

Moulting and wintering grounds of Marsh Warblers *Acrocephalus palustris*: evidence from stable isotopes and ring recoveries

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Abstract. We analysed stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios in Marsh Warbler *Acrocephalus palustris* feathers sampled in Europe and Africa to assess non-breeding habitat selection and location of wintering grounds of different breeding populations. Feather $\delta^{13}\text{C}$ values showed that Marsh Warblers occupy a biome dominated by C_4 vegetation during the stopover in northeastern Africa, whereas C_3 habitats are used during the complete moult in southern Africa. East European Marsh Warblers differed in their stable isotope profiles from other European regions, suggesting a certain level of population segregation in southern Africa. A dual-isotope assignment approach confirmed this difference and helped us restrict the autumn staging areas to lower elevations of the Ethiopian Highlands west of the Rift valley. Available ring recoveries, however, suggested high levels of population mixing both on migration through East Africa and in the final wintering grounds.

Key words: bird migration, feather stable isotopes, ring recoveries, stopover, migratory connectivity, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$

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Over recent decades, dramatic changes in population densities have been documented for long-distance migrants that winter in Africa (Sanderson et al. 2006). To better understand the declines, we should know non-breeding habitat use and the extent of migratory connectivity (degree to which individuals are geographically linked across the annual cycle, Webster et al. 2002). In the case of strong migratory connectivity, individuals of a given breeding population winter close to each other and share similar conditions during winter, whereas low connectivity leads to extensive mixing of individuals that are exposed to diverse selection regimes across the wintering range. Migratory connectivity can thus have important consequences for the ecology and conservation of migratory birds (Sheehy et al. 2010). However, studies assessing the extent of migratory connectivity have been hampered by the extremely low

number of recoveries from conventional ringing (Norris et al. 2006). Stable isotope ratios in avian tissues have therefore been widely used as indicators of geographic origin and habitat use among populations (reviewed by Hobson 2011).

The Marsh Warbler *Acrocephalus palustris* is a small, insectivorous passerine that breeds across the temperate Western Palaearctic region. Birds from the entire breeding range follow the East African migratory pathway, and winter in southeastern Africa (Dowsett-Lemaire & Dowsett 1987). The Marsh Warbler is one of the passerine species whose long autumn journey to southern Africa is known to occur in two stages. A rapid migration to northeast Africa is followed by an interruption for 2–3 months in an unknown area west of the Rift valley where many individuals undergo partial moult. Only in November–December do the birds resume their journey to the final

wintering ground, which is spanning from Kenya and Tanzania through Zambia and Mozambique to South Africa (Pearson et al. 1988, Pearson 1990). There they behave territorially (Kelsey 1989) and undergo complete moult in January–March. In April, they begin northward migration to their Eurasian breeding areas (Dowsett-Lemaire & Dowsett 1987).

Despite long-term ringing efforts, linking the breeding and wintering grounds of populations of this long-distance migrant has been difficult. Here we have analysed stable isotopes in Marsh Warbler feathers to (1) assess autumn and winter habitat use, (2) assign individual Marsh Warblers from several European populations to their southern African wintering sites and (3) more closely determine the location of the autumn staging areas in northeastern Africa (cf. Yohannes et al. 2005). In addition, we estimated the strength of migratory connectivity between breeding and wintering grounds based on ring recoveries. Despite the funnel-shaped migration pattern in East Africa, which implies intensive mixing of breeding populations migrating through a relatively narrow corridor (Pearson et al. 1988), we could not exclude their further segregation in their final wintering grounds.

During breeding seasons 2004–2012, we sampled innermost primaries (P1) of 97 local breeding adult Marsh Warblers at various European sites (Appendix 1). Between 27 April and 30 May 2004, we also collected P1 from 18 birds upon their arrival at Crimea, Ukraine. The European samples were grouped into four broader geographical regions based on their location (North, West, Central and East Europe, see Appendix 1). We also obtained primary and body feathers from the final African wintering grounds in Zambia and South Africa. Unlike the primaries, the body feathers collected in Zambia were thought to have been those grown in the autumn staging areas in northeastern Africa (Appendix 1). To infer the position of the assumed northeast African autumn staging areas, we used published stable isotope profiles from newly grown tertials of 35 adult Marsh Warblers caught at Ngulia, southeast Kenya (Yohannes et al. 2005, 2007).

Feathers were rinsed in a 2:1 chloroform:methanol solution and air-dried in a fume hood. Subsamples of ca. 0.5 mg were weighed into 0.3×0.5-mm tin cups to the nearest 0.001 mg and combusted in an elemental analyser (Eurovector, Milan). The resulting N₂ and CO₂ were separated

by gas chromatography and admitted into the inlet of a continuous-flow isotope-ratio mass spectrometer (Micromass Isoprime, Manchester) to determine ¹⁵N/¹⁴N and ¹³C/¹²C ratios. Measurements are reported in conventional δ-notation relative to the PDB (carbon) and atmospheric N₂ standards in ‰. Replicate assays of internal laboratory standards indicate measurement errors (SD) of ± 0.1‰ and ± 0.2‰ for stable carbon (δ¹³C) and nitrogen (δ¹⁵N) values, respectively. Kolmogorov-Smirnov tests showed that both δ¹³C and δ¹⁵N values conformed to normality (all *p* > 0.14), therefore we fitted linear models (LM) with δ¹³C and δ¹⁵N values as dependent variables and geographic regions as predictors. Mean stable isotope values are presented ± SD.

Feathers grown in the final wintering grounds and those moulted in the autumn staging areas were assigned to isotopic feather clusters derived by Hobson et al. (2012). These regions of similar multi-isotope profiles were previously inferred from a cluster analysis of expected African δ¹³C and δ¹⁵N isoscapes based on plant physiology models (Craine et al. 2009, Still & Powell 2010) and diet–tissue discrimination factors between plants and feather keratin of insectivorous birds (Hobson et al. 2012). We used multivariate normal probability density functions (Royle & Rubenstein 2004) to assess the likelihood that an isotopic cluster represented the origin for a sample, given the values predicted by the two-isotope isoscape as in Table 3 in Hobson et al. (2012) and the covariance between the observed δ¹³C and δ¹⁵N values. The covariance was estimated in the 'mvnmle' package (Gross & Bates 2012). Using expected feather isotope means from the isoscapes and the covariance matrix between isotopes from our feather samples, we estimated the multivariate normal probability densities associated with each potential source population in the 'mvtnorm' package (Genz et al. 2014). We assigned a given feather sample to the isotopic cluster for which the highest likelihood was obtained.

Ring recoveries of Marsh Warblers were gathered from European and African ringing centres and from available published reports. We explored the migratory connectivity between breeding and wintering sites as follows. First, we grouped the winter recoveries into two clusters based on their geographic position and compared the number of birds originating from different European regions (north, west, central) recovered in these two areas using a 2×3 Fisher's exact test. Second, to quantify the strength of migratory

connectivity between breeding and wintering grounds, we calculated Mantel correlation coefficient (r_M) between a breeding and a wintering distance matrix (Ambrosini et al. 2009). In the case of strong connectivity, a strong positive correlation is expected between the two matrices. We generated a breeding and a wintering distance matrix with loxodromic pairwise distances for each individual (calculated in the 'birdring' package; Korner-Nievergelt & Robinson 2014) and quantified the correlation between these two matrices using a Mantel test in the 'ade4' package (Dray & Dufour 2007). We used 9999 permutations to evaluate the statistical significance of the correlation coefficient. All statistical analyses were performed using R 3.0.3 (R Core Team 2013).

Feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values differed among European regions ($\delta^{13}\text{C}$: $F_{3,111} = 3.17$, $p = 0.027$; $\delta^{15}\text{N}$: $F_{3,111} = 2.93$, $p = 0.037$). Marsh Warbler primaries sampled in Ukraine were enriched in ^{13}C and depleted in ^{15}N relative to those collected in most other European regions (Fig. 1, Table 1A). Feathers sampled in Africa also differed ($\delta^{13}\text{C}$: $F_{3,40} = 3.39$, $p = 0.027$; $\delta^{15}\text{N}$: $F_{3,40} = 6.84$, $p < 0.001$). Freshly grown tertials sampled en route in Kenya were enriched in ^{13}C and depleted in ^{15}N compared with primaries from Zambia and South Africa (Table 1B). However, they were similar to the values from body feather $\delta^{13}\text{C}$ of birds caught wintering during February in Zambia (Table 1B).

Primary feathers sampled in Europe ($-20.0 \pm 2.1\text{‰}$, $n = 115$) largely differed in $\delta^{13}\text{C}$ from fresh

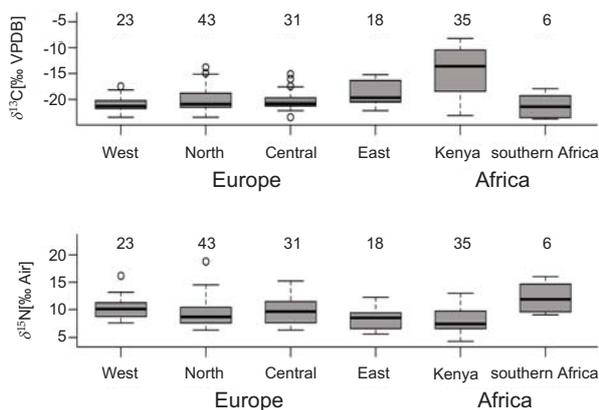


Fig. 1. Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios in Marsh Warbler feathers sampled in four different European regions and in Africa. Primaries from Zambia and South Africa pooled. The central bar of the box indicates the median, the box delimits 25th and 75th percentiles, whiskers show 1.5 times the interquartile range, and circles denote outliers. Sample sizes given above the boxes.

Table 1. Results of linear models exploring differences in feather ^{13}C and ^{15}N values with respect to the sampling regions in (A) Europe and (B) Africa. Differences among regions are expressed as treatment contrasts, the reference level being for (A) East Europe and for (B) Kenya.

	Estimate	SE	t	p
A) Europe				
$\delta^{13}\text{C}$				
(Intercept)	-18.75	0.48	-39.1	< 0.001
North	-1.33	0.60	-2.2	0.030
West	-1.95	0.64	-3.0	0.003
Central	-1.25	0.57	-2.2	0.031
$\delta^{15}\text{N}$				
(Intercept)	8.28	0.53	15.5	< 0.001
North	1.47	0.67	2.2	0.031
West	2.00	0.71	2.8	0.006
Central	0.95	0.64	1.5	0.141
B) Africa				
$\delta^{13}\text{C}$				
(Intercept)	-14.54	0.80	-18.1	< 0.001
Zambia body	-2.46	2.85	-0.9	0.395
Zambia	-6.85	2.85	-2.4	0.021
South Africa	-6.33	2.85	-2.2	0.032
$\delta^{15}\text{N}$				
(Intercept)	8.14	0.38	21.4	< 0.001
Zambia body	2.77	1.35	2.0	0.047
Zambia	2.95	1.35	2.2	0.035
South Africa	5.11	1.35	3.8	0.001

tertials collected in Kenya ($-14.5 \pm 4.8\text{‰}$, $n = 35$; LM: $t = -9.61$, $p < 0.001$), but did not differ from primaries sampled in southern Africa ($-21.1 \pm 2.5\text{‰}$, $n = 6$; Zambia and South Africa pooled: LM $t = -0.95$, $p = 0.344$). European samples ($9.4 \pm 2.3\text{‰}$, $n = 115$) were depleted in ^{15}N compared with those from southern Africa ($12.2 \pm 2.7\text{‰}$, $n = 6$; LM $t = 2.83$, $p = 0.005$), and enriched in ^{15}N compared with those collected in Kenya ($8.1 \pm 2.2\text{‰}$, $n = 35$; LM $t = -2.88$, $p = 0.005$; Fig. 1).

The likelihood assignment approach confirmed that feathers collected in Ukraine differed in their stable isotope profiles from the rest of European samples. A total of 78% of east European samples were assigned to isotopic feather cluster 2 (Table 2), which is distributed over large parts of the species' final wintering grounds (Fig. 2). More than a half of the samples collected in northern and western Europe, however, were apparently grown in places corresponding to cluster 3, with a lower probability of origin from clusters 1 and 2. Feathers from central Europe showed equal probabilities of moult origin from clusters 1–3 (Table 2). None of the European samples were assigned to cluster 4 and only nine of 115 samples to cluster 5.

More than 70% of freshly moulted tertials sampled en route in Kenya in autumn were assigned to cluster 2 (Table 2), which corresponds to an area encompassing the foothills of the Ethiopian Highlands (Fig. 2). Body feathers sampled in Zambia were assigned to clusters 2, 3 and 4. Three of six primaries from southern Africa (originating from regions classified as cluster 2 and 1, respectively – see Fig. 2) were assigned to cluster 3, two to cluster 5 and one to cluster 2, respectively.

A total of 280 long distance recoveries (>100 km) was available. Of these, 133 came from Kenya, among which 87 connected East Africa with places across the Eurasian breeding range (Fig. 3A). Ring recoveries from areas further south (Fig. 3B) formed two clusters: one located in Malawi and Mozambique ($n = 9$), the other in South Africa and Botswana ($n = 5$). The distribution of birds ringed in northern, western and central Europe did not significantly differ between the two winter clusters (Fisher exact test $p = 0.146$). Mantel test showed low and not significant correlation between the breeding and wintering distance matrices ($r_M = 0.207$, $p = 0.110$).

Our results demonstrated that stable isotope ratios from birds sampled at a spring stopover site in southern Ukraine (most likely breeding in eastern Europe) were enriched in ^{13}C and depleted in ^{15}N relative to values obtained from birds breeding further west and north. The likelihood-based assignment approach confirmed that the birds sampled in Ukraine moult in isotopically different habitats (which are likely to be drier compared to wintering habitats of western populations) and might thus geographically segregate from the western breeding populations in their final wintering areas. This suggests that despite the entire Marsh Warbler population gathering in a restricted autumn staging area and migrating

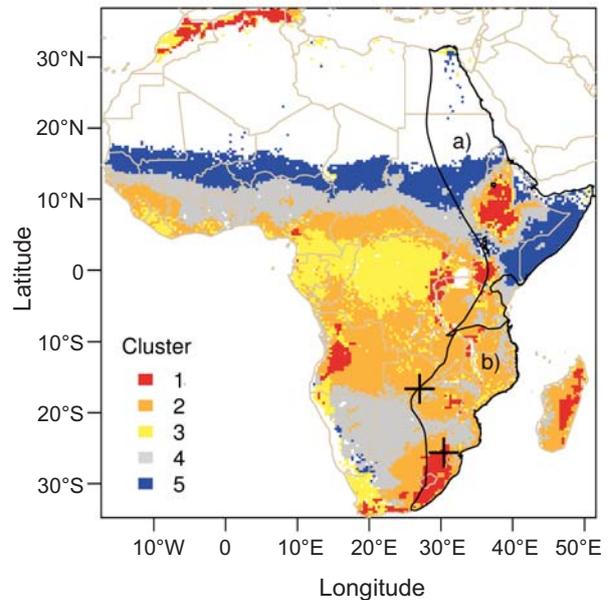


Fig. 2. Isotopic clusters (1–5) resulting from the analysis of African feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes by Hobson et al. (2012) to which Marsh Warbler samples were assigned. Black lines delimit the African non-breeding range: a) migration and autumn staging areas, b) final wintering grounds. Crosses depict the location of sampling sites in southern Africa.

through a narrow corridor in East Africa (Pearson 1982, Pearson et al. 1988), populations from the eastern part of the breeding range may partly segregate south of Kenya.

Ring recoveries roughly conform to this scenario. The numerous East African records demonstrate that the migration through south-eastern Kenya includes birds from across the whole breeding range (Fig 3A). Recoveries further south suggest low levels of migratory connectivity between breeding and wintering grounds, although the available sample sizes are only modest. Unfortunately, no winter recoveries are available to confirm segregation of the eastern populations. The low level of migratory connectivity we found is, however, in agreement with the low genetic differentiation across the species' distribution range (Arbabi et al. 2014).

Global carbon isotope maps for southern Africa exhibit strong latitudinal and longitudinal variation in vegetation $\delta^{13}\text{C}$; and regional terrestrial C_3/C_4 plant distributions show that the local biomes are mostly dominated by C_4 plants (Still et al. 2003). However, $\delta^{13}\text{C}$ values in Marsh Warbler primaries from southern Africa and those from Europe indicate that the species undergoes winter moult in habitats with higher abundance of C_3

Table 2. Assignment of Marsh Warbler feathers collected in Europe and Kenya to the five African isotopic clusters. Values represent likelihoods that the feathers sampled in different European regions (west, north, central, east) and Kenya were grown in the given isotopic cluster within Africa (see Methods and Fig. 2).

Region	Cluster					N
	1	2	3	4	5	
North	0.19	0.23	0.45	0.00	0.13	31
West	0.26	0.13	0.57	0.00	0.04	23
Central	0.30	0.30	0.30	0.00	0.10	43
East	0.05	0.78	0.17	0.00	0.00	18
Kenya	0.06	0.71	0.17	0.00	0.06	35

plants and/or more humid conditions in southern Africa (mean for C_3 plants approx. -27‰ , Farquhar et al. 1989). The relatively low $\delta^{13}\text{C}$ values reported here for most study sites (except for northeastern Africa and body feathers from Zambia) are in agreement with the habitat selection of the species in tropical Africa (dense leafy thickets with herbaceous undergrowth, Dowsett-Lemaire & Dowsett 1987, Kelsey 1989). The higher $\delta^{15}\text{N}$ values observed for the South African study site were most likely affected by anthropogenic input (G. Grieve pers. comm.).

The mean $\delta^{13}\text{C}$ value of Marsh Warbler feathers grown in northeastern Africa was -14.5‰ . Using mean values for C_4 plants (-13‰ , Lajtha & Michener 2007) as endpoint, this indicates a C_4 -dominated carbon source incorporation into the food chain of the species during the partial moult at the autumn stopover site. Alternatively, higher $\delta^{13}\text{C}$ values can also be linked to C_3 plants of drier areas in response to water-use efficiency (e.g. Ehleringer & Cooper 1988). The large range of $\delta^{13}\text{C}$ values (between -23.0‰ and -8.2‰) in the Kenyan samples suggests that although the majority of these feathers sampled must have

been grown in ^{13}C enriched areas, a small proportion (only seven individuals show $\delta^{13}\text{C} \leq -20\text{‰}$) has a relatively lower $\delta^{13}\text{C}$ isotopic signature, showing that the species uses isotopically varying habitats (C_3 - and C_4 -dominated biomes) during its extended stopover in autumn.

Feather $\delta^{13}\text{C}$ values of freshly grown feathers of migrants passing through Ngulia, Kenya, were significantly enriched in ^{13}C relative to all other samples in Europe and Africa (except for body samples from Zambia which, during February, were probably still those grown in autumn staging areas). Adults entering continental Africa through the Sudanese Red Sea coast show no signs of active moult, but most already have fresh body plumage when they reach Kenya, indicating that most birds grow new feathers somewhere in between (Dowsett-Lemaire & Dowsett 1987, D. J. Pearson & G. Nikolaus, pers. comm.). A heavy migration through coastal Sudan and then three months later through Kenya indicates that large numbers of Marsh Warblers make a long stopover in between (Dowsett-Lemaire & Dowsett 1987, Pearson et al. 1988). Vocal mimicry of Afrotropical species suggests that this lies somewhere north

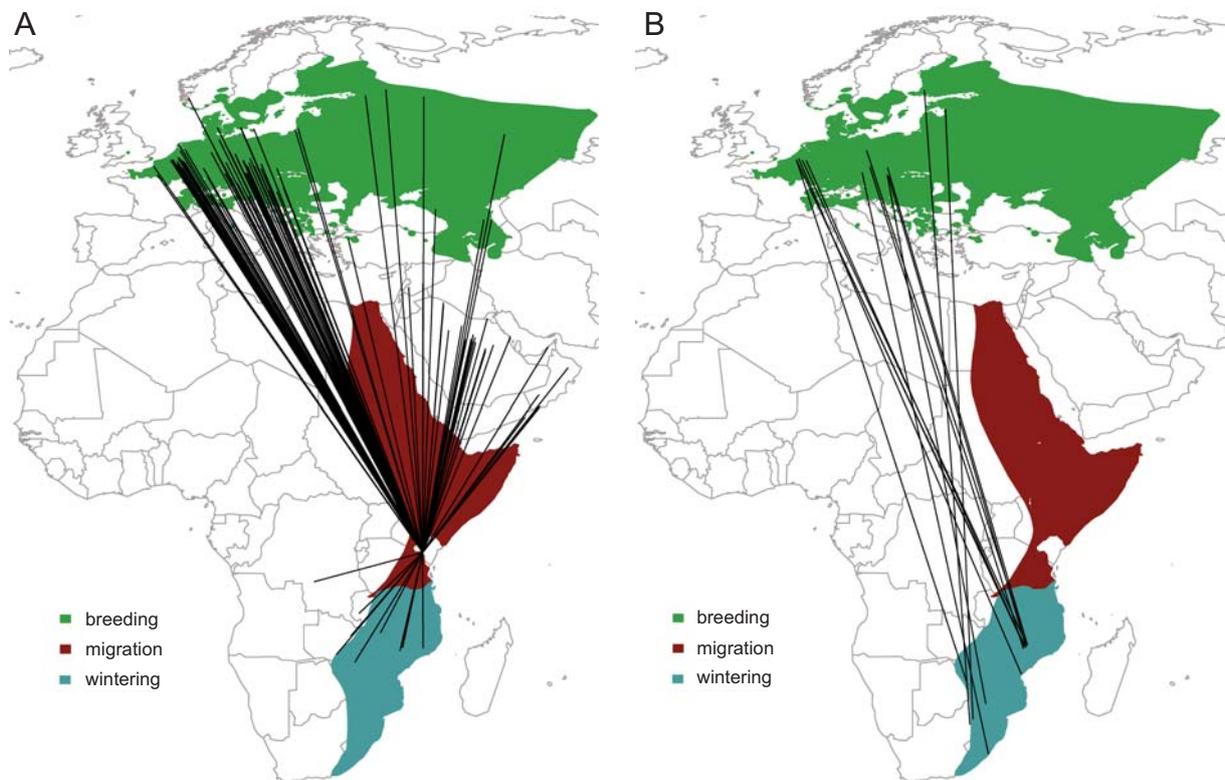


Fig. 3. Long-distance ring recoveries of Marsh Warblers: A — intercepted on autumn passage in eastern Africa ($n = 133$), and B — ringed within the breeding range and found in the final wintering grounds in southern Africa ($n = 14$). Lines connect ringing and recovery sites and do not reflect the exact migration trajectory.

of about 8° N in western Ethiopia (Dowsett-Lemaire 1979). Using stable isotope measurements, Yohannes et al. (2005) concluded that this staging area is probably located between south-eastern Sudan and western Ethiopia. In the present study, by using the feather isotope clusters of Hobson et al. (2012) we have been more effectively able to narrow this down to the lower elevations of the Ethiopian Highlands.

Our findings give evidence that the Marsh Warbler occupies a wider set of habitats on its non-breeding grounds than in Europe. The species winters in a variety of mostly damp habitats in southern Africa, but in northeast Africa, it may inhabit mainly dry, well-vegetated areas. This implies that it is less restricted to a distinct isotopic regime (e.g. C₄ savannas or C₃ lush thickets with rank herbaceous undergrowth) but uses biomes of high isotopic variability. While this assists in assigning moult origin in northeastern and southern Africa, these findings can have importance for the conservation and management of this and other migratory species.

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STRESZCZENIE

[Położenie miejsc pierzenia i zimowisk łożówki na podstawie analizy zawartości trwałych izotopów w piórach i danych obrączkowania]

W celu określenia przyczyn spadków liczebności wielu gatunków dalekodystansowych migrantów zimujących w Afryce, konieczne jest poznanie ich miejsc zimowania oraz wybiórczości siedliskowej w okresie pozalęgowym. Ważnym aspektem jest także zbadanie na ile osobniki z poszczególnych populacji zimują w tych samych miejscach. W przypadku niewielkich ptaków wróblowych nie można zastosować wielu metod badania migracji, a dane z obrączkowania nie są zbyt liczne. W takich przypadkach stosuje się analizę poziomu zawartości stabilnych izotopów w piórach, która pozwala na określenie miejsc, na których występowały ptaki podczas pierzenia.

Łozówka to niewielki owadożerny wróblak, którego areal lęgowy obejmuje zachodnią Palearktykę. Ptaki z całego zasięgu lęgowego wędrują poprzez Afrykę wschodnią na zimowiska

położone w południowo-wschodniej części kontynentu. Migracja jesienna przebiega w dwóch etapach. Po szybkim przelocie na teren północno-wschodniej Afryki następuje dwu-trzymiesięczna przerwa, podczas której ptaki przechodzą częściowe pierzenie. Następnie w listopadzie i grudniu podejmują wędrówkę do docelowych zimowisk, gdzie przechodzą całkowite pierzenie.

W pracy analizowano poziom zawartości izotopów węgla i azotu w piórach łożówki pozyskanych od ptaków z populacji lęgowych w Europie oraz schwytych jesienią i zimą w Afryce (apendyks 1). Dodatkowo użyto opublikowanych danych o zawartości izotopów w przepierzonych lotkach trzyczłonowych ptaków schwytych w Kenii. Na tej podstawie oceniono wybór siedliska na miejscu przystankowym i zimowisku oraz przybliżone położenie miejsc pierzenia częściowego i zimowisk różnych populacji tego gatunku.

Stwierdzono, że łożówki ze wschodniej Europy różniły się profilem izotopowym od reszty europejskich populacji (Fig. 1, Tab. 1). Może to wskazywać na pewną segregację tych populacji na zimowiskach. Lotki trzyczłonowe ptaków schwytych w Kenii różniły się profilem izotopowym od piór ptaków z zimowisk z południa Afryki (Fig. 1, Tab. 1). Uzyskane wyniki porównano z danymi o rozmieszczeniu izolinii roślinności w Afryce, które pozwalają na wydzielenie przestrzennych grup izotopowych (Fig. 2). 70% piór ptaków schwytych w Kenii zostało przypisanych do grupy 2 (Tab. 2). Na tej podstawie stwierdzono, że miejsca pierzenia znajdują się na terenach otaczających Wyżyny Somalijską i Abisyńską (Fig. 2).

Wyniki zawartości izotopu węgla ¹³C wskazują, że w trakcie pierzenia częściowego na miejscu przystankowym łożówki wybierają siedliska z roślinnością C₄ (np. sawanny) zaś w trakcie pierzenia całkowitego na zimowiskach — siedliska z roślinnością C₃ (np. zarośla z bujną roślinnością zielną).

Zebrane dotychczas dane uzyskane z obrączkowania nie wskazują jednak, aby osobniki z poszczególnych populacji europejskich wykorzystywały różne tereny zarówno w trakcie wędrówki jesiennej przez wschodnią Afrykę, jak i na właściwych zimowiskach w południowo-wschodniej Afryce (Fig. 3).

Appendix 1. Sampling sites, number of individuals and assumed moulting origin (based on Winkler & Jenni 2007) of the sampled Marsh Warbler feathers.

Region	Sampling site	Coordinates	Year	Sampling period	N	Presumable moulting origin (feather sampled)
North Europe	southern Finland (several sites)	60.2–61.2°N, 22.1–28.7°E	2010	breeding (Jun/early Jul)	16	southern Africa (primaries)
	Rybachy, Russia	55°09'N, 20°51'E	2004	breeding (Jun)	15	southern Africa (primaries)
West Europe	Cuxhaven, Germany	53°50'N, 08°50'E	2012	breeding (early Jun)	7	southern Africa (primaries)
	Grande-Synthe, France	51°01'N, 02°18'E	2012	breeding (Jun)	5	southern Africa (primaries)
	Chirens, France	45°25'N, 05°33'E	2012	breeding (Jun)	6	southern Africa (primaries)
	Elbeuf, France	49°28'N, 01°23'E	2012	breeding (Jun)	5	southern Africa (primaries)
Central Europe	Osík, Czech Rep.	49°52'N, 16°18'E	2004	breeding (Jun)	15	southern Africa (primaries)
	Hodonín, Czech Rep.	48°54'N, 17°02'E	2004–2012	breeding (Jun)	14	southern Africa (primaries)
	Draganić, Croatia	45°34'N, 15°38'E	2005	breeding (Jun)	14	southern Africa (primaries)
East Europe	Crimea, Ukraine	45°45'N, 32°56'E	2004	spring migration (Apr/May)	18	southern Africa (primaries)
East Africa	Ngulia, Kenya	03°00'S, 38°13'E	2001–2004	autumn migration (Nov/Dec)	35	northeast Africa (fresh tertials)
Southern Africa	Choma, Zambia	16°39'S, 27°02'E	2011	wintering (Feb)	3	northeast Africa (body feathers)
	Pretoria, South Africa	25°37'S 30°24'E	2005	wintering (Dec/Jan)	3	southern Africa (primaries)