies according to the birds' place of origin and the distance to be covered. For example, birds should arrive at their breeding grounds in order to match the timing of optimal food availability for breeding (Lack 1968; van Noordwijk et al. 1995; Jonzén et al. 2007; Newton 2008). Furthermore, males and females or respective age classes may be exposed to different ecological and physiological constraints which may lead to different migration timing. For example, in protandrous bird species, males arrive earlier than females at the breeding grounds (Morbey and Ydenberg 2001; Coppack and Pulido 2009).

In general, migratory birds are faced with a trade-off between minimizing energy expenditure and reducing the total time needed for the journey (Hedenström and Ålerstam 1997). Both early arrival and body condition at arrival have an impact on the reproductive fitness of birds (Potti and Montalvo 1991; Sandberg and Moore 1996; Currie et al. 2000; Smith and Moore 2005), although the relative importance of these factors may differ between sexes and age classes. Since the speed of migration depends to a greater extent on stopover duration than on actual flight speed (Hedenström and Ålerstam 1997), we might expect birds seeking to reduce journey duration to shorten stopovers, thus carrying lower fuel stores, whereas birds aiming to arrive at their breeding grounds in good body condition might travel more

slowly, but carrying higher fuel reserves. However, these strategies are not mutually exclusive and may vary throughout the season. Environmental variables such as adverse weather (e.g., low temperatures or wind drift) may also affect migratory strategies. Timing of migration and physiological correlates vary between populations, sexes, and age classes, and different species may adopt different strategies in order to match their specific requirements. Therefore, investigating the patterns of differential migration within a species is of paramount importance to understand the selective pressures acting at both the individual and population levels.

Differential migration can be observed en route at staging places (Newton 2008) provided that sexes, age classes, and populations can be distinguished from each other. Morphometric measurements are a useful tool for this purpose, since some morphological variables (e.g., body size or wing shape; Lockwood et al. 1998) vary in many species with the distance covered during migration (Chandler and Mulvihill 1990; Marchetti et al. 1995; Fiedler 2005). In addition, the analysis of stable isotopes in feathers has provided valuable information on migratory connectivity and offers a further tool for assigning individual birds to specific breeding populations (Rubenstein et al. 2002; Hobson 2005; Hobson and Wassenaar 2008). Over the past decade, stable hydrogen ratios of feathers have helped to identify migratory connectivity in a range of migratory species (Hobson and Wassenaar 2008), and the analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ has shown the different wintering grounds of two different subspecies of Willow Warbler (*Phylloscopus trochilus*) from Scandinavia (Chamberlain et al. 2000).

The Northern Wheatear (*Oenanthe oenanthe*) is a widespread passerine with a Holarctic breeding range; all populations winter in sub-Saharan Africa (Cramp 1988). It has been shown that populations and sexes differ in their timing of migration (Dierschke et al. 2005), and these findings have been confirmed by laboratory studies which have revealed the endogenous basis of these differences (Maggini and Bairlein 2010; 2012). Previous studies on the Wheatear were focused on northern stopover sites, where birds of different subspecies were easily assigned to their breeding population (Delingat et al. 2011). In this study, we wanted to investigate the migratory patterns of Northern Wheatears at a more southern stopover site placed just after the Mediterranean crossing, offering a unique opportunity to sample staging migrants belonging to a mix of geographical populations, all belonging to the nominate subspecies. In particular, we addressed the following questions:

1. Are differences in the date of passage related to sex, age, and population?
2. Do birds differ in body condition depending on passage date, sex, age, or population?

Methods

Study site

We trapped Northern Wheatears on the island of Ventotene, Italy (40°47'N, 13°25'E, some 50 km off the western Italian coast), during spring 2006. The island is only 1.54 km² in area and is known for attracting large numbers of migrants during spring migration (Spina et al. 1993). Trapping effort was continuous between 1 March and 30 May, and personal observations did not reveal the presence of Wheatears outside this study period. Therefore, we assume to have covered the whole spring migratory season of this species on the island.

Capture protocol

Birds were mostly trapped within a standardized program using a total of 282 m of mist-nets (4 shelves, mesh 16 mm), placed in the macchia vegetation on the southern tip of the island. Additionally, birds were trapped during selected days in an open area on the northern end of the island using spring traps baited with a mealworm. After capture, birds were ringed and morphometric measurements were taken following Bairlein (1995). We measured the length of the primary feathers P2 to P9, the total length of the flattened and stretched wing (maximum chord), tail length, bill length to the skull, bill width, bill depth, and tarsus length. Sex and age were determined from plumage characters (Svensson 1992; Jenni and Winkler 1994). Fat and muscle scores were determined according to Bairlein (1995). Fat scores were given values from 0 to 8, and muscle scores ranged between 0 and 3. Birds were weighed with a precision of ± 0.1 g. For isotopic analysis we sampled the second outermost tail feather (TF5) from every bird.

Stable isotope analysis

Stable-hydrogen isotope ratios of feathers were analyzed at the stable isotope laboratory of the Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany, using an isotope ratio mass spectrometer (Delta V Advantage; Thermo Finnigan, Bremen, Germany) connected to an elemental analyser (HT Elementaranalysator; HEKAtech, Wegberg, Germany) (see Erzberger et al. 2011 for details). We used the international standards IAEA NBS 22 (mineral oil) and IAEA-CH-7 (polyethylene) to determine the stable isotope ratio of the reference gas used in the mass spectrometer. We refer to stable hydrogen isotope ratios in the δ notation, which expresses isotope ratios in relation to an international standard (Vienna Standard Mean Ocean Water for hydrogen) in the unit parts per mil (‰) deviations from the standard.

A small section of feather tissue was clipped from the tip of the feather (350 ± 7 μg) and loaded in silver capsules (IVA Analysetechnik, Meerbusch, Germany), which were allowed to equilibrate with ambient air in a microtiter tray over 1 week. Subsequently, trays were stored for at least 24 h at 50 °C in a drying oven. We used the comparative equilibration method (Wassenaar and Hobson 2003) to account for the amount of exchangeable hydrogen in feather keratin. We used three standards that covered the range of expected $\delta^2\text{H}$ values in our samples. These standards were also used to determine the $\delta^2\text{H}$ of non-exchangeable hydrogen (Wassenaar and Hobson 2000, 2003). The stable hydrogen isotope ratios of the non-exchangeable hydrogen (mean $\delta\text{D}_n \pm 1\text{SD}$) of the standards were: -133.6 ± 1.2 ‰, -109.1 ± 1.2 ‰, and -87.2 ± 1.0 ‰. In the sequential order of one autorun, keratin standards were placed at positions 1–6 (2×3 standards) and at any 9th–11th position (three standards each time). Analytical precision based on the repeated analyses of laboratory keratin standards was always better than 0.851 ‰ (1SD).

Data analysis

We performed a principal component analysis (PCA) to assess the relative importance of morphometric variables for further analysis. Eight variables were included in the PCA: wing length, tail length, tarsus length, bill length to skull, bill depth, bill width, wing pointedness (index C2 in Lockwood et al. 1998), and wing concaveness (index C3 in Lockwood et al. 1998). To assess variation in morphometrics with date, we ran linear models with the first (PCA1) and the second (PCA2) principal components (see “Morphometrics” in the “Results” section), respectively, as response variables and date as the explanatory variable. Age and sex were included in the models as covariates.

To investigate whether there is a link between stable isotope variation and date of arrival, we ran a linear model with $\delta^2\text{H}$ as response variable and date of capture as the explanatory variable. Age, sex, PCA1, and PCA2 were included as covariates.

To investigate variation in body condition with date, we first calculated a body condition index (BCI). BCI was obtained from a PCA of fat score, muscle score, and body mass. In order to correct body mass by size and time of sampling, we used residuals of a linear model with body mass as response variable and PCA1 (as a measure of size) and time of day as covariates. To do this, we had to assume that changes in body mass are linear over the course of the day. This seems to be a good approximation when considering only one mass measurement per individual (Delingat et al. 2009). We then ran a linear model with BCI

as response variable and sex, age, date, PCA1, and PCA2 as explanatory variables.

All response variables were tested for normality with Shapiro–Wilk tests. In all models, non-significant terms were stepwise eliminated until reaching a simplified model, according to the principle of parsimony. The simplified models were tested for heteroscedasticity and non-normality of errors by plotting residuals as described in Crawley (2007). All statistics were performed using the software R 2.8.0 (R Development Core Team 2008).

Results

We trapped 134 Northern Wheatears between 27 March and 13 May 2006. Males passed the island about 3.5 days earlier (median = 16 April) than females (median = 19–20 April). This difference, however, was not significant (Wilcoxon–Mann–Whitney test: $m = 73$, $n = 60$, $W = 1,940$, $p = 0.258$) and, therefore we pooled data (median for adults = 17 April). Second-year birds passed the island at about the same time (median = 16 April) as adults (Wilcoxon–Mann–Whitney test: $m = 47$, $n = 86$, $W = 2129.5$, $p = 0.611$).

Morphometrics

The two first principal components resulting from the PCA were related to overall body size (PCA1) and to wing shape and bill size (PCA2).

PCA1 resulted from the formula:

$$0.379 \times \text{tarsus length} + 0.479 \times \text{wing length} + 0.405 \\ \times \text{bill length} + 0.323 \times \text{bill width} + 0.357 \\ \times \text{bill depth} + 0.471 \times \text{tail length} - 0.071 \times \text{C2} \\ + 0.066 \times \text{C3}$$

PCA2 resulted from the formula:

$$-0.051 \times \text{tarsus length} + 0.508 \times \text{wing length} - 0.431 \\ \times \text{bill length} - 0.199 \times \text{bill width} - 0.380 \times \text{bill depth} \\ + 0.223 \times \text{tail length} - 0.557 \times \text{C2} + 0.096 \times \text{C3}$$

In both formulas, the standardized values of the morphometric variables (subtracting the mean from every value and dividing the difference by the standard deviation) were used. High values of PCA1 indicate larger birds, whereas high values of PCA2 indicate birds with long, pointed wings and smaller bills. PCA1 explained 26.4 % of the total variance in the data (eigenvalue: 2.111), whereas PCA2 explained 19.1 % of the variance (eigenvalue: 1.530).

Shapiro–Wilk normality tests were non-significant for both PCA1 ($W = 0.9949$; $p = 0.920$) and PCA2 ($W = 0.9879$; $p = 0.287$), thus allowing the use of

parametric statistics. PCA1 was significantly correlated with sex, males being larger than females (Table 1a) and date. Smaller birds passed through later in the season (Table 1a; Fig. 1). PCA2 was significantly related to sex (Table 1b) and date. Birds with longer and more pointed wings (representing populations flying longer distances; Delingat et al. 2011), and also smaller bills, passed later in the season than birds from populations flying shorter distances (Table 1b; Fig. 2). The interaction term of sex and date was close to significance ($p = 0.057$; Table 1b), and removing it from the model caused an increase in Akaike Information Criterion (AIC), so we did not drop this term from the final model. The increasing slope in PCA2 with date was steeper in males than in females (Fig. 2).

Stable isotopes

Preliminary data exploration of deuterium values revealed the presence of two outliers in the dataset ($\delta^2\text{H} = -38.0$ and $+11.4$ ‰, respectively). We removed these values from further analysis since feathers with such high $\delta^2\text{H}$ values are likely to have been grown in the African wintering grounds (see, e.g., Bowen et al. 2005), and therefore do not give any indication of the breeding provenance of these two birds. Thus, we performed analysis of deuterium values of a total of 63 birds, which ranged from a minimum of $\delta^2\text{H} = -152.9$ ‰ to a maximum of $\delta^2\text{H} = -54.2$ ‰. After deletion of the two outliers, the Shapiro–Wilk normality test was not significant ($W = 0.9773$, $p = 0.277$), thus allowing the use of parametric statistics. $\delta^2\text{H}$ was significantly correlated with date of passage and PCA2 (Table 2). Birds with long and pointed wings had lower $\delta^2\text{H}$ values and passed the stopover site later in the season (Fig. 3).

Body condition

BCI (the first principal component of a PCA using the standardized values of size-corrected body mass, fat, and muscle scores) was obtained from the formula:

$$\text{BCI} = 0.596 \times \text{fat score} + 0.513 \times \text{muscle score} + 0.619 \\ \times \text{size-corrected body mass}$$

BCI accounted for 62.4 % of the variance and had an eigenvalue of 1.871. Preliminary data exploration of BCI data revealed one outlier (BCI = -5.754). We decided to remove this data point from further analysis because the individual was clearly exhausted (fat and muscle scores = 0, body mass = 16.6 g) and therefore we did not consider it as representative. After deletion of the outlier, the Shapiro–Wilk normality test was not significant ($W = 0.9864$; $p = 0.221$), which allowed us to use parametric statistics for further analysis. BCI was

Table 1 Outcome of the LM with PCA1 and PCA2 as response variables and sex, age and date as covariates

Covariate	df	Sum of squares	Mean of squares	F value	p
Response variable: PCA1 ^a					
Sex	1	70.9	70.9	47.8	<0.001
Date	1	16.3	16.3	11.0	0.001
Residuals	130	192.9	1.5		
Response variable: PCA2 ^b					
Sex	1	7.6	7.6	6.8	0.010
Date	1	46.3	46.3	41.1	<0.001
Sex × date	1	4.1	4.1	3.7	0.057
Residuals	129	145.2	1.1		

Age was deleted from both models during simplification because of non-significance

^a Adj. $r^2 = 0.301$; $F_{2,130} = 29.39$; p of model <0.001

^b Adj. $r^2 = 0.269$; $F_{3,129} = 17.19$; p of model <0.001

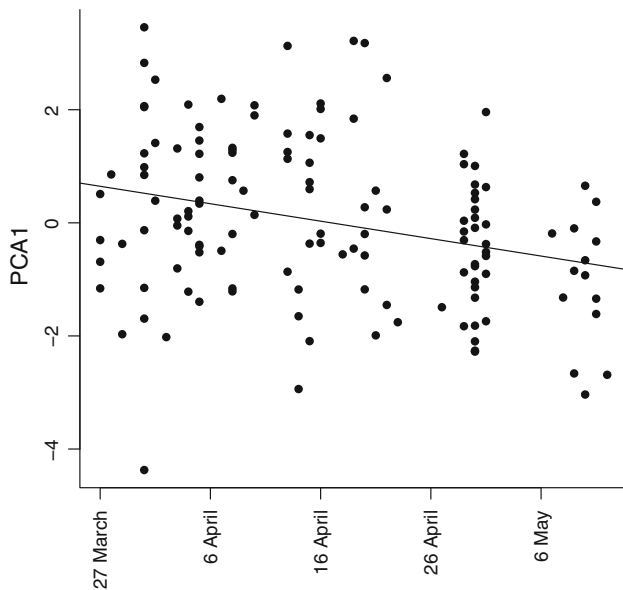


Fig. 1 Variation in body size (as indicated by PCA1) with date in Northern Wheatears (*Oenanthe oenanthe*) in Ventotene in spring 2006. High values of PCA1 indicate larger birds

significantly correlated to age and date (Table 3). Second-year birds were in slightly poorer condition than adults (Fig. 4) and birds passing later in the season were in better condition (Fig. 5).

Table 2 Outcome of the LM with δ^2H as a response variable and date, sex, age, PCA1, and PCA2 as covariates

Covariate	df	Sum of squares	Mean of squares	F value	p
Response variable: δD					
Date	1	1314.1	1314.1	4.3	0.042
PCA2	1	1289.5	1289.5	4.2	0.044
Residuals	62	18875.5	304.4		

Sex, age and PCA1 were deleted from the final outcome of the model because of non-significance

Adj. $r^2 = 0.093$; $F_{2,62} = 4.276$; p of model = 0.018

Discussion

During spring 2006, we observed no significant differences between sexes and age classes in the date of passage of migrating Northern Wheatears on Ventotene. This contrasts with observations of other species (Newton 2008) or of Wheatears at other sites (Dierschke et al. 2005). Protandry is known to occur at the breeding grounds (Currie et al. 2000; Pärt 2001) and to have an endogenous basis in the Wheatear (Maggini and Bairlein 2012). Analysis of data from Ventotene over many years, however, revealed a mean difference in passage dates between males and females of only 1 day (Spina et al. 1994). In our study, the difference in median passage between the two sexes was 3.5 days, albeit the difference was not significant. Possibly, the sex-related or age-related passage times were obscured by the presence of several distinct populations which may differ in their timing of migration, thus leading to a larger variation of passage times and, consequently, to differences that are not statistically detectable.

The morphology of staging Northern Wheatears varied across spring migration on the island of Ventotene. Birds passing the island later were smaller and had proportionately longer, more pointed wings than earlier in the season. The fact that late birds were smaller than early birds could be explained by a higher proportion of migrating females later in the season (although this was not significant in our analysis). Wing length and pointedness have been demonstrated to be related to the overall distance covered on migration between and within species (Chandler and Mulvihill 1990; Marchetti et al. 1995; Fiedler 2005; Förschler and Bairlein 2011). In this study, we were able to give further support to this assumption by analyzing the stable hydrogen ratios in sampled feathers. Birds with longer and more pointed wings had the lowest values of δ^2H , indicating their provenance from breeding grounds further away. When considering the potential breeding ranges of wheatears passing through Ventotene in spring (which most probably lie to the NE, Spina and Volponi

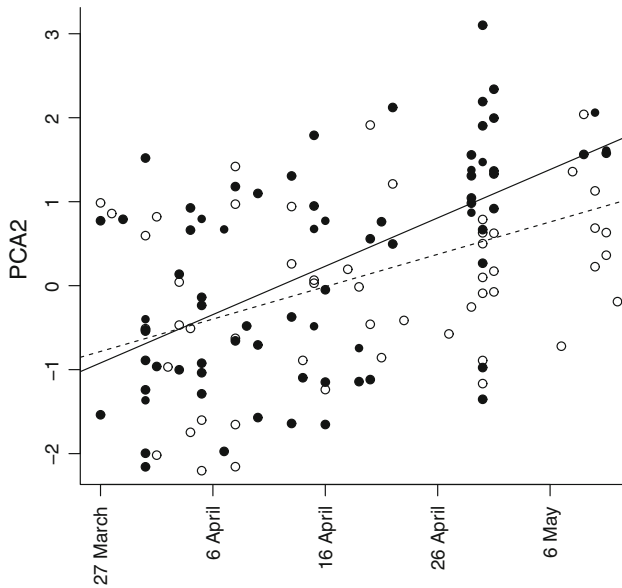


Fig. 2 Variation in PCA2 with date in Northern Wheatears on Ventotene in spring 2006. High values of PCA2 indicate birds with longer and more pointed wings, and smaller bills. *Filled dots and continuous line: males; white dots and dashed line: females*

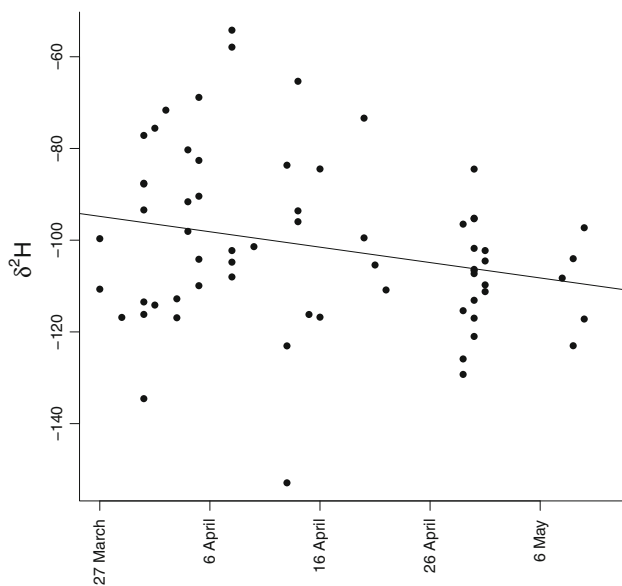


Fig. 3 Variation in $\delta^2\text{H}$ with date in Northern Wheatears on Ventotene in spring 2006. Low values of $\delta^2\text{H}$ indicate provenance from more distant breeding ranges, such as northern Scandinavia or western Siberia

2008), decreasing values of $\delta^2\text{H}$ are found towards the north or towards the east, i.e. in northern Scandinavia or western Siberia (Bowen et al. 2005; West et al. 2009). Thus, our data clearly indicate that birds migrating over longer distances pass through Ventotene later in the season, reflecting later arrival dates at the breeding grounds. Central European birds already occupy their breeding

Table 3 Outcome of the LM with BCI as a response variable and date, sex, age, PCA1 and PCA2 as covariates

Covariate	<i>df</i>	Sum of squares	Mean of squares	<i>F</i> value	<i>p</i>
Response variable: BCI					
Age	1	11.5	11.5	8.1	0.005
Date	1	18.9	18.9	13.4	<0.001
Residuals	127	179.3	1.4		

Sex, PCA1 and PCA2 were deleted from the final outcome of the model because of non-significance

Adj. $r^2 = 0.1315$; $F_{2,127} = 10.76$; *p* of model <0.001

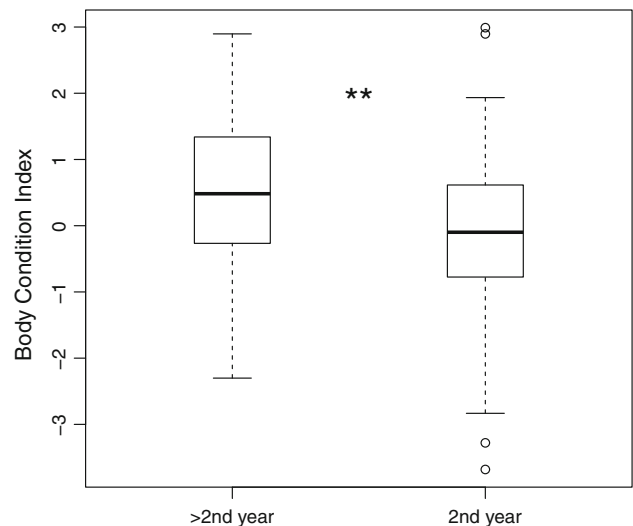


Fig. 4 Body condition of adult (>second year) versus second-year wheatears on Ventotene in spring 2006, as indicated by a body condition index (BCI) calculated using a PCA with fat and muscle scores, and size-corrected body mass as factors. The *horizontal lines* show the median BCI value for both age classes, the bottom and top of the *boxes* show the 25 and 75th percentiles, respectively. *Whiskers* show 1.5 times the interquartile range of the data. *Stars* indicate the significance level, $**p < 0.01$

territories in April, whereas northern Scandinavian and Siberian birds are not on territory before the end of May (Suter 1988). The birds observed on Ventotene later in the season most probably originate from these areas. Differences in phenology of migrating birds belonging to different populations are known from a wide range of species (Lack 1968; van Noordwijk et al. 1995; Jonzén et al. 2007; Newton 2008; Conklin et al. 2010), and this study provides additional data supporting the idea that this is a general pattern.

Almost all Wheatears examined on Ventotene were in relatively good body condition. As only 1 bird out of 134 captures was found to be clearly exhausted, we are confident that our analysis was representative. Second-year birds were in slightly poorer condition than adults.

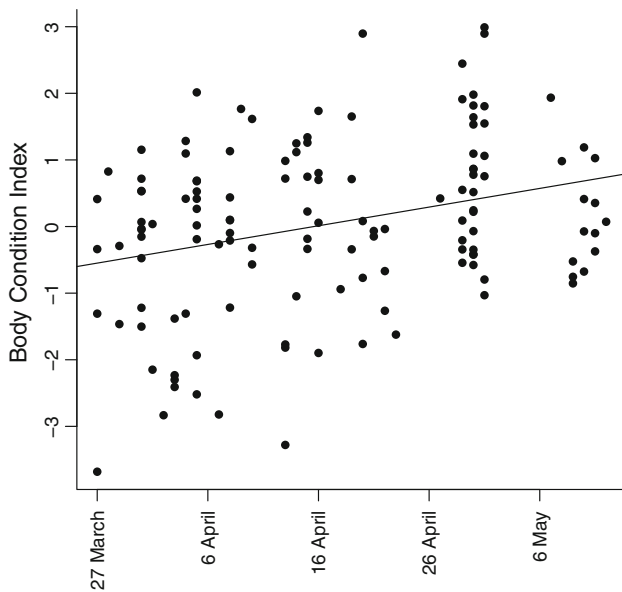


Fig. 5 Variation in BCI with date in Northern Wheatears on Ventotene in spring 2006

However, the difference was relatively small (Fig. 4) and can be explained by age-related migratory history or experience. Birds migrating for the first time might be less efficient in adjusting their energy accumulation and consumption in response to environmental conditions (e.g., Pilastro and Magnani 1997; Woodrey and Moore 1997). Furthermore, birds arrived in better body condition when staging on Ventotene later in the season. This can be explained in several ways: (1) birds passing through later in the season may have allocated more time in refuelling at stopover sites than earlier passage migrants; (2) birds passing through later may have accumulated larger energy stores prior to migration; or (3) all birds may have embarked on the Mediterranean crossing with the same amount of reserves, but birds passing later may have been more efficient in using fuel stores during sea crossing thanks to their longer and more pointed wings. Previous studies of both captive and wild Wheatears have shown that the normal migratory strategy used by this species is daily stopover with refueling (Delingat et al. 2006) and that increased fuel loads are accumulated only prior to the crossing of ecological barriers (Delingat et al. 2008; Maggini and Bairlein 2010). These studies do not report correlations between fuel load and overall distance to be covered for Northern Wheatears (Maggini and Bairlein 2010). Thus, we believe that the Wheatears arriving on Ventotene accumulated just enough reserves on the coast of North Africa in order to cross the Mediterranean, irrespective of the distance to their breeding range further to the north or east. Wheatears are opportunists in terms of food choice (Suter 1988) and, therefore, they can expect to

find refueling opportunities almost anywhere along their migration route. The same pattern can be observed in other species migrating through continental Europe (Bairlein 2003). Therefore, it seems likely that the differences in body condition observed in Wheatears on Ventotene are a consequence of their different wing morphology, although we cannot completely rule out the possibility that birds facing a longer flight are also carrying more energy reserves.

The results of this study indicate that different populations within a bird species adjust their migration schedule to reach their breeding grounds at an appropriate time. The data suggest that more northern and/or eastern populations of Northern Wheatears migrate later than conspecifics breeding in more southern areas. The observed pattern at the stopover sites may shed new light on what we observe in Northern Wheatears at their breeding grounds, in particular since environmental or climatic changes along migratory routes could affect some individuals or populations more than others.

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