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Fuelling strategies differ among juvenile Sedge and Reed Warblers along the eastern European flyway during autumn migration

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In this study, we investigated fattening strategies of juvenile Sedge and Reed Warblers during their autumn migration. We analysed fat scores of birds captured at five ringing sites situated between the southern Baltic Sea coast and Asia Minor. In Eastern Europe these two species had similarly low fat reserves. Their fat load increased in the Balkans. Remarkable differences between the species were noted in Asia Minor, where fat reserves of Sedge Warblers were more than two-fold higher compared to Reed Warblers. As high as 90% of Sedge and only 30% of Reed Warblers captured in Asia Minor had the potential capability to cross the Mediterranean Sea in one non-stop flight. Moreover, two-thirds of those Sedge Warblers were able to continue their long flight without refuelling and reach the southern edge of the Sahara desert, while in Reed Warblers only 6% of individuals were potentially able to use the same strategy. The results of the study show clear differences in potential flight ranges of the studied species, revealing different fattening strategies of the Sedge and Reed Warbler in the Balkans and Asia Minor. Majority of Sedge Warblers refuel well before the Sahara desert indicating their potential for long non-refuelling steps while crossing two large ecological barriers, whereas the majority of Reed Warblers accumulate small fat reserves, which may indicate migration with short-steps through Cyprus and/or along the eastern coast of the Mediterranean Sea. Similar interspecific differences were reported from well-studied western European route and thus our results indicate consistent migration strategies of Sedge and Reed Warblers along these two migratory flyways in the Western Palearctic, the western and the eastern one.

1. Introduction

Seasonal migration is an energetically demanding process and thus migration strategy employed by a given bird species is largely dependent on the spatio-temporal distribution of the abundance of preferred prey (Alerstam 1990, Bibby & Green 1981, Schaub & Jenni 2001, Chernetsov 2006). Long-distance migrants adopt different strategies during their migration between breeding and wintering sites (Biebach 1990, Herremans 1991, Schaub & Jenni 2000a,b). Seasonal fattening prior to migratory flights is one of key components of those strategies. Even species of the same genus like *Acrocephalus* or *Sylvia* warblers may adopt different fattening strategies as was shown in many studies on main migratory routes in Western-Palearctic bird migration system (e.g., Bibby & Green 1981, Yohannes *et al.* 2009, Ożarowska 2015). Such differences were also documented at the intraspecific level, like in Garden Warblers (*Sylvia borin*) migrating along the western and eastern European routes (Bairlein 1991). Moreover, the presence of ecological barriers, like deserts, high mountains or seas, where refuelling is hampered or impossible, is another major factor shaping bird migration strategies (Moreau 1961, Schaub & Jenni 2000a, Alerstam 2001, Adamík *et al.* 2016).

Autumn avian migration from European breeding grounds to African winter quarters occurs across the whole width of two, large ecological barriers: the Mediterranean Sea and Sahara desert (Yom-Tov 1984, Biebach 1992, Newton 2008), yet several species show a migratory divide between populations within Europe following different directions (Hedenström & Petterson 1987, Bairlein 1991, Shirihai *et al.* 2001, Kennerley & Pearson 2010). Those species cross the Mediterranean region along three main migratory routes of Western-Palearctic migration system, i.e., the western, through the Iberian Peninsula, the central through the Italian Peninsula, or the south-eastern route, through Asia Minor and the Middle East (Basciutti *et al.* 1997, Fransson *et al.* 2006, Trierweiler *et al.* 2014). Among passerines, a high proportion of nocturnal long-distance migrants, which use the eastern route, do not circumvent the eastern Mediterranean, but cross the open water in a broad front, opposite to the western route, which leads mostly over land through the Iberian Peninsula and the Strait of Gibraltar (Zehtindjiev & Liechti 2003). All three main flyways lead then through the Sahara desert, which is the most extensive barrier for long-distance Palearctic passerines, and hardly any refuelling opportunities exist there (Moreau 1961, 1972, Fransson *et al.* 2006, Yohannes *et al.* 2009).

In this study, we investigated fat reserves expressed as fat score of juvenile Sedge Warbler (*Acrocephalus schoenobaenus*) and Reed Warbler (*Acrocephalus scirpaceus*) during their autumn migration. These are two common, insectivorous and habitat specialist species (Zink 1973, Cramp 1992, Kennerley & Pearson 2010). Both exhibit a migratory divide in Europe. In the Reed Warbler, there is a prominent division between the western and eastern flyway, whereas Sedge Warblers move on a broader front, and some populations migrate along the central one as well (Zink 1973, Cramp 1992, Csörgő *et al.* 2009, Procházka *et al.* 2008, 2017). Our knowledge about the Sedge and Reed Warbler migration, like in other long-distance passerines in Western Palearctic, is based mainly upon the studies conducted along the western European flyway (Bibby & Green 1981, Hilgerloh & Wiltschko 2000, Bermejo & Puente 2002, Arizaga *et al.* 2011a).

The studies carried out on the eastern European route are scarce in comparison to western and central flyways and mostly report on the phenology and migration dynamics (Akriotis 1998, Zehtindjiev *et al.* 2010), with only a few studies focusing on migration strategies of passerines in this region (Biebach *et al.* 2000, Fransson *et al.* 2008, Yohannes *et al.* 2009, Ożarowska 2015). This is in spite of the fact that at least for the Reed Warbler, a higher absolute number of individuals follows the eastern route compared to the western one (Procházka *et al.* 2017). Therefore, the studies on the eastern migratory flyway are necessary to understand the whole pattern of the Western-Palearctic migratory system of this species (Fransson *et al.* 2006).

By studying the amount of fat reserves accumulated by autumn migrating juvenile Sedge and Reed Warblers at the stop-over sites located between the Baltic Sea and Asia Minor, we aimed to compare their fattening strategies in this vast region. We also examined whether these species

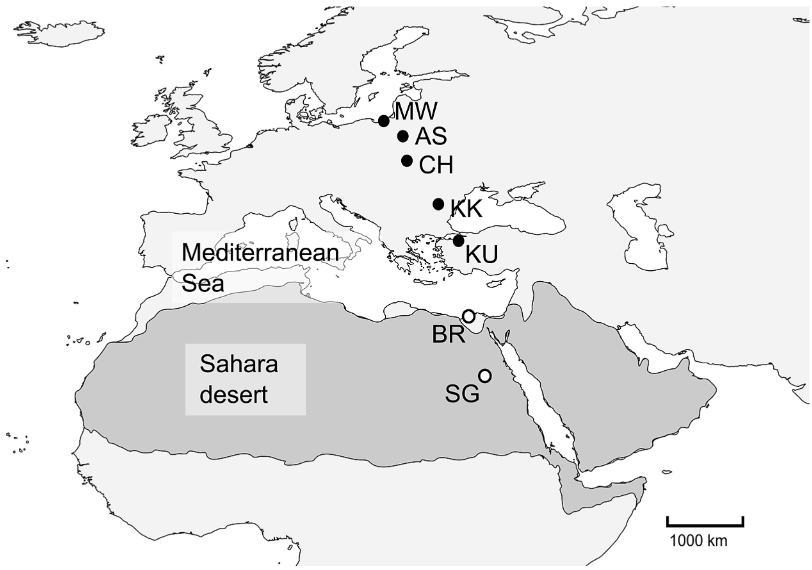

Fig. 1. Location of five ringing stations (filled circles): MW – Mierzeja Wiślana, AS – Siemianówka, CH – Cholgyni; KK – Kalimok; KU – Kuscenneti. The extension of the Sahara and deserts of the Arabian Peninsula is shown as shaded area. Two other sites mentioned in the Discussion section are also shown (open circles): BR – Burullus and SG – Saluga Ghazal.

were potentially able to perform a long-distance flight without refuelling from the southernmost stop-over sites in the studied region to the southern edge of two ecological barriers, the Mediterranean Sea and Sahara desert.

2. Material and methods

2.1. Study area and fieldwork

Birds were captured at five ringing stations, located in Poland, Ukraine, Bulgaria and Turkey between 2001 and 2008 during the autumn migration season. These stations work within the South-East European Bird Migration Network (SEEN) and are located from the southern Baltic coast to Asia Minor: Mierzeja Wiślana, Siemianówka, Cholgyni, Kalimok and Kuscenneti (Fig. 1, Table 1). The total range between the northernmost and southernmost station was equal to 1,850 km. At every station, the reedbeds were one of the main habitats, with admixture of bushes and trees. Ringing recovery distribution shows that in the Balkans (Kalimok) and northern part of the Mediterranean Sea (Kuscenneti) two studied species follow eastern migration flyway heading south (Csörgő *et al.* 2009, Procházka *et al.* 2017, P. Zehtindjiev & M. Ilieva – unpublished data). Whereas in Mierzeja Wiślana, Siemianówka and Cholgyni, majority of migrating Reed Warblers head towards west, while Sedge Warblers head south and/or south-east (Busse 1987, Bønløkke *et al.* 2006, Bairlein *et al.* 2014, Valkama *et al.* 2014, Procházka *et al.* 2017).

The dates of the fieldwork at four out of five ringing stations (Table 1), were adjusted to migration phenology of the studied species in a given area (Jakubas *et al.* 2002, Zakala *et al.* 2004, Jakubas & Wojczulanis-Jakubas 2010, Zehtindjiev *et al.* 2010). Only in Mierzeja Wiślana and Kuscenneti, we missed the beginning of the *Acrocephalus* migration period, but still its main part was covered (Akriotis 1998, Jakubas *et al.* 2002, Kozłowska *et al.* 2009, Erciyas *et al.* 2010). Juvenile Sedge and Reed Warblers start migration through Europe in late July, and their main migration period is in August and September (Cramp 1992, Kennerley & Pearson 2010). In general, migrants reach the southernmost areas of the continent later in the season in respect to the northern latitudes (Kennerley & Pearson 2010), thus we assumed that the later start of catching period at Kuscenneti had no significant influence on the obtained results.

During the fieldwork, the standard SEEN methodology was applied, i.e.: constant mist-netting, standard set of biometric measurements, including weight measured with accuracy to 0.1 g with an electronic balance and subcutaneous fat score (*FS*) assessment according to the Busse's nine-step scale, i.e., between 0 (no visible fat) and

Table 1. Ringing stations (abbreviations and geographic coordinates are given in brackets), studied years and the number of ringed individuals of the studied species.

Ringing station	Studied years	Catching dates	Species	*N*
Mierzeja Wiślana (MW)	2001–2008	12 Aug–31 Oct	Reed Warbler	5,578
(54°21'N, 19°19'E)			Sedge Warbler	569
Siemianówka (AS)	2002–2008	1 Aug–24 Oct	Reed Warbler	393
(52°55'N, 23°50'E)			Sedge Warbler	1,063
Cholgyni (CH)	2001–2004	2 Aug–2 Sep	Reed Warbler	930
(49°58'N, 23°38'E)			Sedge Warbler	1,476
Kalimok (KK)	2001–2004	4 Aug–28 Oct	Reed Warbler	462
(41°00'N, 26°26'E)			Sedge Warbler	942
Kuscenneti (KU)	2002–2003	26 Aug–18 Oct	Reed Warbler	738
(40°14'N, 28°02'E)			Sedge Warbler	76

8 (whole belly, flanks and furculum covered with fat; after Busse & Meissner 2015). As in other studies (e.g., Schaub & Jenni 2000a, Bayly & Rumsey 2007, Ożarowska 2015) we considered only first captures, retraps were excluded. Such approach provides homogeneity of the sample. Besides, the number of retraps was low, ranging from 3 to 16% in two studied species. Age of the captured birds was identified according to plumage characteristics (Svensson 1992). Due to low numbers of adult birds at some stations, the analyses were conducted on first-year individuals only (in immature plumage), hereafter juveniles (Table 1). Moreover, in many species, age classes differ in migration strategies (Bibby & Green 1981, Bayly & Rumsey 2007, Jakubas *et al.* 2014).

2.2. Statistical analysis

We used analysis of variance (ANOVA) in general linear modelling (GLM) with a logarithm link function and normal error distribution to relate the fat score to the species (two categories: Reed Warbler and Sedge Warbler) and consecutive ringing station arranged in geographical order (five categories), followed by the Spjotvoll-Stoline post-hoc test to assess the differences in mean fat score of individuals of each species captured at different ringing stations. Statistical analyses were performed using the STATISTICA 12 software (StatSoft 2014).

As stations worked in different years, we pooled data from all available years (Table 1). But, beforehand, to check for a possible effect of year on fattening in Sedge and Reed Warblers, we ran an additional analysis for two years, 2002 and 2003, when all stations were operating. We used general linear modelling (GLM) with a logarithm link function and normal error distribution. The aim of this analysis was to check whether the same pattern was found in this short period and if it was similar, then this would further support pooling of data from all available years.

2.3. Estimation of potential flight ranges

Potential flight ranges were calculated only for the two southernmost stations, Kalimok and Kuscenneti due to their proximity to two main geographical barriers: the Mediterranean Sea and Sahara desert. To assess theoretical flight ranges of Sedge and Reed Warblers, we applied the Flight programme ver. 1.24 by Pennycuick (2008). We assumed the passage at an altitude of 1,000 m a.s.l. in still air of density 1.11 kg m^{-3} (Pennycuick 2008). The migration simulation requires an estimate of the individual mass when migration starts, and also of its fat fraction, which is the ratio of the mass of consumable fat to the body mass (Pennycuick 2008). Similarly to Bayly & Rumsey (2007) and Ożarowska (2015), we did not run calculations for each bird separately, but for a group of birds representing a given fat score. For assessing the flight range, three wing parameters were also required: wing span (WS), wing area (WA) and aspect ratio (AR). WS and WA were taken from the available

Table 2. Results of GLM ANOVA of the effect of the species and consecutive ringing station on fat score of Sedge and Reed Warblers.

Ringing station	*SS*	*df*	*MS*	*F*	*p*
Intercept	19114.8	1	19114.8	10647.9	< 0.001
Ringing station	2338.8	4	584.7	325.7	< 0.001
Species	932.8	1	932.8	519.6	< 0.001
Ringing station × Species	578.0	4	144.5	80.5	< 0.001
Error	21450.6	11949	1.8		

literature data for females and males of the studied species (Hedenström & Møller 1992).

As we did not sex captured birds, then we calculated WS and WA as a mean for both sexes, while AR was calculated using the procedure in the Flight programme (Reed Warbler: WS = 0.1946 m, WA = 0.00773 m^2, AR = 4.90 and Sedge Warbler: WS = 0.1947 m, WA = 0.00747 m^2, AR = 5.07). The lean body mass was estimated by averaging body masses of all individuals with no fat visible under the skin (*FS* = 0; Arizaga *et al.* 2011a). Fat fraction, which is needed to run simulations, was calculated for birds representing each fat class, using the fat mass (i.e., the difference between mean body mass of all individuals representing given fat score and mean lean body mass), divided by mean body mass of birds representing the given fat score.

We calculated the potential flight range of Sedge and Reed Warblers representing each fat score. Then based on the minimum fat score, which was equal to fat load sufficient to potentially cross the first (Mediterranean Sea) or both barriers together (Mediterranean Sea and Sahara desert), we estimated the percentage of birds with fat load sufficient to reach south-eastern coasts of the Mediterranean or south-eastern edge of the Sahara desert in potentially one non-refuelling step. The width of belt of the Mediterranean Sea between the Balkans/Asia Minor and north-eastern Africa was estimated as 600 km. According to Fransson *et al.* (2006), the width of the eastern part of the Sahara desert is around 1,800 km.

It should be noted that flight ranges' calculations reflect the potential migratory distance for a given fraction of birds and are based on the assumption of one-step flight in still air conditions. Hence, the obtained results should be treated as possible covered distances. Nevertheless, such calculations are widely used and provide the basis to understanding the evolutionary and ecological significance of bird migration strategies (e.g., Ellegren & Fransson 1992, Rubolini *et al.* 2002, Salewski *et al.* 2010, Ożarowska 2015).

3. Results

3.1. Fat score

When comparing data collected in 2002 and 2003, i.e., during two years when all stations were operating, there was no significant difference in mean fat score of Reed Warblers captured at different stations (Wald = 0.098, p = 0.75; Supplementary Fig. S1). In Sedge Warblers, birds had somewhat higher fat loads in 2002 (Wald = 5.138, p = 0.023), but the general pattern, i.e., distinct increase in fat stores of individuals captured at the southernmost stations was the same (Supplementary Fig. S2). Then in further analyses we pooled data from all available years.

At three northernmost ringing stations in Eastern Europe (Mierzeja Wiślana, Siemianówka and Cholgyni) the Sedge and Reed Warbler accumulated low fat reserves. Mean fat score increased significantly in both species at Kalimok, with distinct increase in Sedge Warblers documented at the southernmost station Kuscenneti (Fig. 2). The Sedge and Reed Warbler differed in their mean fat reserves and we found significant effects of the species, consecutive station and interaction between the species and consecutive station on fat score (Table 2). Sedge Warblers, in general, accumulated higher fat reserves than Reed Warblers (GLM ANOVA, $F_{1,933}$ = 519.6, $p < 0.001$).

Both species increased their fat stores at southern latitudes and the highest mean fat scores were

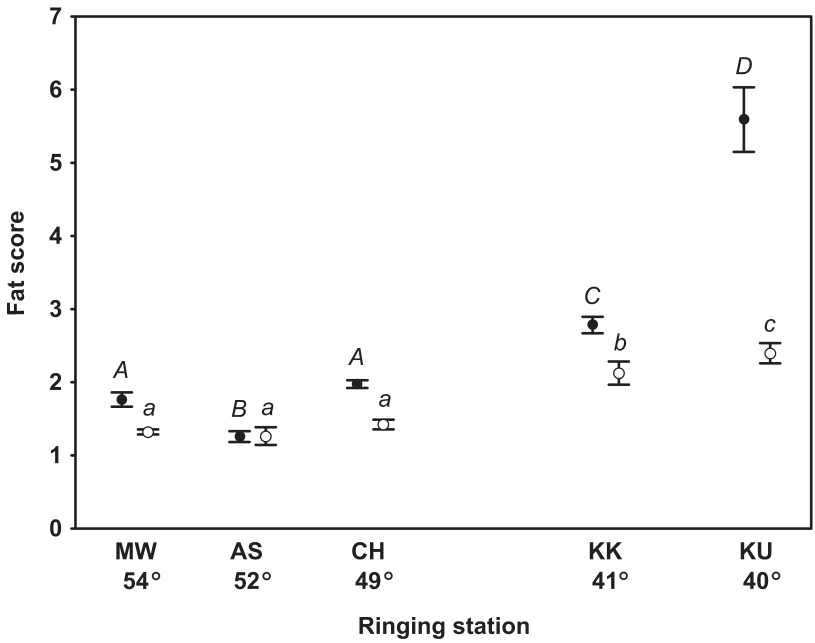

Fig. 2. Mean fat scores of juvenile Sedge Warblers (black dot) and Reed Warblers (open dot) captured at five ringing stations arranged in geographical order (for the abbreviations see Table 1). The statistically significant differences between mean fat scores within the species are denoted with different letters (capital letters for Sedge and lower case letters for Reed Warblers; Spjotvoll-Stoline post-hoc test, $p < 0.02$ in all cases). Vertical lines show the 95% confidence intervals.

recorded in Kuscenneti, the most distant south-eastern ringing station (Spjotvoll-Stoline post-hoc test, $p < 0.02$ in all cases; Fig. 2). Among the three northernmost ringing stations, there were no differences in mean fat score in the Reed Warbler, while in the Sedge Warbler significantly lower amount of accumulated fat was documented in Siemianówka (Spjotvoll-Stoline post-hoc test, $p < 0.02$ in all cases; Fig. 2).

3.2. Flight range

Among individuals potentially capable to reach the southern edge of the Mediterranean Sea from the northernmost stations, there were only two Sedge Warblers, while none of Reed Warblers had the fat load high enough to cover this distance. At Kalimok we recorded low fractions of Sedge and Reed Warblers potentially capable of crossing the Mediterranean Sea. These fractions were similar in both species (χ^2 test, $\chi^2 = 3.52$, $df = 1$, $p = 0.061$; Table 3). At Kuscenneti, this fraction increased about 6 times in Sedge Warblers and about 3 times in Reed Warblers compared to Kalimok, and was significantly higher in the Sedge Warbler (χ^2 test, $\chi^2 = 96.04$, $df = 1$, $p < 0.001$).

We found also a different proportion of high fattened Sedge and Reed Warblers, potentially capable to reach the southern edge of the Sahara desert. In Reed Warblers captured at Kalimok, there were no individuals capable of crossing both barriers, while in the Sedge Warbler that fraction constituted about 5% of birds. At Kuscenneti, the majority of Sedge Warblers, which were potentially able to cross the Mediterranean Sea, had already enough fat stores to fly much further south and cross the Sahara desert as well. The fraction of Sedge Warblers potentially capable to overfly both barriers constituted about two thirds of all Sedge Warblers captured at Kuscenneti, while in the Reed Warbler this fraction was only 6% ($\chi^2 = 248.26$, $df = 1$, $p < 0.0001$).

4. Discussion

Long-distance migrants exhibit varied fattening strategies, as they cover long distances between their breeding and wintering grounds (Schaub & Jenni 2000a,b, Alerstam 2003, Fransson *et al.* 2006, Ożarowska 2015). In Eastern Europe, carrying low fat reserves is a common phenomenon among passerines migrating across this region in autumn (Bairlein 1991, Schaub & Jenni 2000b, Ścisłowska & Busse 2005, Jakubas & Wojczula-

Table 3. Fractions (%) of Sedge and Reed Warblers with fat reserves sufficient for a potential non-refuelling flight along the eastern flyway from two selected stations (Kalimok and Kuscenneti) up to the south-eastern edge of two barriers: the Mediterranean Sea and the Sahara desert. Minimum fat score (FS_{min}) and minimum mean body mass ($Mass_{min}$) allowing for barrier crossing are given.

	Sedge Warbler			Reed Warbler		
Barrier/station	%	FS_{min}	$Mass_{min}$ ± SD	%	FS_{min}	$Mass_{min}$ ± SD
Mediterranean Sea						
Kalimok	15.6	5	12.62 ± 0.89	11.8	5	12.69 ± 0.79
Kuscenneti	86.6	3	13.40 ± 2.26	30.2	3	11.73 ± 0.97
Sahara desert						
Kalimok	5.4	7	15.67 ± 1.78	–	–	–
Kuscenneti	67.1	6	15.62 ± 1.32	5.9	7	14.74 ± 1.43

nis-Jakubas 2010, Ożarowska 2015). Indeed, the results of our study from three northernmost stations located in Eastern Europe (Mierzeja Wiślana, Siemianówka and Cholgyni) also support these findings. At these latitudes, migrants do not encounter any large unhospitable areas/barriers, availability of food resources is reasonably high, and consequently the flight cost may be minimized, then all these geographical and ecological factors favour carrying low fat reserves in general (Lindström & Alerstam 1992, Alerstam 2001, Fransson *et al.* 2006).

However, at the same time some species, and the Sedge Warbler in particular at least in Western Europe, gain high fuel loads in southern Great Britain and northern France, so well before arriving to the edge of the barrier to be crossed, when still passing over zones with abundant food supplies (Bibby *et al.* 1976, Bibby & Green 1981). It seems that the fattening strategy of the Sedge Warbler migrating along the eastern route might differ slightly from what we observe in Western Europe, as was also shown for Garden Warblers (Bairlein 1991). These two routes differ in topography, wind conditions and refuelling possibilities, which may influence species migration strategy. On the western route, the majority of long-distance migrants head towards the Iberian Peninsula, cross only a small stretch of the Mediterranean Sea and finally cover the shorter distance over the Western Sahara with more oases and vegetation compared to desert areas further east (Biebach *et al.* 1986, Schaub & Jenni 2000a, Zehtindjiev & Liechti 2003). On the eastern route, on the other hand, migrants benefit from favourable autumn tailwinds for crossing the eastern Mediterranean Sea and then Egyptian desert (Erni *et al.* 2005).

In our study prominent differences in fat reserves of Sedge and Reed Warblers were documented more southerly, at Kalimok and Kuscenneti, located in the Balkans and Asia Minor, with Sedge Warblers carrying clearly higher fat load. Two-thirds of Sedge Warblers in Kuscenneti had enough fat reserves to successfully reach the Sahel zone, enabling them to cross two large barriers in potentially one non-refuelling step, whereas among Reed Warblers there were only a few such individuals.

These clear differences indicate that Sedge Warblers gain considerable fat reserves already before the Mediterranean Sea, as opposed to the majority of Reed Warblers which carry low fat load. This is in agreement with the results of Fransson *et al.* (2006) from Lesbos, a Greek island located 100 km from Kuscenneti, documenting high mean body mass of Sedge Warblers captured there (Lesbos: 15.9 g, Kuscenneti: 14.8 g). Other studies from Greece and Turkey (Akriotis 1998, Erciyas *et al.* 2010) also reported Sedge Warblers as carrying high fat load migrants, contrary to Reed Warblers with low fat reserves.

These results also agree with the findings of the studies on Reed Warblers migrating along the western route, which showed that many birds gained fat reserves in the northern Africa, i.e., at the northern edge of the Sahara desert (Biebach 1990, Arizaga *et al.* 2011b, Andueza *et al.* 2014). The observed pattern, i.e., Sedge Warblers accumulating very high fat reserves, while Reed Warblers carrying low fat load in south-eastern Europe and Asia Minor indicates difference in their fattening strategy and consequently the migration strategy they employ. Sedge Warblers may accomplish migration with larger fat reserves in few, but long steps, while Reed Warblers may minimize their energy expenditure and travel with low fat reserves as long as they encounter favourable conditions to replenish fat reserves, which would be associated with time or energy minimization hypotheses, respectively (Lindström & Alerstam 1992, Alerstam *et al.* 2003).

On the other hand, experimental study, which included supplementary feeding, showed that Reed Warblers were time-minimisers. Yet their fuelling behaviour was unlikely to be shaped by selection for time minimization only, but it was also foraging intensity-dependent predation risk that resulted in fuelling rates not being maximized (Bayly 2006).

On migration, Reed Warblers are able to exploit a much broader range of habitats than Sedge Warblers (Schaub & Jenni 2000a,b), which enable them to stopover in drier habitats in the Mediterranean region, like *Tamarix* sp. bushes (Glutz von Blotzheim & Bauer 1991). Sedge Warblers are more confined to marshy areas and rarely occupy arid habitats (Bibby *et al.* 1976, Cramp 1992, Kennerley & Pearson 2010). The migration strategy of Sedge Warblers in Europe has been linked mainly to superabundance of plum-reed aphids *Hyalopterus pruni*, the temporarily and spatially restricted food source that enables birds to accumulate extensive fat reserves and make long non-refuelling flights to sub-Saharan Africa (Bibby *et al.* 1976, Bibby & Green 1981, Chernetsov & Manukyan 2000, Bayly 2007). The Reed Warbler, on the other hand, is not a food-specialist and can feed on different kinds of arthropods, which are distributed more evenly. Its migration over the western and central part of the continent is slower and takes course in short stages (Bibby & Green 1981, Ormerod 1990, Bensh & Nielsen 1999, Chernetsov & Manukyan 1999, Schaub & Jenni 2001).

Ringing recoveries of Sedge and Reed Warblers from the eastern route are scarce (Shirihai 1996, Cepák *et al.* 2008, Csörgő *et al.* 2009, Kralj *et al.* 2007, 2013, Valkama *et al.* 2014), and the pattern of crossing the Mediterranean Sea by these species during autumn migration is less clear compared to the western migration flyway. According to the recovery distribution, Reed and Sedge Warblers were recorded on the southern Greek islands, on Cyprus, along the eastern Mediterranean coast, and at Egyptian coasts (op. cit.). Autumn radar studies of Zehtindjiev & Liechti (2003) showed, that high proportion of passerine nocturnal migrants flying along the eastern route do not circumvent, but cross eastern Mediterranean Sea on a broad front towards Libyan and Egyptian coasts. They commonly rely on support of consistent favourable tail-winds which effectively decrease energetic costs of migration enabling barrier crossing with lower fat deposits (Biebach 1992, Zehtindjiev & Liechti 2003, Erni *et al.* 2005).

Besides, the ringing recoveries of Reed Warbler indicate, that the network of islands in this part of the Mediterranean may divide sea crossing into shorter steps and thus enable migrants to reduce open sea crossing to even less than 400 km (for example from Crete or Cyprus). Additionally, migrating Reed Warblers are able to feed in the Mediterranean region in habitats other than reeds (Schaub *et al.* 2001). When considering all these facts it seems probable that the proportion of Reed Warblers which reach the northern African coasts departing from the Balkans and Asia Minor may be underestimated in our study. Flight range estimations indicated that majority of highly fattened Sedge Warblers when initiating flight from Asia Minor had enough fat reserves to reach the southern edge of the Sahara desert. White et *al.* (2013) showed that although Sedge and Reed Warblers were scarce visitors in one of the northern Egyptian oases, Sedge Warblers had much higher fat reserves when compared to Reed Warblers (mean fat score: 4.6 and 1.7, respectively).

This suggests that some Sedge Warblers continue the Sahara crossing with high fat reserves or only stop in vast reedbeds in the Nile Delta (Zaniewicz & Chruściel 2011), whereas Reed Warblers continue southward migration with lower fat deposits, stopping more often and replenish fat reserves en route. Besides, it seems that at least those Reed Warblers, which migrate along the Nile Valley, deposit fuel reserves gradually (Ożarowska *et al.* 2010), and not just in front of the Sahara as was previously suggested by Schaub &

Jenni (2000a), and Yohannes *et al.* (2009). According to Ożarowska *et al.* (2010), the proportion of Reed Warblers with high fat reserves was distinctly higher in Saluga-Ghazal (ca., 70%), near Aswan at the Nile River in the southern Egypt, than in Burullus (less than 30%) in the northern part of the Nile Delta – two sites located ca. 1,000 km apart (SG and BR, respectively in Fig. 1).

Moreover, Reed Warblers were one of the most numerous migrants in Saluga-Ghazal, while Sedge Warblers were scarce there (Hasseb *et al.* 2004). Sedge Warblers as habitat specialists may not find suitable feeding conditions along the Nile Valley, while Reed Warblers as opportunists could fatten effectively there. Thus at least some Reed Warblers migrating along the eastern flyway may successfully utilise the Nile River valley with its narrow belt of agricultural land and humid vegetation as the refuelling corridor towards sub-Saharan Africa, which was also suggested by Biebach (1990) and Akriotis (1998).

In general, the results of the present study showed that two studied species migrating through the northern part of the study area carried low fat reserves, while they distinctly differed in those reserves when approaching the first barrier, the eastern part of the Mediterranean Sea. Low fat loaded Reed Warblers seem to adopt short-step strategy there, circumventing along the eastern coasts or with favourable tail-winds cross the sea and then, at least some, utilize the Nile Valley to replenish fat reserves en route to cross the Sahara desert (Ożarowska *et al.* 2010). High fat loaded Sedge Warblers, on the other hand, are able to directly cross two barriers from Asia Minor in a long non-refuelling step. Similar interspecific differences in fattening strategies of the studied species (long-step vs. short-step migration) were previously reported from the western flyway (Bibby & Green 1981, Schaub & Jenni 2000a,b, Arizaga *et al.* 2011b). It seems that the migration strategies of the Reed and Sedge Warbler are consistent over the vast Euro-Asia region.

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Ruoko- ja rytikerttusen syysmuuton aikaiset ruokailustrategiat Itä-Euroopan muuttoreitillä

Tutkimme ruokokerttusen ja rytikerttusen ruokailustrategiota syysmuuton aikana. Rasvaindeksejä analysoitiin viidellä rengastusasemalla, eteläiseltä Itämereltä ja Vähä-Aasiaan. Kummallakin lajilla oli alhainen rasvaindeksi Itä-Euroopassa, ja korkeampi indeksi Balkanin niemimaan rengastusasemalla. Vähä-Aasiassa ruokokerttusella havaittiin kaksi kertaa korkeampi rasvaindeksi kuin rytikerttusella. Täten 90 % ruokokerttusista ja vain 30 % rytikerttusista pystyvät todennäköisesti ylittämään Välimeren ilman pysähdyksiä.

Arvioimme lisäksi että kaksi kolmannesta ruokokerttusista todennäköisesti pystyy lentämään Saharan eteläpuolelle ilman pysähdyksiä, kun taas rytikerttusista vain noin 6 %. Tulokset osoittavat selviä eroja potentiaalisissa lentomatkoissa ja ruokailustrategioissa tutkituilla lajeilla Vähä-Aasiassa. Suurin osa ruokokerttusista ruokailee kauan ennen Saharan ylittämistä ja pystyy täten lentämään pitkiä yhtäjaksoisia matkoja sekä Balkanvuoriston että Saharan yli.

Rytikerttuset sen sijaan kerryttävät vain vähäisiä rasvavarastoja, ja tekevät mahdollisesti lyhyitä lentomatkoja Kyproksen kautta ja/tai Välimeren itärannikkoa seuraillen. Vastaavia lajienvälisiä eroja on havaittu myös kyseisten lajien Länsi-Euroopan muuttoreitiltä. Tuloksemme viittaavat siis samanlaisiin muuttostrategioihin lajien läntisellä ja itäisellä muuttoreitillä pohjoisella pallonpuoliskolla.

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Online supplementary material

Supplementary Fig. S1. Mean fat scores of juvenile Reed Warblers in 2002 and 2003.
Supplementary Fig. S2. Mean fat scores of juvenile Sedge Warblers in 2002 and 2003.