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**Change in migration phenology and biometrics of two sister *Sylvia*
species in Hungary**

**Szilvia Kovács^{1,*}, Tibor Csörgő², Andrea Harnos^{1,3},
Péter Fehérvári¹ and Krisztina Nagy³**

Concise title: Change of migration phenology of *Sylvia* spp.

¹ **Szent István University, Faculty of Veterinary Science, Department of Biomathematics
and Informatics
H-1078, István utca 2., Budapest, Hungary**

² **Eötvös Loránd University, Faculty of Science, Department of Anatomy, Cell- and
Developmental Biology
H-1117, Pázmány Péter sétány 1/C., Budapest, Hungary**

³ **Hungarian Academy of Sciences – Corvinus University of Budapest, Adaptation to
Climate Change Research Group
H-1118, Villányi út 29-43., Budapest, Hungary**

*** e-mail: kovacs.szilvia@aotk.szie.hu, tel.: +36 (1) 478-4213, fax: +36 (1) 478-4217**

ABSTRACT

The distribution area and the timing of migration of many bird species have changed recently, presumably due to climatic factors. In our study we estimated the effect of climate change on migration phenology and biometrics of two sister *Sylvia* species: the medium distance migrant Blackcap (*Sylvia atricapilla*) and the long distance migrant garden warbler (*Sylvia borin*). We used the data of 52 440 Blackcaps and 6 943 Garden Warblers caught and ringed at the Ócsa Bird Ringing Station (47°15'N, 19°15'E) in Hungary between 1984 and 2008. The age and in case of blackcaps the sex groups were handled separately. The timing of the spring migration of garden warblers shifted earlier, whereas it did not change in blackcaps during the study period. We presume- in accordance with other observations concerning blackcaps in West-Europe- that it probably has changed earlier than the 80's. The timing of autumn migration shifted about two weeks later in all age and sex groups of blackcaps. We found significant correlation in the timing of autumn migration of sex groups, the sign of the differences between the timing of males and females changed. Juvenile garden warblers shifted their autumn migration 13 days later, but adults did not. Mean body mass decreased while mean wing length increased suggesting a change in the composition of the trans-migrant population. We hypothesise that due to climate change the breeding range of these species expanded northwards, producing an increased ratio of long-winged northern individuals in the trans-migrant populations.

KEY WORDS: garden warbler, blackcap, climate change, migration phenology, biometrics

Zusammenfassung

Veränderungen in Zugphänologie und Biometrie zweier Grasmückenarten in Ungarn

Bei vielen Vogelarten haben sich jüngerer Zeit Verbreitung und Zugphänologie verändert, vermutlich als Folge des Klimawandels. In dieser Studie untersuchten wir die Wirkung von klimatischen Veränderungen auf die Phänologie und Biometrie der Zuges zweier Grasmückenarten, nämlich des Mittelstreckenziehers Mönchsgrasmücke (*Sylvia atricapilla*) und des Langstreckenziehers Gartengrasmücke (*Sylvia borin*). Wir untersuchten 52.440 Mönchsgrasmücken und 6.943 Gartengrasmücken, die von der Beringungsstation Ócsa (47°15'N, 19°15'E) zwischen 1984 und 2008 gefangen und beringt wurden. Altersgruppen und bei Mönchsgrasmücken zusätzlich Geschlechtsgruppen wurden unabhängig behandelt. Der Zeitraum des Frühlingszuges der Gartengrasmücke verschob sich nach vorne, während er sich bei der Mönchsgrasmücke im Verlauf der Studie nicht änderte. Wir nehmen an, unterstützt durch andere Beobachtungen von Mönchsgrasmücken in Westeuropa, dass bei ihnen diese zeitliche Verschiebung schon vor den 1980er Jahren erfolgte. Der Zeitpunkt des Herbstzuges verschob sich bei der Mönchsgrasmücke in allen Alters- und Geschlechtsgruppen um etwa zwei Wochen nach hinten. Wir fanden signifikante Veränderungen im Zeitpunkt des Herbstzuges, wobei die Vorzeichen der Veränderung bei Männchen und Weibchen verschieden waren. Junge Gartengrasmücken verschoben ihren Herbstzug um 13 Tage nach hinten, Altvögel hingegen nicht. Ihre mittlere Körpermasse verringerte sich, während sich die mittlere Flügellänge erhöhte, was auf eine Änderung in der Zusammensetzung der durchziehenden Population hindeutet. Wir nehmen an, dass sich die Brutgebiete dieser Arten auf Grund des Klimawandels nach Norden verschoben haben, wodurch mehr nördliche, langflügelige Individuen auftreten.

71 **INTRODUCTION**

72 One of the most intriguing questions is to what extent living organisms are able to adapt to
73 rapid environmental changes (Berteaux et al. 2004). Global and regional warming play an
74 important role in distribution shifts in many taxa including birds (Root et al. 2003; Gordo
75 2007). In birds specifically, climate change may alter the geographic distribution of species
76 (Huntley et al. 2007), influence the timing and phenology of migration (Lehikoinen et al.
77 2004, Tøttrup et al. 2006; Zalakevicius et al. 2006), moult (e.g. Pulido and Coppack 2004)
78 and breeding (e.g. Crick and Sparks 1999; Charmantier et al. 2008). The rate and direction of
79 changes may differ among species and between populations of the same species (Bearhop et
80 al. 2005; Catry et al. 2006). Even age and sex groups may react differently (Catry et al. 2007).

81 In case of European birds, climate change may cause northward shifts in the breeding
82 areas (Huntley et al. 2007). These changes depend on the migration strategy of the species
83 concerned. The migration of long distance migrants is predominantly under genetic control
84 (Gwinner and Wiltschko 1978) allowing a slower adaptation to rapid changes compared to
85 residents, short-range or facultative migrants (Both and Visser 2001). Spring migration
86 shifted earlier, in particular in species with more generalized diet, shorter migration distance,
87 more broods per year, and less extensive prenuptial moult (Végyvári et al. 2009).

88 The prediction is obvious for spring migration due to the advantages of early breeding
89 (Crick and Sparks 1999; Dunn 2004). The timing of spring migration shifted earlier at most of
90 the examined species. In case of good weather conditions earlier arrival is beneficial, since
91 earlier birds can occupy better territories and can raise their reproductive success (Forstmeier
92 2002).

93 In autumn, the causes of the shifts are more complicated as birds generally optimize for
94 survival and could use different strategies to adapt to the changing environment. Departures
95 may occur earlier under a warming climate if nesting is completed earlier, or even later if the

extended season encourages additional nesting attempts (Jenni and Kéry 2003). Advanced spring migration and delayed autumn migration of several passerine species have been detected at our study site (Miholcsa et al. 2009).

Blackcaps have a large Palearctic distribution area. The southern populations are resident, the northern and eastern populations of European blackcaps are long-range migrants while the Central European populations are partial or medium-distance migrants (Cramp and Brooks 1992). Blackcaps breeding in Hungary are medium-distance migrants, their main wintering range covers the Eastern Mediterranean Basin, but birds may overwinter in any part of the Mediterranean region. Cross migrant blackcaps at our study site originate from northern populations, thus are long-distance migrants (Csörgő and Gyurácz 2009 a). In Western Europe the spring arrival of blackcaps shifted earlier according to the studies of Lungberg and Endholm (1982) and Tøttrup et al. (2006), similar shift have been observed in Central Eurasia by Askayev et al. (2009), while the timing of autumn migration is delayed (Nowakowski 1999).

Garden warbler has the most northern distribution area in the Palearctic region amongst the Sylvidae warblers (Cramp and Brooks 1992). According to ring recovery data, birds from our study area migrate through the Apennine Peninsula towards Africa (Csörgő and Gyurácz 2009 b). Their wintering grounds cover the Sahel region south from the Sahara (Cramp and Brooks 1992; Grattarola 1999). In Northern and Western Europe and Central Eurasia the timing of spring migration of the garden warblers shifted earlier (Hüppopp and Hüppopp 2003; Jonzén et al. 2006; Sparks et al. 2007, Askayev et al. 2009), the timing of autumn migration did not change in Denmark (Tøttrup et al. 2006) and in Switzerland (Jenni & Kéry 2003).

In our study we analyzed the changes in timing of migration of two Sylvia warbler species at an Eastern European stopover site. We hypothesize that birds shift their migration earlier in spring and later in autumn. We suppose it can be a possible effect of recent climate change. We propose that the changes depend on age and moulting strategy in autumn.

Furthermore, we analyzed the change in differences in migration peaks of the two sex groups of blackcaps as we hypothesize that the two sex groups may use different migration strategy. Additionally, we used wing length and body mass in order to examine how these biometric parameters have changed during the last 25 years. In our view the biometric changes could be explained by the changes in the composition of populations passing through the area, thus indirectly showing the possible effects of climate change.

2. MATERIALS AND METHODS

1.1. Location and data

Data were collected in Central Hungary (47°15'N, 19°15'E) at the Ócsa Bird Ringing Station. The station is situated within the Ócsa Landscape Protection Area, a coherent part of the Danube-Ipoly National Park. The site is at the edge of a postglacial peatbog. The surrounding is highly variable comprising all habitat types from reedbeds to closed forests. The study area has a typical continental climate with cold winters and warm summers. Our bird ringing database contains data of 25 years (1984–2008). Mist-netting and ringing were conducted at the same locations, using the methodology of Szentendrey et al. (1979) throughout the whole study period. We used the records of 13 049 adult and 39 391 juvenile blackcaps (*Sylvia atricapilla*) trapped and ringed between February-November and 1 968 adult and 4 975 juvenile garden warblers (*Sylvia borin*) ringed between April-October within the study period. Only data from first captures were used. We distinguished two age groups by features published by Svensson (1992). 1st calendar year birds are referred to as juveniles, older birds as adults. In blackcaps we could determine the sex of birds by cap colorization (Svensson 1992). All birds were measured by a few experts who follow the same methodology (Szentendrey et al. 1979) to eliminate inter-observer bias. The right 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 individuals. Visual fat scores were estimated following the scale of Kaiser (1993), ranging from zero (no visible fat) to eight (whole belly covered with fat). We used the data of birds whose fat scores fall into the linear range of the Kaiser scale in biometric analysis.

1.2. Statistical analysis

Bird migration phenology has been traditionally described by measures of central tendency (mean, median and mode) and spread (first and last observations, or 5% and 95% percentiles). We defined arrival times as the day of the year when the birds were caught at the first time and characterized the annual timing of migration by the location of the peak of the kernel smoothed arrival distribution curves (Fig. 1). Kernel smoothing was used to reduce the effects of missing observations (Silverman 1986; Knudsen et al. 2007).

Peaks of smoothed curves were identified separately for each species by season and age group and in blackcaps also by sex. To detect a shift in the timing of annual peaks during the study period, we applied linear regression analysis. The estimated shift in timing was calculated from the regression equations as the number of years times the estimated per year change (regression coefficient). Shift was regarded as significant if the corresponding linear regression was significant.

Quantile regression (Cade and Noon 2003) was used to estimate trends in 10%, 25%, 50%, 75% and 90% percentiles of the distribution of arrival times from 1984 to 2008. As different quantiles may represent different population segments which may have different responses to the changing environment, quantile regression can provide an insight to different trends of migration timing of early and late arrivals. Shift in timing and significance was determined same as for linear regression.

We analysed the relationship between migration peaks of the two species and of the two age groups of blackcap by Spearman's rank correlation (Hollander and Wolfe 1973). Furthermore we tested the changes in differences between migration peaks of male and female blackcaps by linear regression.

Concerning changes in body condition, we first applied a linear model to estimate body mass from fat score and wing length. We used wing length to control for body size. Extra deposited fat was defined as the difference between actual (observed) body mass and body mass belonging to 0 fat score estimated from the linear model. Changes in average extra deposited fat from 1984 to 2008 were estimated by linear regression weighted by sample size.

The changes in average wing length were determined by linear regression. Additionally in case of garden warblers we used quantile regression to explore changes in the annual distribution of this parameter. To see the differences between an early (1984–1990) and a late (2002–2008) period smoothed density plots were applied.

All statistical analyses were made by the R 2.9.2 program (R Development Core Team 2007).

3. RESULTS

3.1. Changes in timing of migration

No significant shift was found in spring migration peak of blackcaps ($p = 0.5$ and $p = 0.08$ for males and females, respectively). Peak of spring migration of garden warblers shifted 9 days earlier ($p = 0.016$). Quantile regression detected a shift of 8 days at the beginning of the migration period (10% and 25% quantiles) while the median passage date (50% quantile) changed by 6.5 days. For late arrivals (75 and 90% quantiles) the changes

were not significant (Table 1 and Fig. 2a). In the timing of autumn migration of blackcaps the largest delay was detected in adult males (17 days, $p = 0.02$), whereas the smallest occurred in juvenile males (11.5 days, $p = 0.02$). Females of both age groups shifted their peak time 14 days later on average (adults: $p = 0.035$; juveniles: $p = 0.025$). We found similar results by quantile regression for all groups (Table 2). In autumn the time of peak migration of garden warblers did not change significantly in adults ($p = 0.1$), whereas it shifted 14 days later ($p = 0.05$) in juveniles. Juvenile garden warblers migrated later than adults in the whole study period. Therefore the difference of median passage dates between the two age groups increased from 2 to 14 days from 1984 to 2008. In juveniles about the same delay was found for all quantiles in autumn (Table 1).

There was no significant correlation in the peak of migration of the two species neither in spring, nor in autumn. Migration peaks of male and female blackcaps correlated significantly in autumn (adults: $r = 0.55$ $p = 0.028$, juveniles: $r = 0.81$ $p < 0.0001$). In autumn the differences between migration peak of adult male and female blackcaps increased significantly between 1984-2008: estimated differences between males and females were -5 days for 1984 and 7.6 days for 2008 ($p = 0.006$).

3.2. Changes in biometrics

The extra deposited fat decreased significantly from 1984 to 2008 in each age and sex group of both species in autumn (Table 3), however it did not change in spring. The average wing length of adult blackcaps and garden warblers showed a significant increase in both seasons (0.04 mm/year, $p = 0.05$ for blackcap males in both season and 0.03 mm/year, $p = 0.05$ for blackcap females in both season, 0.05 mm/year, $p = 0.01$ for garden warblers in spring and 0.06 mm/year, $p = 0.005$ for garden warblers in autumn). Although median wing

length of adult garden warblers did not change significantly, wing length distribution shifted toward larger wing lengths (Table 4, Fig. 3, 4). We have not observed remarkable size differences between sexes.

4. DISCUSSION

The distribution area and the timing of migration of many bird species has changed recently, presumably due to climatic factors (Gordo 2007). In our study we pointed out some possible consequences of climate change on the migrating populations of blackcaps and garden warblers caught at the Ócsa Bird Ringing Station in Hungary.

The timing of spring migration of many long and medium distance migrants shifted earlier (e.g. Gordo and Sanz 2005, Sparks and Tryjanowski 2007). The reason of this changing trend could be the optimization to reproduction. In spring birds benefit from the early arrival and could increase their reproductive success in case of favourable spring weather conditions (Forstmeier 2002; Dunn 2004). In spite of the possibility of prosperous consequences of advanced spring migration neither sex groups of blackcaps altered their spring arrival timing significantly during our study period. The reason may be that this species migrates very early in spring and earlier arrival could be non-adaptive as local weather is highly unfavourable preceding the observed arrival dates. In Hungary the first blackcaps arrive in late February, however a handful of recent observations of overwintering birds suggest that a minor fraction of the population may have become sedentary (Csörgő and Gyurácz. 2009 a). Nevertheless in early spring (late February, early March) the weather in Hungary can be very cold sub-zero temperatures and snow is often characteristic of this period. If these unfavourable circumstances occur permanently, the survival rate of birds is very low. We presume - similarly to the observations in Western Europe - that the spring

migration of blackcaps has already shifted earlier before our study period in the previous decades. According to the observations in Northern and Western Europe e. g. in Sweden the timing of spring migration of blackcaps shifted on average 5 days earlier between 1965–1979 compared to the 1941–1950 period (Lundberg and Endholm 1982). A Danish study pointed out that the median of arrival dates of blackcaps showed greater shift than those of its related species between 1976 and 1997 (Trottrup et al 2006). In Central Eurasia a study reported on 6 days earlier shift in first arrival date of blackcaps between 1957-2008 (Askeyev et al. 2009). The first garden warblers arrive to Hungary in the second half of April, the peak of migration is in the middle of May (Csörgő and Gyurácz 2009 b). We found that the spring migration of garden warblers shifted 6.5 days earlier in Ócsa. Similarly to our results, Jonzén et. al. (2006) showed a 7 days average shift of spring migration of garden warblers in Sweden (Falsterbo, Ottenby) between 1980–2004. In Germany (Helgoland) the mostly Scandinavian originated cross migrant garden warblers shifted their spring migration on average 7.4 days earlier between 1960 and 2000 (Hüppopp and Hüppopp 2003). In England (Sussex) the first arrival date of garden warblers occurred on average 16.8 days earlier during 42 years long study period (Sparks et al. 2007), however, it only shifted 4 days earlier during 51 years in Central Eurasia (Kazan) (Askeyev et al. 2009) and did not change significantly in Lithuania (Vilnius) between 1971–2004 (Zalakevicius et al. 2006).

Contrary to the observations in Central Eurasia (Askeyev et al. 2007, Askeyev et al. 2009), there was no significant correlation in the peak of migration of the two sister species neither in spring, nor in autumn at our study site. However, the lack of correlation in our data is not surprising as blackcaps in Central Eurasian are long-distance migrants, while they are medium distance migrants in Eastern Europe. Blackcaps in Central Eurasia arrive on average at the same time with garden warblers (Askeyev et al. 2009), while there is a marked difference in arrival dates in Europe.

After the dispersion period of early August the autumn migration of blackcaps starts in late August and the peak of migration is in the first half of September at our study site (Csörgő and Gyurácz. 2009 a). The autumn passage of blackcaps takes two months, thus the detected approximately two weeks shift is remarkable in all sex and age groups.

Both species alter their foraging strategy before autumn migration, they switch from insects to fruits e.g. elderberry at our study site. The change of main food source may cause inexperienced juveniles to spend more time with food deposition than adults. Adult blackcaps – contrary to juveniles and garden warblers – have postnuptial moult, therefore they stay longer, like the inexperienced juveniles. Presumably this is the reason of the approximately two weeks shift in both age groups. Another observation on the timing of autumn migration of blackcaps was a 3 days delay in North Poland in the period between 1985–1998 (Nowakowski 1999). Blackcaps favour late migration as a consequence of increasing temperature and improved food availability on the breeding grounds (Coppack et al. 2001).

In small bird species, energy-demanding life cycle stages, such as breeding, moult and migration are separated in time. Thus, there is a strong correlation between the timing of postjuvenile moult and migration of blackcaps (Pulido and Coppack 2004). The longer stopover time may be beneficial as it provides sufficient time to complete life cycle components such as moult and allows to prepare for migration (Pulido and Coppack 2004).

We found significant correlation between autumn migration peaks of the two sexes. We hypothesize that it may be due to similar responses of the sexes to annual changes of climatic parameters. Interestingly, the sign of the differences between the timing of autumn passage of adult males and females changed significantly. It means that in the early years of study period the males had earlier migration peaks compared to females and recently females leave earlier the study site and males staying longer. These results may imply that the two sex groups of blackcaps could use slightly different migration and refuelling strategies. Possibly, females place more importance on energy-maximization, in order to ensure successful reproduction

(Tryjanowski et al. 2004). On the other hand males are the territory defenders and that they generally arrive ahead of females to the breeding territories (Izhazi 1998, Gustin 1999). Catry et al. (2007) have presented convincing evidence on differential distance migration of sexes in chiffchaffs, with females moving further than males. In blackcaps was found a significantly larger proportion of females in samples of British birds that wintered in Africa (Catry et al. 2006). If this sexual difference in sex-ratios on wintering grounds occurs, males can leave the breeding ground later, than females. In case weather is highly favourable on stopover site males can stay even longer and the differences between sexes increase.

In contrast to blackcaps, winter moulting adult garden warblers must fit this highly energy consuming life-cycle component into a relatively short winter, hindering delayed departure from the breeding grounds (Hedenström et al. 2007). They gain weight faster and hence migrate earlier than juveniles. In this species, the timing of autumn migration of adults did not change during the past 25 years, while juveniles shifted their timing 13 days later. The autumn migration commences in early August at our study site. The peak of autumn passage is in early September and the last individuals leave the ringing site at the beginning of October (Csörgő and Gyurácz 2009 b). Considering that the duration of autumn passage of garden warblers at our study site is two months, our results of a 13 day shift in the migration peak of juvenile garden warblers are non-negligible.

In contrast to our results the passage times of the last 5% of garden warblers in autumn shifted earlier in Denmark (Christiansø) (Tøttrup et al. 2006). The last passage date also shifted earlier in England (Oxfordshire) between 1971–2000 (Cotton 2003). However these studies cannot be compared with our results, as they have not handled the age groups separately during their analysis, while we have found large differences in the timing of adults and juveniles.

Both species deposit large amounts of fat before autumn migration. The average body mass of blackcaps is 18.7 grams in Sweden and 21 grams on Cyprus (Fransson et al. 2006).

327 Around 16% of body mass of garden warblers from South Sweden consist of deposited fat
328 (Ellergen and Fransson 1992). In Greece the average body mass of juveniles is approximately
329 20 grams (Fransson et al. 2008), while south from the Sahara it is around 17 grams (Ottosson
330 2005).

331 As the published data shows that there could be large differences in mean body mass
332 and in average deposited fat -depending on the distances between two stopover sites and the
333 distance between their current stopover site and the wintering grounds- among migrating
334 populations. On the other hand the pattern of refueling is strictly defined in a population.
335 Therefore, the change in average deposited fat of species at a stopover site could indicate the
336 changes in population composition of cross migrating birds. Remarkable decrease was found
337 in extra deposited fat in all age and sex groups of blackcaps and in adult and juvenile garden
338 warblers at the Ócsa stopover site (Table 3). This decrease could mean a drop with more than
339 one fat score on average. As we have only analysed the first capture data of every individual,
340 and as arriving migrants are predominantly caught shortly after arrival, our data represents the
341 condition of newly arrived birds. Additionally the amount and availability of food for these
342 species could not have changed in this rate at our study area between 1984-2008, thus, it
343 signifies a change in the population composition of cross migrating birds.

344 A correlation was observed between length of migration route and wing length and
345 wing morphology of migrating birds (Lockwood et al. 1998). The wing of northern breeders
346 having longer migration route until the wintering ground is longer and more pointed than that
347 of southern breeders with shorter migration route. This theory is supported by the data of
348 blackcaps on the Iberian Peninsula, where the wing length of cross migrants is larger on
349 average than that of residents (Perez-Tris 2001). According to the data of Western
350 Mediterranean ringing stations there are differences in wing length and body mass among
351 garden warbler populations (Grattarola 1999). Our study indicates that the wing length of
352 blackcaps increased on average and the distribution of wing length shifted toward longer

winged birds regarding garden warblers (Table 4, Fig 3, Fig 4). We detected a large change in wing length (average shift of 0.8-1.3 mm), which cannot be explained by local adaptations. There are many studies, which have been reported morphological changes hypothesised as related to climatic variables (Kaňuščák et al. 2004, Tryjanowski et al. 2004). In accordance with our results long-term decrease in body weight and increase in wing length was found for ringed blackcaps in Britain between 1968 and 2003 (Yom-Tov et al. 2006).

We detected that the average body mass decreased and the average wing length increased in the migrating population during the study period. In our view this is explained by the change in the composition of individuals originating from different populations, by the increasing rate of northern originated birds among the trapped birds. Therefore a northward shift in the distribution or a larger reproductive success of these species in northern breeding territories, as the effect of climate change, is probable (Huntley et al. 2007). Our theory is supported by the positive correlation between warming weather conditions and the reproductive success in the populations of other northern breeder species (Møller 2002). The population sizes in northern breeding grounds of blackcaps and garden warblers have increased in the previous decades (Jiguet et al. 2010). According to our results there is a remarkable shift in the timing of migration in autumn and spring in case of two species. Garden warblers advanced their spring migration and the autumn migration of garden warbler juveniles and blackcaps was delayed.

In addition, our results may indirectly show the effects of climate change on extending breeding range northwards as on the predicted distribution map for blackcaps in the Climatic Atlas of European Breeding Birds, or effects on increasing reproductive success in northern breeding territories like in case of the prediction for garden warblers (Huntley et al. 2007).

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378

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382

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Tables

Table 1: Shift in timing of migration of garden warblers (*Sylvia borin*) estimated by quantile regression. Estimated number of shifted days (d) from 1984 to 2008 and p-values (p) are represented. Negative numbers represent earlier arrivals.

quantiles	spring		autumn adult		autumn juvenile	
	d	p	d	p	d	p
10%	-8.0*	0.005	8	<0.001	16	<0.001
25%	-8.0	0.001	3	0.311	9	<0.001
50%	-6.5	0.096	1	0.142	13	<0.001
75%	-7.5	0.052	0	0.922	16	<0.001
90%	1.5	1.000	2	0.901	7	<0.001

*e.g. -8.0 (upper left cell in the table) means that the shift of the 10% quantile of the distribution was 8 days earlier on average in 2008 than in 1984.

Table 2: Shift in timing of migration of blackcaps (*Sylvia atricapilla*) estimated by quantile regression. Number of days shifted (d) from 1984 to 2008 and p-values (p) are represented.

quantiles	autumn adult				autumn juvenile			
	male		female		male		female	
	d	p	d	p	d	p	d	p
10%	17.0	<0.001	12.5	<0.001	10.5	<0.001	8.0	<0.001
25%	13.5	<0.001	12.5	<0.001	9.5	<0.001	7.5	<0.001
50%	12.5	<0.001	14.0	<0.001	11.5	<0.001	12.5	<0.001
75%	12.5	<0.001	12.5	<0.001	11.0	<0.001	15.5	<0.001
90%	9.0	<0.001	14.5	<0.001	10.0	<0.001	16.0	<0.001

Table 3: Change in annual average extra deposited fat in autumn in each group of garden warblers (*Sylvia borin*) and blackcaps (*Sylvia atricapilla*) from 1984 to 2008 estimated by linear regression. The changes in grams, slopes (grams/year) and p-values are represented.

	garden warbler		blackcap			
	autumn adult	autumn juvenile	autumn adult		autumn juvenile	
			male	female	male	female
change (g)	-1.5	-1.1	-0.7	-0.8	-1.0	-0.9
slope	-0.061*	-0.046	-0.029	-0.032	-0.042	-0.036
p-value	<0.001	0.026	0.006	<0.001	<0.001	<0.001

*e.g. -0.061 in the table means that the decrease of extra deposited fat was 0.061 per year on average from 1984 to 2008.

Table 4: Changes (d) of wing length (mm) of adult garden warblers (*Sylvia borin*) from 1984 to 2008 in spring and in autumn estimated by quantile regression. The changes (mm), slopes (mm/year) and p-values are represented.

	spring adult			autumn adult		
quantiles	slope	d	p-value	slope	d	p-value
10%	0.08	2.0	0.012	0.07	1.8	<0.001
25%	0.05	1.3	0.024	0.06	1.5	<0.001
50%	0.00	0.0	1.000	0.00	1.0	1.000
75%	0.00	0.0	1.000	0.06	1.5	<0.001
90%	0.06	1.5	0.037	0.06	1.5	<0.001

562 **Figures**

563

564 **Fig. 1** The daily number of mist-netted juvenile garden warblers (*Sylvia borin*) caught in 2008
565 and the smoothed line fitted by kernel smoothing

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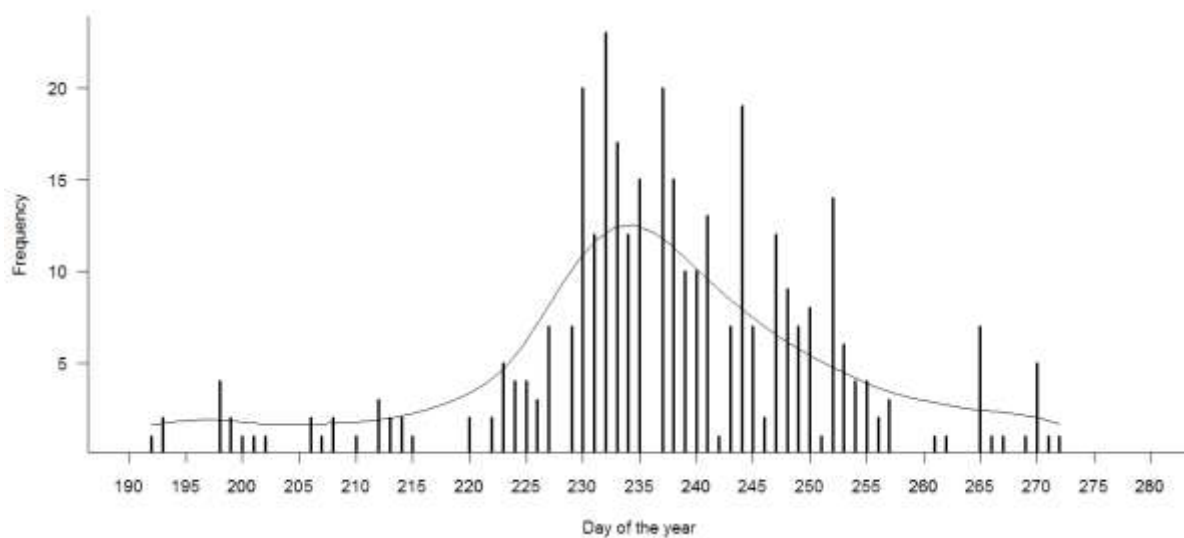
567 **Fig. 2** Scatter plot of capture times (day of the year) vs. year. Lines were fitted by quantile
568 regression (10, 25, 50, 75, 90%; significant – solid lines, non-significant - broken lines) to the
569 arrival times of spring migration of adult (a) and autumn migration of juvenile garden
570 warblers (*Sylvia borin*) (b)

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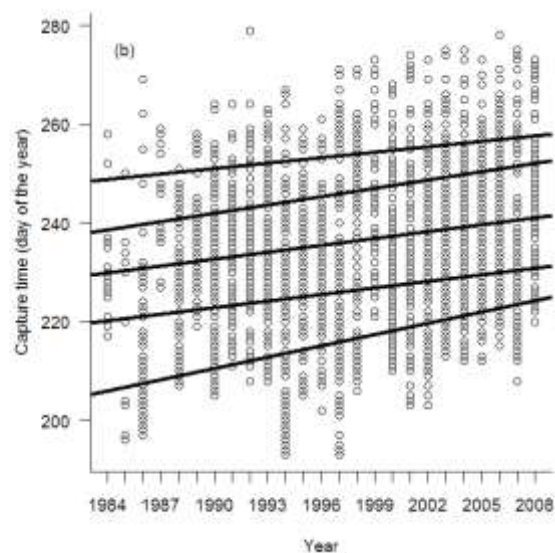
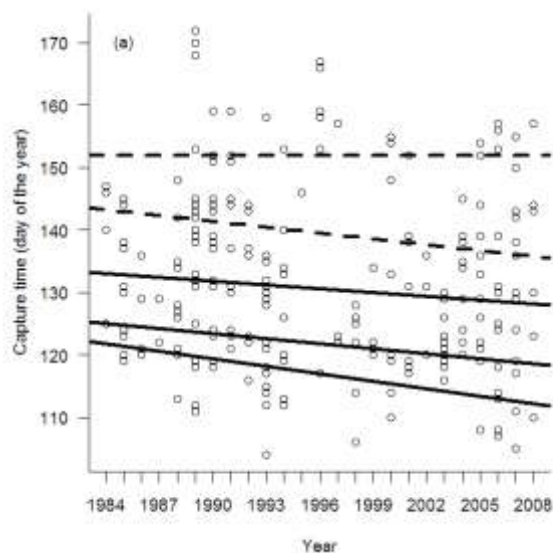
572 **Fig. 3** Wing length (mm) changes of adult garden warblers (*Sylvia borin*) captured in spring
573 (a) and in autumn (b) and fitted lines (quantile regression 10, 25, 50, 75, 90%; significant –
574 solid lines, non-significant – broken lines). Data points are jittered

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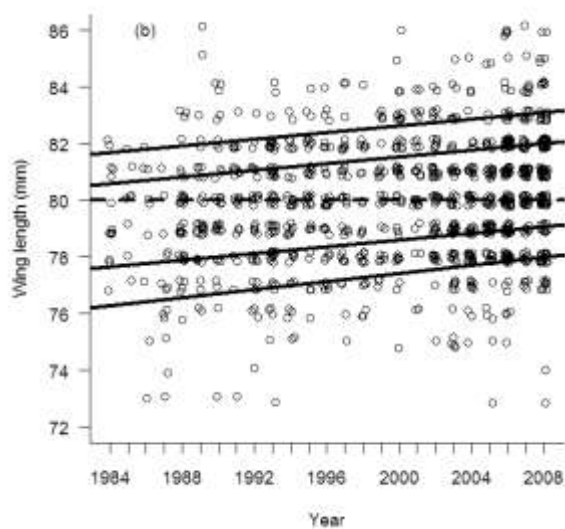
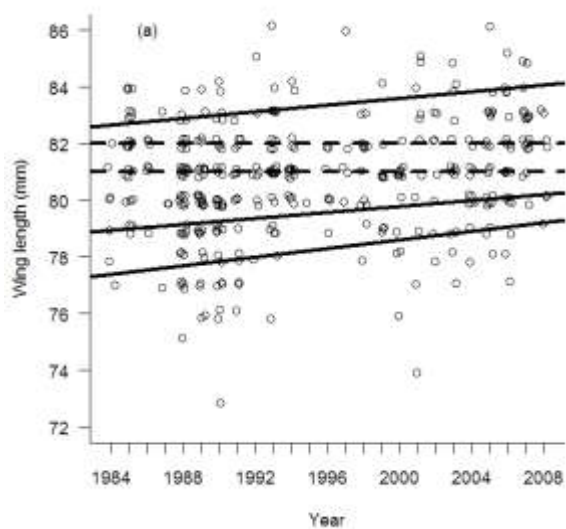
576 **Fig. 4** Smoothed density distributions of wing length (mm) of adult garden warblers (*Sylvia*
577 *borin*) captured between 1984 and 1990 (solid lines) and between 2002 and 2008 (broken
578 lines) in spring (a) and in autumn (b)



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