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CHANGE OF TIMING OF AUTUMN MIGRATION IN *ACROCEPHALUS* AND *LOCUSTELLA* GENUS

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Our research was done on trans-Sahara migrant *Acrocephalus* and *Locustella* species caught in Ócsa (Hungary) with standardized conditions between 1987–2004. We have constructed the cumulative diagram of the migration for adults and juveniles for every year and we have established the dates of the 50 and 90% percentiles. We have represented these data in the function of years and the average temperatures of August. On these distributions we have made linear regressions and studied their parameters. The very close related species react to the climate change in different degrees and direction. Although the study period is short, we have found some significant changes in the timing of migration and correlations with the temperature. The early migrating species have advanced their autumn migration and the later-migrating species have delayed it. The migration strategies of the species are very complex, so it is hard to give a uniform explanation for the changes.

Key words: bird, migration, long-distance migrant, trans-Sahara migrant, climate change, global warming

INTRODUCTION

In the last century the average temperature of the atmosphere has increased 0.7 °C (IPCC 2007). More and more unambiguous consequences of global climate change on bird migration are coming to light. Studies from North America and Western Europe show that the majority of passerines, short-, medium-, and long-distance migrants alike, arrive and breed earlier in the spring, and these changes can be related to earlier springs and higher temperatures (BOTH & VISSER 2001, COPPACK *et al.* 2001, SPARKS & MASON 2004, HÜPPOP & HÜPPOP 2005, SOKOLOV & GORDIENKO 2006). The connection between the external conditions (temperature, precipitation) and the timing of the migration is very strong at the short- and medium-distance migrants, hence in their case – in contrast with long-distance migrants – it's easy to interpret these changes. The autumn migration of long-distance migrants are less studied and understood, it is triggered by photoperiodic changes and it has a strong genetic control (BERTHOLD 1988, 1994, 1996, PULIDO *et al.* 1996). The shift of the autumn migration is less evident, than in the case of the spring migration, but several researches managed to demonstrate that during the last few decades the timing of autumn migration of many species has also changed (HANLA *et al.* 1986, GATTER 1992). The results of these studies are often controversial, the trends of different species can be opposite (SPARKS & MASON 2004, HÜPPOP & HÜPPOP 2005). General trends cannot be determined, but it seems that the autumn passage delays in short-distance migrants (JENNI & KÉRY 2003, THORUP *et al*. 2007), while in long-distance migrants the timing can change in both ways (JENNI & KÉRY 2003, THORUP *et al*. 2007). Explanations for both directions can be given: the departure of long distance migrants can advance due to the selection pressure to cross the Sahel before its seasonal dry period (JENNI & KÉRY 2003) and/or because of the earlier end of the vegetation period and high insect abundance caused for instance by the earlier drying out of marshes. (ROOT *et al*. 2003). The departure can delay, because the longer and warmer autumns allow birds to stay and feed longer on their breeding grounds, accordingly they can start their migration in a better physical condition, increasing their chance of survival.

Trying to clarify this fuzzy situation we undertook a long-term study of the dynamics of autumn migration of six long-distance migrant trans-Sahara passerine species. The aims of this investigation were (1) to detect changes in the timing of migration; (2) to study the relations between temperature and departure dates; and (3) to detect possible differences between and within species in the timing of autumn departure.

Being aware of these facts, we have made predictions, how the autumn migration of the studied species could be influenced by the climate change: (1) due to the earlier springs and longer summers the breeding period will extend, the migration will delay; (2) due to the earlier springs and higher temperatures the marshes dry out earlier, the migration will advance in time because of the earlier lack of food.

MATERIALS AND METHODS

Ócsa Landscape Protected Area is a Ramsar Site about 30 km south of Budapest (Hungary). It is a 3,600 ha wetland, a postglacial relict of a former Danube bed with very diverse vegetation (from reed beds with open water surface to closed forest) caused by human activities (agriculture, peat farming), primer- and secondary succession. The birds were captured with 70 Japanese-type (length: 12 m, height: 2.5 m, shelves: 5, mesh: 16 mm) mist nets, placed in different vegetation types, by standardized conditions. Birds are trapped from 10th of July till the end of October every year, covering the whole migration of these species. The age of every individual is determined, birds are measured and weighed.

From the 156 species and more then 230,000 individuals caught at Ócsa we have examined six trans-Saharan migrant *Acrocephalus* and *Locustella* species – Marsh Warbler (*Acrocephalus palustris*), Reed Warbler (*Acrocephalus scirpaceus*), Sedge Warbler (*Acrocephalus schoenobaenus*), Great Reed Warbler (*Acrocephalus arundinaceus*), Savi’s Warbler (*Locustella luscinioides*) and River Warbler (*Locustella fluviatilis*) – caught between 1987–2004. We have chosen these species, because they prefer marshes, habitats which are considered to be highly affected by climate change.

Studying these birds we can understand better the effects of global warming on many other species, too, which are using these types of habitats on their migration routes as roosting and feeding areas.

Because the migrating strategy of the juveniles can differ from the migration of adults in these species (GYURÁCZ & CSÖRGŐ 1991), birds were separated in two age groups: juveniles – birds hatched that year; adults – birds hatched in previous years. Individual's age was determined by tongue patches and feather characteristics (SVENSSON 1992). It would be very interesting to study separately males and females, too, but unfortunately in these species determining the sex is rarely possible. Cumulative diagrams of the migration were constructed for adults and juveniles for every year and the dates of the 50% and 90% percentiles were established (Fig. 1). The 50% percentile represents the median, the 90% percentile represents the end of the migration. We didn't choose the 100 percentile (last individual) for the end of migration, because the last 10% of birds are mainly week individuals in bad condition, not representative for the main migrating population, the dates of their departure vary strongly, this would only corrupt the statistics.

These data were illustrated in the function of years (Fig. 2) and the average temperatures of August (Fig. 3). On these distributions linear regressions have been made and their parameters were studied. The temperature data was obtained from a weather station of the National Meteorology Service, located in Pestszentlőrinc, 25 km north from the study area. We have chosen the temperature of August, because these bird species depart very early; the majority of individuals migrate in the above mentioned month.

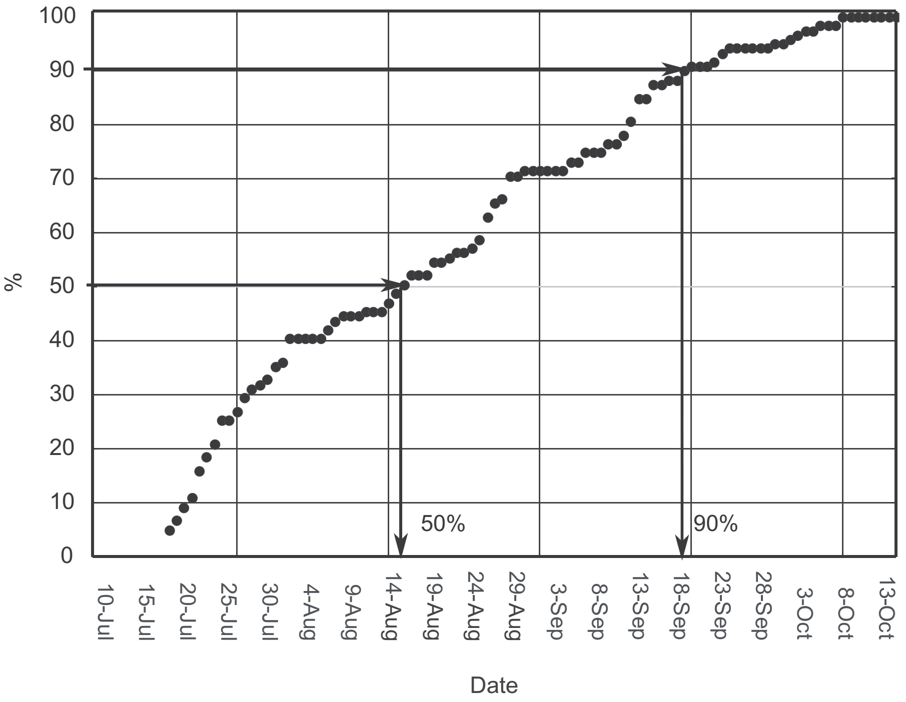

Fig. 1. Cumulative curve of juvenile Sedge Warbler in 1999 and the 50% and 90% percentiles

Table 1. Chronological order according to autumn migration data of the species (average for all the years)

	50%		90%	
	Species	Date	Species	Date
Adult	River Warbler	14 July	River Warbler	3 August
	Great Reed Warbler	24 July	Great Reed Warbler	9 August
	Marsh Warbler	24 July	Marsh Warbler	12 August
	Reed Warbler	25 July	Reed Warbler	15 August
	Savi's Warbler	26 July	Sedge Warbler	26 August
	Sedge Warbler	29 July	Savi's Warbler	28 August
Juvenile	Savi's Warbler	24 July	Savi's Warbler	20 August
	River Warbler	28 July	River Warbler	27 August
	Marsh Warbler	1 August	Marsh Warbler	28 August
	Great Reed Warbler	1 August	Great Reed Warbler	31 August
	Reed Warbler	2 August	Reed Warbler	4 September
	Sedge Warbler	15 August	Sedge Warbler	14 September

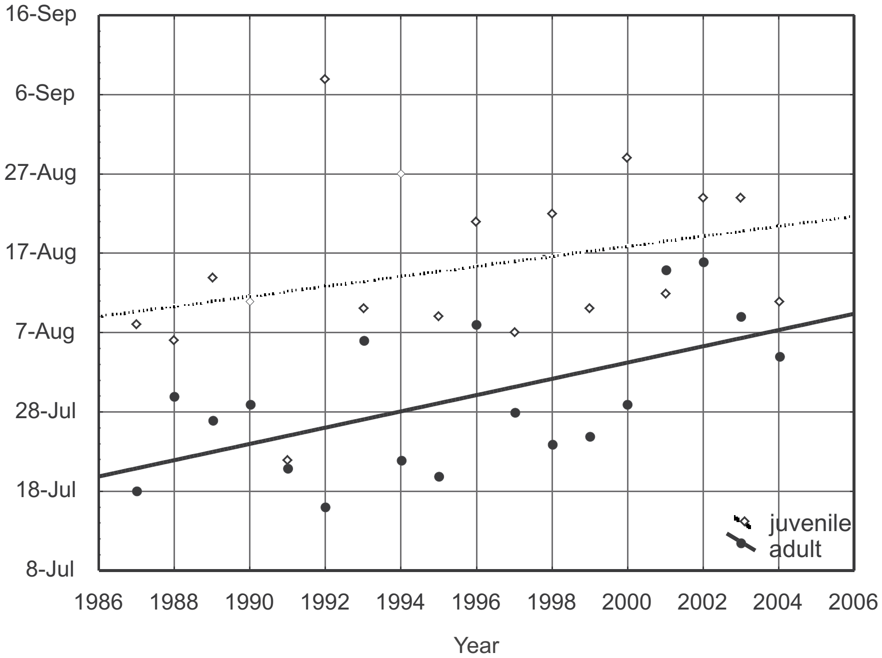

Fig. 2. Connection between the 50% percentiles of the autumn migration and the consecutive years (Sedge Warbler). (equations: juvenile: $y = 36585.9026 + 0.6326x$, $r = 0.3068$, $p = 0.2156$; adult: $y = 35786.687 + 1.0248x$, $r = 0.5907$, $p = 0.0098$)

In the table that contains the results (Table 2), the species are in the chronological order of their migration. (The order of species was different for the two age groups, so we have considered the bigger sample size of the migration of juveniles authorative.)

For the calculations we used Statistica 7 and Microsoft Excel software package.

RESULTS

Although the study period is not too long, we have found some significant changes in the timing of migration and correlations with the temperature. The very close-related species react to climate change in different degrees and directions. Early migrating species seem to migrate earlier and the later-migrating species later.

1. In time, the autumn migration of the two *Locustella* species has been advanced, the migration of the four *Acrocephalus* species (except juvenile Marsh Warblers) has been delayed. This change is significant in the case of the adult Savi-, the juvenile Reed- and the adult Sedge Warbler.

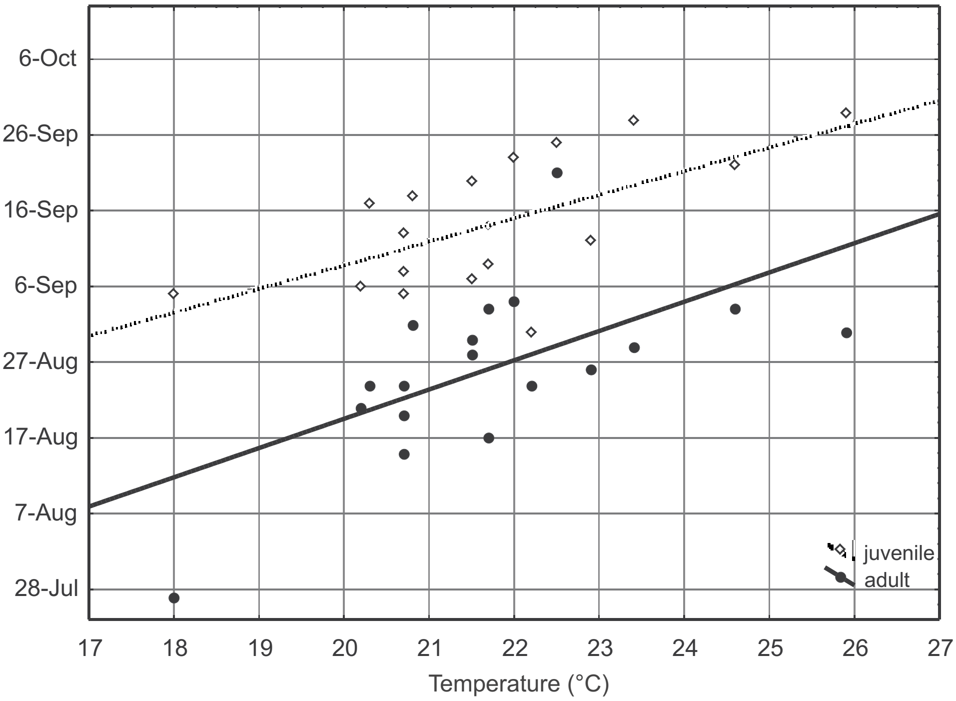

Fig. 3. Connection between the change of the 90% percentiles and the average August temperatures (Sedge Warbler) (equations: juvenile: y = 37810.7946 + 3.1145x, r = 0.6344, p = 0.0047; adult: y = 37775.1912 + 3.8655x, r = 0.6077; p = 0.0075)

2. In the case of River-, Marsh- and Sedge Warbler the timing of migration correlates stronger with the average August temperatures than with the consecutive years. This correlation is significant at the Sedge Warbler. We have also found

Table 2. Changes in the timing of departure and their correlations with average August temperature (bold = significant correlation)

Change of timing	Species	Age (number of specimens)	Regressions with years					
			50%			90%		
			slope	r	p	slope	r	p
-	Savi's Warbler	adult (n=467)	–0.675	–0.43	0.072	–0.880	–0.47	**0.049**
		juvenile (n=2836)	–0.398	–0.42	0.082	–0.090	–0.10	0.683
-	River Warbler	adult (n=73)	–0.389	–0.34	0.179	–0.632	–0.19	0.475
		juvenile (n=502)	–0.321	–0.19	0.443	–0.217	–0.09	0.711
ad – juv +	Marsh Warbler	adult (n=1286)	–0.399	–0.25	0.317	–0.658	–0.30	0.234
		juvenile (n=3042)	0.058	0.06	0.813	0.041	0.030	0.905
+	Great Reed Warbler	adult (n=388)	0.497	0.47	0.050	0.832	0.39	0.105
		juvenile (n=825)	–0.388	–0.28	0.259	0.705	0.43	0.072
+	Reed Warbler	adult (n=2828)	0.379	0.38	0.125	0.281	0.21	0.408
		juvenile (n=7732)	0.421	0.56	**0.017**	0.513	0.51	**0.032**
+	Sedge Warbler	adult (n=2134)	1.025	0.59	**0.010**	0.068	0.04	0.864
		juvenile (n=7591)	0.633	0.31	0.216	–0.356	0.27	0.277
			Regressions with August average temperatures					
			50%			90%		
			slope	r	p	slope	r	p
-	Savi's Warbler	adult (n=467)	–0.453	–0.01	0.703	–2.349	–0.42	0.086
		juvenile (n=2836)	–0.214	–0.07	0.769	–0.619	–0.23	0.346
-	River Warbler	adult (n=73)	–0.956	–0.28	0.275	2.870	0.28	0.274
		juvenile (n=502)	–1.690	–0.34	0.173	–1.123	–0.16	0.523
ad – juv +	Marsh Warbler	adult (n=1286)	1.790	0.37	0.129	2.199	0.33	0.186
		juvenile (n=3042)	0.983	0.34	0.169	1.782	0.43	0.073
+	Great Reed Warbler	adult (n=388)	0.016	0.01	0.985	1.160	0.24	0.328
		juvenile (n=825)	0.454	0.11	0.667	–1.694	–0.43	0.078
+	Reed Warbler	adult (n=2828)	0.363	0.12	0.638	0.566	0.14	0.583
		juvenile (n=7732)	0.113	0.05	0.846	1.436	0.47	**0.050**
+	Sedge Warbler	adult (n=2134)	0.785	0.15	0.553	3.866	0.61	**0.008**
		juvenile (n=7591)	4.209	0.68	**0.002**	3.115	0.63	**0.005**

significant connection between the 90% percentile date of juvenile Reed Warblers and average August temperature.

3. Differences have been found within species at the Marsh Warbler: adults migrate earlier, juveniles later. There is also a difference between the age groups of the Savi's Warbler: juveniles depart first, adults last among the six species (Table 1).

DISCUSSION

Several researchers and observations demonstrate that both short- and long distance migrant birds arrive earlier in spring to their breeding territories as the winters are becoming milder, and shorter, and food is available sooner (BOTH *et al.* 2004, HÜPOPP & HÜPOPP 2005).

In the interest of occupying territory and breeding, the spring migrations goal is to reach the breeding site as soon as possible, its' optimization is aimed at reproduction. In contrast with this, the autumn migration is slower and protracted, the

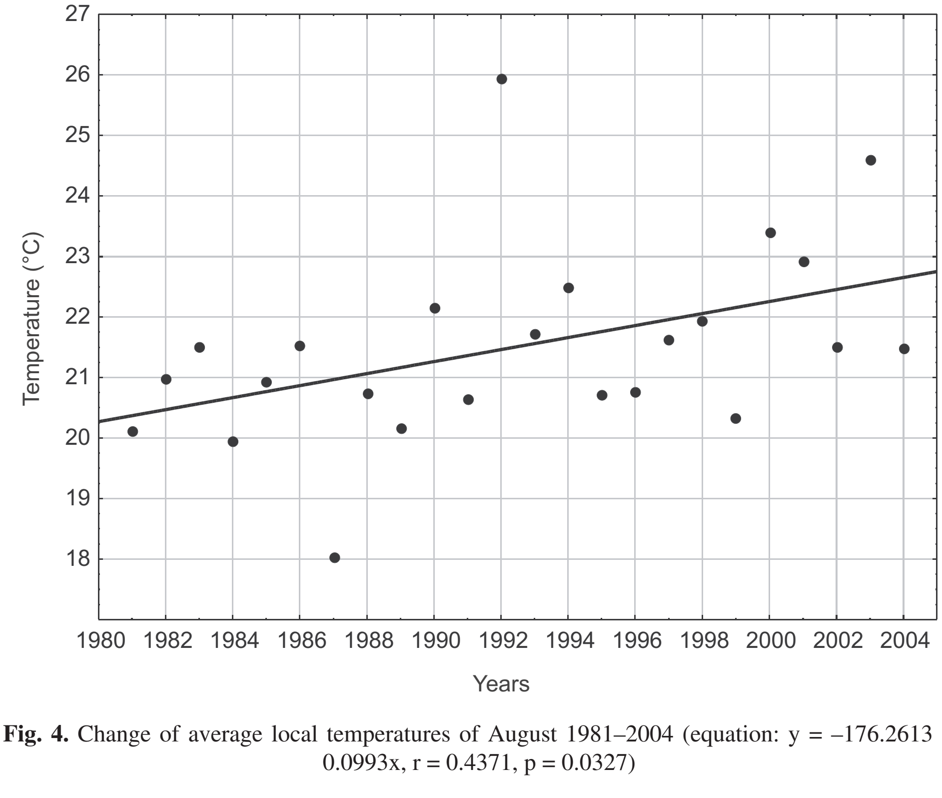

Fig. 4. Change of average local temperatures of August 1981–2004 (equation: $y = -176.2613 + 0.0993x$, $r = 0.4371$, $p = 0.0327$)

birds optimize on many factors, their goal is to survive. Therefore the variance of the changes and trends in the timing of migrations is much bigger (HÜPPOP & HÜPPOP 2005), hence we expect that the timing of autumn migration will be both advanced and delayed. Both cases have advantages and disadvantages: it is not worth to leave earlier, because the weather is favorable in the breeding territory and food is available for a while, there is more time to prepare for the migration (COPPACK *et al.* 2001). On the other hand leaving too late can be dangerous, because in time weather is more and more unpredictable, anomalies are stronger and more frequent (BEZZEL & JETZ 1995).

The autumn migration behavior of long-distance migrants is very diverse, it can be influenced by the moulting and migrating strategies (fat accumulation, timing, route, direction, speed etc.), territoriality on migration route and wintering area (MOORE & YONG 1991), food and other ecological demands, which can differ strongly between species, and moreover they can be age- and sex-dependent (KELSEY 1988, YOUNG 1988, CANTOS & TELLERIA 1994, STUTCHBURY 1994, WOODREY & MOORE 1997).

Although the studied species are very closely related, we can't give a uniform explanation for the changes. The different directions and strength of the detected trends are not surprising, namely we can't expect that climate change will affect equally different species and age groups.

A long-term study showed that the arrival and breeding of Reed Warblers has advanced in two decades and juveniles fledge earlier (BERGMANN 1999). So yearlings have more time to prepare for the migration and they theoretically could depart earlier (COPPACK *et al.* 2001, COPPACK & BOTH 2002). However, we found that juvenile Reed Warblers, like the other *Acrocephalus* juveniles, migrate later. This can be explained with their partial moult before leaving the breeding area. It seems that it is profitable for these birds to allocate more time in this very energy-(food) demanding exertion. Reed Warblers migrate slowly in the autumn because they have to invest energy in moult and migration, too. In the comparison of some European ringing stations it became evident, that this species dwell long in Europe, where while they moult, they migrate slowly without accumulating fat. By the time they arrive to the Mediterranean, they finish their moult, they start to accumulate fat and their migration speed also grows (SHAUB & JENNI 2001).

Further examination is necessary to decide weather the timing of the partial moult has been delayed, or the duration of the moult has been dilated, or both. Contrary to *Acrocephalus* juveniles *Locustella* juveniles don't make a partial moult before departure (SVENSSON 1992), hence they migrate earlier.

Differences in moult strategies between age groups can result in differences in migration within species: juvenile Savi's Warblers depart first, while adults leave last among the six studied species. The explanation might be that among the analyzed species only adult Savi's Warblers begin a complete moult before migration (KELEMEN *et al.* 2000). Because of its bigger energy-demand this process takes much more time than the partial moult of the other species, hence they leave last.

In the case of short- and medium distance migrants the distance between their breeding and wintering area is small, the weather conditions are similar in the two places. So the birds can judge at the end of the winter, when the circumstances are adequate in their breeding territory to return. In their case the migration is triggered by external factors, the timing of departure is just a physiological response given to the environmental conditions, it has no such strong genetic control, as in the case of long- distance migrants (BERTHOLD 1988, 1994, 1996).

In contrast, the distance between the wintering and breeding areas of long-distance migrants can be many thousand kilometers, so they can't estimate what kind of weather it is "at home", according to our knowledge their departure is triggered by the photoperiodic changes (COPPACK *et al.* 2001) and it is under strong genetic control (BERTHOLD & QUERNER 1981, BERTHOLD 1988, 1994, 1996, PULIDO *et al.* 1996). Despite the fact that climate change does not affect the photoperiod, there are alterations in the timing of migration. Moreover, in some species the date of the 50% and 90% percentiles correlates stronger with August average temperatures than with the consecutive years, in some cases this correlation being significant.

Considering these facts, we cannot decide, whether the plasticity of long-distance migrants is higher then we thought, or the directional selection on the population's genetic pool caused by climate change was so fast, that it produced genetic changes in the population in just 18 years. In the case of individual optimization the bird adjusts its migration to the actual weather. This is a physiological response given to the external conditions, it doesn't produce genetic changes in the population. In the case of directional selection the genetically determined timing of migration changes in the population, because individuals, who are more adequate to the effects of climate change, are favored by selection. In time this causes genetic changes in the population.

With the changing climate beside the slow rise of average data the extremities increase. For example in the Carpathian Basin the average August temperature in the last two and a half decades increased significantly with 2.5 °C, and showed a very strong fluctuation (between 18–26 °C; Fig. 4 (National Meteorology Service)). This 2.5°C rise is much higher than the rise of yearly average temperature in Hungary, so climate change could have a stronger effect on early migrating passerines than we can expect. This strong fluctuation can weaken the force of directional selection and the importance of physiological responses given to the external factors could grow.

According to our results, both predictions seem to be partially true. The departure of the studied long-distance migrants both advanced and delayed during the 18 year long study period. The delay of the migration at the studied species seems to deny that earlier lack of food at the breeding area would cause the advance in departure. It seems more probable that the migration of some species may advance due to the selection pressure to cross the Sahel before its seasonal dry period (JENNI & KÉRY 2003). According to our results if the long-distance migrants moult before migration, it is optimal to spend more time on this energy-demanding process and to leave in better physical condition, this way delaying the departure.

The timing of autumn migration can be influenced by many other factors beside the above mentioned, like population size, density, weather conditions during the breeding season etc. In the future we plan to make some further studies involving more species and factors, hoping that the effects of climate change on bird migration will be better understood.

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