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Changes in migration phenology and biometrical traits of Reed, Marsh and Sedge Warblers

Research Article

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Abstract: Global environmental processes like climate change could severely affect population level migratory behaviour of long range migrant birds. We analyzed changes in migration phenology and biometrics of three closely-related long-distance migrant *Acrocephalus* species. We used the records of 12 063 Sedge, 12 913 Reed, and 5 409 Marsh Warblers caught and ringed between 1989-2009, at a Hungarian stopover site. Quantile regressions were used to analyse the changes in spring and autumn migration phenology. Median spring arrival date of Sedge and Reed Warblers shifted 6.5 and 7.5 days earlier, respectively. Autumn arrival of all species shifted one (Reed and Marsh Warblers) or two (Sedge Warbler) weeks later. Mean body mass of adult Reed and Marsh Warblers decreased in spring (by 0.3 and 0.2 grams, respectively) and in autumn (by 0.8 and 0.2 grams, respectively) while body mass of adult Sedge Warblers decreased only in autumn (by 0.4 grams). Mean wing length of all species increased significantly (range of change: 0.6-1 mm). Despite the fact that the studied species are closely related, all three have remarkably different migration strategies. However, similar patterns can be observed in the studied parameters, indicating that global processes may have general effects on these species, albeit through markedly different mechanisms.

Keywords: *Acrocephalus • Climate change • Timing of migration • Wing length • Body mass, • Phenology*

1. Introduction

Birds are one of the best monitored taxa, and consequently with long-term standard datasets exist around the world [1]. These datasets enable us to track long-term changes in avian populations and to correlate these changes to global environmental processes. Recently, several researches reported shifts in the timing of migration of different bird species as possible consequences of climate change [2-5]. In general, long-distance (*i.e.* wintering south of the Sahara) migrants could react later to rapid alterations of the environment compared to short-range or facultative migrants [6, but see further comments in 7], as the migration of these species is predominantly under genetic control [8]. However, studies on the shift in migration phenology and its relation to climate change are often controversial [2,3,6,9-12]. The direction and degree of changes strongly depend on migration strategy, length of migration routes, timing of moult, or on the geographical position of the source data [4,10,11,13].

Despite the controversial results, generally the timing of spring migration of many long distance migrants has shifted to become earlier [e.g. 14]. Advanced arrival can

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be beneficial because birds can commence breeding earlier, hence optimizing their reproduction and increasing reproductive success [2,4,10,11,15-20].

On the other hand, less information is available on the impact of global processes on the phenology and ecology of post-nuptial migration [21,22]. The changes of timing during autumn migration are even more confusing than in spring. Although some studies of long-distance migrants found earlier departure in recent, warmer years, most report that migrants have not changed or even delayed their departure date [2]. The trends of changes in autumn migration timing usually have greater variability across populations and geographic distribution of a given species than in spring [10,21]. Birds could favour late autumn migration as a consequence of increasing temperature and improved food availability on the breeding grounds [23], thus optimizing survival. However, the optimal migration strategy may differ not just among species, but also amongst populations, age/sex groups and individuals [24-27].

Intriguingly, only a handful of studies have assessed mid to long-term changes in biometrics [28]. For example [29] and [30] have linked the changes in body mass and wing length of passerine birds to climate change through Bergman's rule. On the other hand, changes in these parameters may just as well indicate altered migration strategies, expanding breeding ranges and/or migration routes in long distance migrants [28]. The basic concept behind these hypotheses is that birds with longer, more pointed wings generate more power with less energy and migrate faster compared to shorter winged birds [31]. Thus, populations of the same species may have different wing shapes and wing lengths, related to the distances covered during migration. For example, Reed Warblers breeding in the northern extent of the species' distribution have considerably longer average wing lengths as compared to southern populations [32].

In the current study we examined changes in migration phenology and biometrics of three closely related long-distance migrant *Acrocephalus* species; the Sedge (*A. schoenobaenus*), the Reed (*A. scirpaceus*) and the Marsh Warbler (*A. palustris*) at a Central European study site. These birds share wetlands as breeding habitats, however, on a finer scale Reed Warblers prefer homogeneous reed-beds, Sedge Warblers prefer heterogeneous reed-beds and hedges, while Marsh Warblers prefer herbaceous vegetation [33]. Although all three species are closely related and have similar habitat preferences, they show markedly different migration strategies.

Reed Warblers have two distinct wintering areas: in Southeast and in Western Africa [34], and individuals of the Carpathian Basin population may utilize both areas [35]. This species arrives in April and stays until September (adults) or October (juveniles) [36]. Reed Warblers migrate in small steps, often refuelling their deposits [37] and maintain territorial behaviour at stopover sites and on the wintering grounds [33,38]. The northern populations of Reed Warblers avoid the Carpathians on migration, thus the local breeding population can be regarded as a Carpathian Basin isolate. Therefore, we presumed that all individuals trapped at the study site are from a homogeneous population breeding within the Carpathian Basin [36].

Sedge Warblers winter in the sub-Saharan region, and cross the Sahara with a long, non-stop flight. They are non-territorial at stopover sites [38] and are considered to be less territorial compared to the other two studied species during wintering [33]. These birds arrive to the study site in April and stay until September (adults) or October (juveniles). The northern Sedge Warbler populations pass through Hungary during autumn migration, thus unlike Reed Warblers, the individuals trapped at our study site may originate from several differently behaving populations [39].

Marsh Warblers winter in Southeast Africa and all European populations perform a funnel-shaped step migration, crossing into Africa *via* the East-Mediterranean in large steps [40,41]. Birds arrive only in May and stay until the end of September at our study site [42]. This species does not defend territories at stopover sites, but is territorial on wintering grounds [33]. Marsh Warblers travel large distances between re-fueling sites and stop only a handful of times during migration [43]. Populations originating Northwest of the Carpathian Basin pass through the region during autumn migration [42]. In Sedge and Marsh Warblers, there are only a few ring recoveries from other European or North-African stopover sites south of the Carpathian Basin, thus the ringing site of this study is considered to be an important refuelling area for both species [36,39,42].

In general, the timing of spring and autumn migration of the three species shifted earlier in the last few decades throughout Europe [9,10,13,19,22,44,45]. However, we have previously shown delayed autumn migration at our study site for most other long-range migrant species [26,28]. It is important to consider that these studies differ in applied methodology, study periods, and they have been carried out at different latitudes. All of these factors may interact and may lead to different conclusions and explanations for the observed changes [46,47].

In the current study, we analysed the changes that have happened during the past two decades (1989-2009) in migration phenology, body mass and wing

length of these trans-Saharan migrant species. We hypothesize that global environmental processes affect parameters describing the migration of the three studied, closely related species. We also hypothesize that these patterns will be similar, despite the fact that the three species have markedly different migration strategies. Revealing alterations in the timing of migration and biometrics at a Central European breeding and stopover site may contribute to a more coherent understanding of the population level migratory behaviour of different species, and may help shed light on possible effects of global processes like climate change.

2. Experimental Procedures

2.1 Study area and data

Data were collected by the Ócsa Bird Ringing Station Society near Ócsa, (47°15'N, 19°15'E), in central Hungary. The site is situated in the Ócsa Landscape Protected Area, belonging to the Danube-Ipoly National Park. The ringing station itself is at the edge of a post-glacial bog with mosaic, heterogeneous vegetation ranging from reedbeds to forests. Minor habitat alterations have occurred (e.g. due to habitat succession) during the 21 years of the study period, but in general the aquatic habitat types of the study site have remained unchanged. Thus, our results are unlikely to be biased by local habitat effects. Mist-netting and ringing were conducted using a standard methodology [48] at the same locations throughout the study period. We used the records of 12 063 Sedge, 12 913 Reed, and 5 409 Marsh Warblers caught and ringed between 1989 and 2009. Only data from the first capture was used, therefore a given individual's data is used only once in this study. Adult (hatched previous years) and juvenile (hatched that year) birds were distinguished by the abrasion of primary feathers, tongue spots and plumage colour [49] and were treated separately during the analyses.

All birds were measured by a few experts following the same standard methodology [48] to eliminate inter-observer bias. The left wing length (to the nearest millimetre using the ruler) and the body mass (to nearest 0.1 g using a digital balance) were measured for each individual. Autumn wing length measurements may be biased by feather abrasion, as all of the studied species complete a full moult (*i.e.* moulting major flight feathers) in the wintering grounds. Thus, we only analysed the data of birds whose feather wear scores were either 0 (no visible damage on feather) or 1 (minor wear visible on the feather). Visual fat scores were estimated following the Kaiser scale; ranging from zero (no visible fat) to eight (whole belly covered with fat) [50]. We used data from birds whose fat scores fell into the linear range of the Kaiser scale in the conducted biometric analyses.

2.2 Statistical analysis

Quantile regressions were used to estimate trends in 10%, 25%, 50%, 75% and 90% percentiles of the distribution of arrival times (day of the year). In quantile regression, separate regression lines are fitted for each of the specified quantiles of the distribution, thus allowing the estimation of separate trends for birds arriving in different segments of the migration wave [51]. The interpretation of slope and significance is similar to linear regressions: negative slopes indicate shift toward earlier migration, and positive slopes toward prolonged migration.

Spring migration overlaps with the breeding period, while in autumn, the migration and the dispersion of juvenile birds overlap in all three study species. To avoid bias, the timing of spring migration was calculated using data of birds captured before 1st June (in Sedge and Reed Warblers) or 25th June (in Marsh Warblers) and the timing of autumn migration in all three species was calculated using data from birds captured after the 10th July. We excluded all migration periods (*i.e.* spring or autumn trapping seasons) when less than 10 individuals of a given species were trapped.

To estimate the differences in timing of autumn migration between adults and juveniles, we included age (adult or juvenile) in the quantile regression models (with 50% percentile).

To quantify changes in mean body mass and mean wing length we initially subsetted the data to the first and last five years (periods between 1989-1993 and 2005-2009) and compared the means of the two groups using Welch two sample t-tests. Using the five years on both ends of the study period gave enough data to eliminate year effects, but are separated markedly enough to give robust results on the differences in means of body mass and wing lengths. We used the R 2.10.0 program (R Development Core Team, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2010, http://www.r-project.org) for all statistical analyses. The significance level was set to 0.05 and assumptions of statistical tests were checked for all analyses conducted.

3. Results

3.1 Changes in timing of migration

During the 21 years of the study period, the median (50% percentile) spring passage day of Sedge Warblers shifted by 7.5 (from 5th May to 28th April) and Reed

Warblers shifted 6.5 days earlier (from 4th May to 28th April); moreover, regression lines of all other quantiles were nearly parallel with these changes (Figure 1, Table 1). No significant changes were detected in the case of Marsh Warblers.

In autumn, the median passage dates of adult and juvenile Sedge Warblers shifted 14.5 and 16 days later (from 27th July to 10th August in adults and from 13th August to 28th August in juveniles). The arrival dates of adult and juvenile Reed Warblers shifted 9 and 5.5 days later (from 25th July to 3rd August and from 3rd August to 8th August in the case of adults and juveniles, respectively). The arrival dates of adult and juvenile Marsh Warblers shifted 7 and 9 days later (from 20th July to 27th July in adults

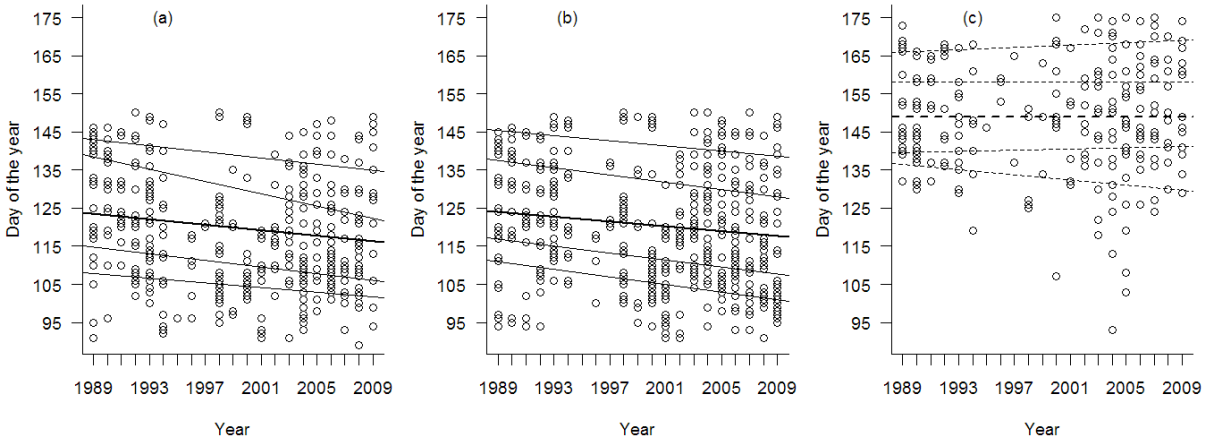

Figure 1. Scatter plot of capture time (day of the year) *versus* year. Lines were fitted with a quantile regression (10, 25, 50, 75, 90%; solid lines significant, broken lines non-significant) on the first capture dates of spring migration of Sedge (a), Reed (b) and Marsh Warblers (c).

		Spring, adults		Autumn, adults		Autumn, juveniles	
	Quantile	d	*P*-value	d	*P*-value	d	*P*-value
Sedge Warbler							
	10%	-6.3	<0.001	18.0	<0.001	21.0	<0.001
	25%	-9.2	<0.001	19.5	<0.001	23.8	<0.001
	50%	-7.5	<0.001	14.5	<0.001	15.8	<0.001
	75%	-16.8	<0.001	2.8	<0.001	18.0	<0.001
	90%	-8.4	<0.001	0	1	8.4	<0.001
	df	966		2149		8942	
Reed Warbler							
	10%	-10.5	<0.001	0	1	-3.0	<0.001
	25%	-9.7	<0.001	4.4	<0.001	0	1
	50%	-6.5	<0.001	8.8	<0.001	5.7	<0.001
	75%	-9.9	<0.001	8.7	<0.001	6.3	<0.001
	90%	-7.0	<0.001	7.0	<0.001	6.0	<0.001
	df	1564		2788		8555	
Marsh Warbler							
	10%	-7.0	0.099	0	1	0	1
	25%	1.5	0.441	5.3	<0.001	4.2	0.006
	50%	0	1	7.0	<0.001	8.8	<0.001
	75%	0	1	7.6	<0.001	9.0	<0.001
	90%	3.2	0.055	1.3	0.692	12.6	<0.001
	df	465		1428		3510	

Table 1. Shift in timing of migration of the three *Acrocephalus* spp. estimated by quantile regression. *d*: Number of days shifted during the examined period (1989-2009), df: degrees of freedom.

and from 30th July to 8th August in juveniles). Additionally, the second half of the population (50%, 75% and 90% quantiles) of both adult and juvenile Reed Warblers and juvenile Marsh Warblers left the study site significantly later, while the first part of the population (10% quantiles) left it significantly earlier or did not shifted the timing of migration, resulting in a longer autumn migration period (Table 1). In adult and juvenile Sedge Warblers, and juvenile Marsh Warblers, the regression lines of the different quantiles were parallel (Table 1).

We found that the juveniles of the studied species left the area later on average, compared to adult birds in all three species. This difference was largest in Sedge Warblers (17.3 days) and smallest in Reed Warblers (6.8 days), while juvenile Marsh Warblers left the study site 9.4 days later, than adults (quantile regression with 50% percentile, P<0.001 in all cases).

3.2 Changes in biometrics

Comparing the first and last five years of the study period, the average spring body mass of Reed Warblers and Marsh Warblers decreased significantly (by 0.3 g and 0.9 g, respectively), while the body mass of Sedge Warblers has not changed. We also found significant differences in adult birds of all three species during autumn migration. Adult Sedge, Reed and Marsh Warblers decreased their body mass by 0.6 g, 0.8 g, and 0.2 g on average, respectively. The mean body mass of juvenile Reed Warblers decreased significantly (by 0.2 g), while the juveniles of the other two species did not show such remarkable changes (Table 2).

The average wing length of adult Sedge Warblers and Marsh Warblers has increased significantly by 0.9−1.0 mm during both spring and autumn migration. The wing length of adult Reed Warblers increased significantly in both seasons. The change in spring was only 0.6 mm, while in autumn it was similar to the degree of change showed by the other two species: 1.0 mm. The average wing length of juvenile Sedge, Reed and Marsh Warblers increased significantly with 0.5 mm, 0.6 mm and 0.7 mm, respectively (Table 3).

4. Discussion

4.1 Changes in timing of migration

4.1.1 Spring migration

We detected earlier spring arrival in Sedge and Reed Warblers, in accordance with previous findings of earlier arrival of both species in Western Europe [e.g. 9,10,13,45].

A plausible explanation would be that winters are becoming milder and shorter − as a possible consequence of climate change – thus, food is available sooner [9,52]. The magnitude of changes observed for both species is similar, approximately 1 week. Although Reed Warblers analysed in the current study are Carpathian Basin isolates, while Sedge Warblers are cross migrants, they both occupy similar habitats throughout their breeding range. Thus, general environmental effects may be altering the conditions of the breeding habitat, generating similar spring arrival date responses for both species.

On the other hand, Marsh Warblers did not shift their spring arrival. The timing of spring migration of Marsh Warblers is highly variable among locations, according

		Sedge W.	Reed W.	Marsh W.
Spring adults	1989-1993	12.02 (1.04)	11.89 (1.03)	12.76 (1.30)
	2005-2009	12.00 (1.14)	11.61 (1.04)	11.89 (1.03)
	P-value	0.334	<0.001	0.023
	df	537	821	282
Autumn adults		Sedge W.	Reed W.	Marsh W.
	1989-1993	12.08 (1.45)	12.66 (0.80)	12.91 (1.34)
	2005-2009	11.50 (0.94)	11.84 (1.00)	12.67 (1.20)
	P-value	<0.001	0.004	0.050
	df	210	621	306
Autumn juveniles		Sedge W.	Reed W.	Marsh W.
	1989-1993	11.29 (1.08)	11.59 (0.92)	12.35 (1.42)
	2005-2009	11.27 (1.13)	11.41 (0.95)	12.45 (1.50)
	P-value	0.647	<0.001	<0.001
	df	2704	3407	941

Table 2. Average (SD) body mass of Sedge Warblers, Reed Warblers and Marsh Warblers during the first and the last five years of the study period (periods between 1989−1993 and 2005-2009), and their comparison using *t*-tests, df.: degrees of freedom.

Spring adults		Sedge W.	Reed W.	Marsh W.
	1989-1993	67.7 (1.9)	67.1 (1.8)	68.7 (1.7)
	2005-2009	68.6 (2.1)	67.7 (1.9)	69.6 (1.9)
	P-value	<0.001	<0.001	<0.001
	df	510	796	283
Autumn adults		Sedge W.	Reed W.	Marsh W.
	1989-1993	66.2 (1.9)	65.9 (1.8)	68.1 (1.8)
	2005-2009	67.2 (2.0)	66.9 (1.8)	69.1 (2.1)
	P-value	<0.001	<0.001	<0.001
	df	212	477	365
Autumn juveniles		Sedge W.	Reed W.	Marsh W.
	1989-1993	66.2 (1.7)	65.6 (1.8)	67.6 (2.1)
	2005-2009	66.7 (1.7)	66.2 (1.8)	68.3 (2.0)
	P-value	<0.001	<0.001	<0.001
	df	2529	3192	835

Table 3. Average (SD) wing length of Sedge Warblers, Reed Warblers and Marsh Warblers during the first and the last five years of the study period (periods between 1989−1993 and 2005-2009), and their comparisons using t-tests, df.: degrees of freedom.

to observations in Europe. In general, only Northern European populations advanced their spring migration. For example, the median arrival date of Marsh Warblers shifted 7 days earlier during spring migration between 1980−2004 at four study sites in Scandinavia [19]. However, the fact that Marsh Warblers did not alter their arrival may be attributed to their habitat. This species breeds only in the herbaceous vegetation zone of wetlands in the Carpathian Basin [53], a habitat type that becomes suitable for breeding only in May. Thus, the advantages of arriving earlier are not as pronounced compared to the early spring period. The other two species nest in the inner zones of reedbeds, hence they can commence their reproduction a month earlier [36,39,42]. In Scandinavia, the spring begins later therefore the vegetation becomes suitable for breeding later. The impacts of climate change on the environment could be remarkable in May at the northern extent of the species' range. Earlier arrival in these areas may yield advantages in reproduction, explaining the observed changes, and the lack of altered arrival dates at our study site.

4.1.2 Autumn migration

We found that the timing of autumn migration of all studied species shifted later; Sedge Warblers prolonged their migration by two weeks, while Reed and Marsh Warblers prolonged migration by a week. Contrary to our results, other Western European studies report an earlier departure in Sedge and Reed Warblers [10,13,22], while there is no data published on the timing of post-nuptial migration of Marsh Warblers. In most studies, no distinction has been made between adult and juvenile birds, making comparisons even more difficult or impossible. The changes and trends could be different among age groups and there is a large variability in the ratio of age groups at different places during autumn migration. For example, it may be biased towards juveniles in front of barriers as young, inexperienced birds need more time to prepare to get over these obstacles. Therefore, contradictory results reported from geographically distinct locations within Europe are not surprising.

Not only delayed, but more extended autumn migration periods were observed in adult and juvenile Reed Warblers at our study site. While the other two studied species breed once in a breeding season, Reed Warblers can have second clutches in the Carpathian Basin [36,39,42]. Earlier spring arrival suggests that the overall time allocated for reproduction increases, hence the ratio of second clutches may also have increased in the past two decades. The increased number of second clutch fledglings amongst autumn migrants may yield a delayed and extended autumn migration pattern. Indeed, juveniles left the study site significantly later than adults. Possible underlying reasons for delayed juvenile autumn migration may be that yearling birds perform a partial post-fledging moult in autumn and they allocate considerable time to successfully complete it [26]. Moreover, juvenile birds usually need more time to accumulate sufficient fat compared to the more experienced adults [54], and thus, may have an altogether slower mean migration speed. M. Woodrey [55] suggests that a plausible reason of the observed delay may be attributed to behavioural advantages, as

socially subordinate juveniles can avoid competition with dominant adults when they delay their passage. The increased rate of second clutches may also affect adult migration phenology. One would expect that raising a second clutch is energetically demanding, thus adults may consequently delay autumn migration.

4.2 Changes in biometrics

4.2.1 Changes in body mass

We showed considerable decrease in mean body mass between the first and the second part of the study period in all examined species, amongst most age groups and in both migration periods.

Reed warblers were 0.3 g lighter on average in spring. These birds have remarkably different migration strategies compared to the other studied species as they migrate in small steps [37,38] and use two alternative and geographically-distinct wintering areas. Reed Warblers captured in Uganda measured on average 12.4 g [Pearson 1971 in 33], 10.6 g in Israel [56], 11 g in Gibraltar [Finlayson 1981 in 33] and 11.7 g in Eastern Baltic during spring migration [57]. Considering the variation in body mass of the species at different stages of migration and wintering, the observed 0.3 g change is remarkable. For instance, it is not surprising that birds lose substantial (30-50%) weight after crossing a barrier; however, we only used the data of a single site, and hence even seemingly minor deviations could have severe impact. However, there is no data from the Carpathian Basin on the ratio of easterly and westerly migrating individuals, thus hindering the construction of biologically relevant inference of our results. Nevertheless, the observed pattern may indicate altered migration strategies (*i.e.* change in the ratio of east-west migrants) or may be a result of environmental changes on the wintering grounds and/or at the stop-over sites.

It seems that the fact that Marsh Warblers also decreased their body mass in spring supports this theory. The latter species follows an easterly funnel migration, presumably staging in similar areas as Reed Warblers. O. Gordo *et al.* [58] have shown that the stop-over sites are becoming more arid, thus the amount of available prey is presumably decreasing. If there is an easterly gradient in the degradation of habitat quality, Marsh Warblers would be more affected, while only the proportion of Reed Warblers migrating *via* the Eastern route would have lowered body mass. The 0.3 g decrease in body mass of Reed Warblers, and the 1 g decrease in case of Marsh Warblers, may indicate that such a gradient exists.

Intriguingly, mean body mass of Sedge Warblers did not change significantly in spring. These birds cover long distances and stop only a few times during migration [38], thus they need to deposit a large amount of fat before crossing barriers like the Sahara or the Mediterranean Sea. The deposited fat is burned, resulting in considerable average weight difference measured before and after certain barriers. For example, 35% of Sedge Warblers are more than 13 g in Nigeria [59]. After crossing the Sahara birds are 10.6 g in Algeria and they arrive weighing 11.2 g in England [Williamson 1968 in 33]. Climate change is known to increase the extent of the Sahara [60]. The lack of decrease in body mass, despite the fact that Sedge Warblers have to cover longer distances, indicates either the existence of an evolutionary coping mechanism and/or that the stop-over sites preceding their arrival to the study site have not changed in the past two decades.

During autumn migration adults of all three species show decreased body mass. Coupled with the fact that they also prolonged the timing of migration, these alterations may indicate adverse changes at the breeding sites and/or European stop-over sites. Arid summers and severe droughts may cause the depletion of invertebrate densities [61]. Migrating birds may compensate for the decreased food availability by either departing earlier − or if this is not possible − by prolonging their migration. In general, the latter seems to apply to all three studied species as the delay in autumn migration is accompanied by considerable average weight loss. Considering Reed Warblers, the increased ratio of second clutch breeders may also have led to a similar pattern.

On the other hand, the decrease in body mass of juveniles of all three species was less pronounced. Marsh Warbler juveniles even showed a 0.1g increase, although probably this is biologically less relevant. Juveniles are on average lighter than adults in case of all three species. Thus, we presume that the lack of pronounced change in average body mass of juveniles is simply because it cannot be further decreased without serious adverse consequences on survival. However, if the current trend continues we hypothesize that juvenile post-migration mortality will increase, resulting in demographic changes throughout the breeding range of all three species.

4.2.2 Changes in wing length

The average wing length of all three studied species has increased significantly in spring and in autumn in all age groups. A significant northward shift in the breeding area of several species has been shown [62-64]. Possibly, a similar northward shift has happened in Sedge and Marsh Warblers, as predicted by B. Huntley *et al.* [65]. Additionally, the observed increase in wing length might also reflect the fact that the size of the northern breeding

populations has increased [e.g. 63], and/or that the reproductive success of birds breeding in northern areas can be greater [66].

An alternative − but not exclusive − explanation would be based on the selection forces for longer winged individuals. These forces may facilitate the observed increase as the distances between stopover sites are increasing and/or the wintering grounds are becoming more arid [67]. The direction of autumn migration of Sedge Warblers breeding north of the Carpathians is almost 180° [35]; birds migrate through Italy [68] and possibly are crossing the Mediterranean Sea and the Sahara with non-stop flights. The extent of the Sahara is increasing continuously [60], resulting in selection forces for longer-winged individuals. In this case, the ratio of longer winged individuals captured at our study site may increase, producing the observed pattern. Most likely both the increased rate of Northern individuals and the selection forces for longer winged individuals synergistically interact and produce a general increase in mean wing lengths. The increased mean wing length could well be an evolutionary coping mechanism, compensating for larger travel distances without noticeable mean weight loss.

However, Reed Warblers are Carpathian Basin isolates and have two migration routes, both avoiding the Sahara; hence, these hypotheses would not predict wing length changes. Possibly, the observed pattern shows a shift in the ratio of easterly and westerly migrating individuals, as the eastern flyway is presumed to be longer. Alternatively, this pattern may indicate that the sex ratio within the population has changed. Males have longer wings and larger body mass than females in both age groups [27]. Juvenile males may benefit from staying longer on the breeding grounds by discovering territories for subsequent years, as they may choose their future nesting locations [69,70]. A study from Hungary supports this hypothesis, as the recapture rate of male Reed Warblers in the natal area was higher than of females [71]. An increasingly male biased sex ratio of ringed birds at the study site might also produce the observed increase in mean wing length.

In general, we found changes in timing of migration and biometrics of Sedge, Reed and Marsh Warblers. Explaining these changes can be confusing or in some cases even contradicting, however our results show that these species have altered their population level migratory behaviour. The large sample size allows us to show the changes in detail and presumably helps fill in a knowledge gap on these species from Central Europe. The results may also allow us to evaluate future changes in population dynamics, and help explain and/or predict changes in distribution ranges.

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References

[1] Moller A.P., Fiedler W., Berthold P., Effects of climate change on birds, Oxford University Press Inc., USA, New York, 2010

[2] Lehikoinen E., Sparks T.H., Zalakevicius M., Arrival and departure dates, Adv. Ecol. Res., 2004, 35, 1-31

[3] Crick H.Q.P., Sparks T.H., Changes in the phenology of breeding and migration in relation to global climate change, Acta Zool. Sinica, 2006, 52, 154-157

[4] Gordo O., Why are bird migration dates shiftling? A review of weather and climate effects on avian migratory phenology, Clim. Res., 2007, 35, 37-58

[5] Rubolini D., Moller A.P., Rainio K., Lehikoinen E., Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species, Clim. Res., 2007, 35, 135-146

[6] Both C., Visser M.E., Adjustment to climate change is constrained by arrival date in a long-distance migrant bird, Nature, 2001, 411, 296-298

[7] Tryjanowski P., Kuźniak S., Sparks T., What affects the magnitude of change in first arrival dates of migrant birds?, J. Ornithol., 2005, 146, 200-205

[8] Berthold P., Control of bird migration, Chapman and Hall London, 1st ed., London, 1996

[9] Hüpopp O., Hüpopp K., North Atlantic Oscillation and timing of spring migration in birds, Proc. R. Soc. London B. Biol. Sci., 2003, 270, 233-240

[10] Tottrup A.P., Thorup K., Rahbek C., Changes in timing of autumn migration in North European songbird populations, Ardea, 2006, 94, 527-536

[11] Zalakevicius M., Bartkeviciene G., Raudonikis L., Januaitis J., Spring arrival response to climate

change in birds: a case study from Eastern Europe, J. Ornithol., 2006, 147, 326-343
[12] Knudsen E., Lindén A., Both C., Jonzen N., Pulido F., Saino N., et al., Challenging claims in the study of migratory birds and climate change, Biol. Rev. Camb. Philos. Soc., 2011, 86, 928-946
[13] Cotton P.A., Avian migratory phenology and global climate change, PNAS, 2003, 100, 12219-12222
[14] Gordo O., Sanz J.J., Phenology and climate change: a long-term study in a Mediterranean locality, Oecologia, 2005, 146, 484-495
[15] Kokko H., Competition for early arrival in migratory birds, J Anim. Ecol., 1999, 68, 940-950
[16] Forstmeier W., Benefits of early arrival at breeding grounds vary between males, J. Anim. Ecol., 2002, 71, 1-9
[18] Dunn P.O., Breeding dates and reproductive performance, Adv. Ecol. Res., 2004, 35, 69-87
[19] Jonzén N., Lindén A., Ergon T., Knudsen E., Vik J.O., Rubolini D., et al., Rapid advance of spring arrival dates in long-distance migratory birds, Science, 2006, 312, 1959-1961
[20] Gienapp R., Leimu R., Merilä J., Responses to climate change in avian migration time -microevolution versus phanotypic plasticity, Clim. Res., 2007, 35, 25-35
[21] Jenni L., Kéry M., Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants, Proc. R. Soc. London B., 2003, 270, 1467-1471
[22] Péron G., Henry P-Y., Provost P., Dehorter O., Julliard R., Climate changes and post-nuptial migration strategy by two reedbed passerines, Clim. Res., 2007, 35, 147-157
[23] Coppack T., Pulido F., Berthold P., Photoperiodic response to early hatching in a migratory bird species, Oecologia, 2001, 128, 181-186
[24] Catry P., Bearhop S., Lecoq M., Sex differences in settlement behaviour and condition of Chiffchaffs Phylloscopus collybita at a wintering site in Portugal. Are females doing better?, J. Ornithol., 2007, 148, 241-249
[25] Tryjanowski P., Sparks T.H., The relationships between phenological traits and brood size of the white stork Ciconia ciconia in western Poland., 2008, Acta Oecol., 33, 203-206
[26] Miholcsa T., Tóth A., Csörgő T., Change of the timing of autumn migration in Acrocephalus and Locustella genus, Acta Zool. Acad. Sci. H., 2009, 55, 175-185
[27] Jacubas D., Wojczulanis-Jacubas K., Sex- and age-related differences in the timing and body condition of migrating Reed Warblers Acrocephalus scirpaceus and Sedge Warblers Acrocephalus schoenobaenus, Naturwissenschaften, 2010, 97, 505-511
[28] Kovács Sz., Csörgő T., Harnos A., Fehérvári P., Nagy K., Change in migration phenology and biometrics of two conspeci?c Sylvia species in Hungary., J. Ornithol., 2011, 152, 365-373
[29] Salewski V., Hochachka W.M., Fiedler W., Global warming and Bergmann's rule: do central European passerines adjust their body size to rising temperatures?, Oecologia, 2010, 162, 247-260
[30] Yom-Tov Y., Yom-Tov S., Wright J., Thorne C.J. R., Du Feu R., Recent changes in body weight and wing length among some British passerine birds, Oikos, 2006, 112, 91–101
[31] Lockwood R., Swaddle J.P., Rayner J.M.V., Avian wing shape reconsidered: wingtip shape indices and morphological adaptation to migration, J. Avian Biol., 1998, 29, 273-292
[32] Peiró I.G., Intraspecific variation in the wing shape of the long-distance migrant Reed Warbler Acrocephalus scirpaceus: effects of age and distance of migration, Ardeola, 2003, 50, 31-37
[33] Cramp S., Brooks D.J., Handbook of the Birds of Europe and Middle East and North Africa: The Birds of the Western Palearctic Volume VI: Warblers, Oxford University Press, Oxford, 1992
[34] Fransson T., Stolt B.O., Migration routes of North European Reed Warblers Acrocephalus scirpaceus, Orn. Svec., 2005, 15, 153-160
[35] Csörgő T., Ujhelyi P., Migration strategies of Acrocephalus species from an analysis of recaptures, In: Gyurácz J (Ed.), The 3rd Scientific Meeting of the Hungarian Ornithological and Nature Conservation Society, (1991, Szombathely, Hungary), Hungarian Ornithological and Nature Conservation Society, 2011, 111-122, (in Hungarian)
[36] Csörgő T, Gyurácz J., Reed Warbler in Csörgő T., Karcza Zs., Halmos G., Magyar G., Gyurácz J., Szép T., et al. (Eds.), Hungarian Bird Migration Atlas, Kossuth Kiadó Zrt., Budapest, 2009, (in Hungarian)
[37] Balança G., Schaub M., Post-breeding migration ecology of Reed Acrocephalus scirpaceus, Moustached A. melanopogon and Cetti's Warblers Cettia cetti at a Mediterranean stopover site, Ardea, 2005, 93, 245-257
[38] Bibby C.J., Green R.E., Autumn migration strategies of Reed and Sedge Warblers, Ornis Scand., 1981, 12, 1-12
[39] Csörgő T., Gyurácz J., Sedge Warbler in Csörgő T, Karcza Zs, Halmos G, Magyar G, Gyurácz J, Szép T, et al. (Eds.), Hungarian Bird Migration

Atlas, Kossuth Kiadó Zrt., Budapest, 2009, (in Hungarian)
[40] Dowsett-Lemaire F., Dowsett R.J., European Reed and Marsh Warblers in Africa: migration patterns, moult and habitat, Ostrich, 1987, 58, 65-85
[41] Pearson D.J., Palaearctic passerine migrants in Kenya and Uganda: temporal and spatial patterns of their movements, In: Gwinner E. (Ed.), Bird migration: physiology and ecophysiology, Springer-Verlag, Berlin, 1990
[42] Csörgő T., Gyurácz J., Marsh Warbler in Csörgő T., Karcza Zs., Halmos G., Magyar G., Gyurácz J., Szép T., et al. (Eds.), Hungarian Bird Migration Atlas, Kossuth Kiadó Zrt., Budapest, 2009, (in Hungarian)
[43] Thorup K., Rabol J., The orientation system and migration pattern of long-distance migrants: conflict between model predictions and observed patterns, J. Avian Biol., 2001, 32, 111-119
[44] Bergmann F., Long-term increase in numbers of early-fledged Reed Warblers (Acrocephalus scirpaceus) at Lake Constance (Southern Germany), J. Ornithol., 1999, 140, 81-86
[45] Spottiswoode C.N., Tottrup A.P., Coppack, T., Sexual selection predicts advancement of avian spring migration in response to climate change, Proc. R. Soc. London B., 2006, 273, 3023-3029
[46] Sparks T., Tryjanowski P., The detection of climate impacts: some methodological considerations, Int. J. Climatol., 2005, 25, 271-277
[47] Knudsen E., Lindén A., Ergon T., Jonzén N., Vik J., Knape J., et al., Characterizing bird migration phenology using data from standardized monitoring at bird observatories, Clim. Res., 2007, 35, 59-77
[48] Szentendrey G., Lövei G., Kállay Gy., 1979: The „Actio Hungarica" bird ringing netwok, Állattani Közl., 1979, 66, 161-166, (in Hungarian)
[49] Svensson L., Identification guide to European Passerines, 4th ed., Ugga, Stockholm, 1992
[50] Kaiser A., A New Multi-Category Classification of Subcutaneous Fat Deposits of Songbirds, J . Field Ornithol., 1993, 64, 246-255
[51] Cade B.S., Noon B.R., A gentle introduction to quantile regression for ecologists, Front. Ecol. Environ., 2003, 1, 412-420
[52] Askeyev O.V., Sparks T.H., Askeyev I.V., Tryjanowski P., Spring migration timing of Sylvia warblers in Tatarstan (Russia) 1957-2008, Cent. Eur. J. Biol., 2009, 4, 595-602
[53] Csörgő T., Passerine bird species of the hedge vegetation and swamp zones, In: Vásárhelyi, T. (Ed.), Animal world of reed beds, Hungarian National History Museum, Budapest, 1995, 138-144, (in Hungarian)
[54] Akriotis T., Post-breeding migration of Reed and Great Reed Warblers breeding in south-east Greece, Bird Study, 1998, 45, 344–352
[55] Woodrey M., Age-dependent aspects of stopover biology of passerine migrants, Stud. Avian Biol., 2000, 20, 43–52
[56] Yosef R., Chernetsov N., Longer is fatter: body mass changes of migrant Reed Warblers (Acrocephalus scirpaceus) staging at Eilat, Israel, Ostrich, 2005, 76, 142-147
[57] Bolshakov C., Bulyuk V., Chernetsov N., Spring nocturnal migration of Reed Warblers Acrocephalus scirpaceus: departure, landing and body condition, Ibis, 2003, 145, 106-112
[58] Gordo O., Brotons L., Ferrer X., Comas P., Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds?, Glob. Change Biol., 2005, 11, 12-21
[59] Aidley D.J., Wilkinson R., The annual cycle of six Acrocephalus warblers in a Nigerian reed-bed, Bird Study, 1987, 34, 226-234
[60] Le Houérou H.N., Climate change, drought and deserti?cation, J. Arid Environ., 1996, 34, 133-185
[61] Bale J.S., Masters G.J., Hodkinson I.D., Awmack C., Bezemer T.M., Brown V.K., et al., Herbivory in global climate change research: direct effects of rising temperature on insect herbivores, Glob. Change Biol., 2002, 8, 1-16
[62] Thomas C.D., Lennon J.J., Birds extend their ranges northwards, Nature, 1999, 399, 213
[63] BirdLife International, Birds in Europe: population estimates, trends and conservation status, Birdlife Conservation Series 12, Birdlife International, Cambridge, 2004
[64] Brommer J.E., The range margins of northern birds shift polewards, Ann. Zool. Fennici, 2004, 41, 391-397
[65] Huntley B., Green R., Collingham Y., Willis S.A., Climatic Atlas of European Breeding Birds, The RSPB and Lynx Edicions, Barcelona, 2007
[66] Jiguet F., Devictor V., Ottvall R,. Van Turnhout C., Van der Jeugd H., Lindström A., Bird population trends are linearly affected by climate change along species thermal ranges, Proc. R. Soc. London B., 2010, 277, 3601-3608
[67] Ktitorov P., Tsvey A., Mukhin A., The good and the bad stopover: behaviours of migrant Reed Warblers at two contrasting sites, Behav. Ecol. Sociobiol., 2010, 64, 1135-1143
[68] Spina F., Bezzi E.M., Autumn migration and orientation of Sedge Warbler (Acrocephalus schoenobaenus) in Northern Italy, J. Ornithol., 1990, 131, 429-438

[69] Brewer R., Harrison K.G., The time of habitat selection by birds, Ibis, 1975, 117, 521–522
[70] Morton M.L., Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the mountain White-crowned Sparrow, Condor, 1992, 94, 117–133
[71] Vadász Cs., Német Á., Karcza Zs., Loránt M., Bíró Cs., Csörgő T., Study on breeding site fidelity of Acrocephalus warblers in Central Hungary, Acta Zool. Acad. Sci. H., 2008, 54, 167–175