

# Spatial and temporal differences in the blood parasite fauna of passerine birds during the spring migration in Bulgaria

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**Abstract** Species composition and prevalence of the blood parasites of three migratory *Acrocephalus* species of warblers (*Acrocephalus arundinaceus*, *Acrocephalus scirpaceus* and *Acrocephalus schoenobaenus*) were studied during spring period in Bulgaria. For each of the studied species, we compared the parasite fauna during their spring migration at three study sites in search of infection patterns in time and space. Spatial differences were registered in the blood parasites and their prevalence for two of the studied species—*A. arundinaceus* and *A. scirpaceus*, whereas for the third one—*A. schoenobaenus*, there were no significant differences. The parasite species *Haemoproteus belopolskyi* was present in migrating *A. arundinaceus* only at Kalimok station, but not at the other two sampling locations. *Plasmodium* prevalence in *A. arundinaceus* migrating through Kalimok was also different between years. A decrease of *H. belopolskyi* prevalence was detected for *A. schoenobaenus* at Petarch during the spring of 2006. On the contrary, *Plasmodium* (*Haemamoeba*) sp. infections of the same bird species increased during the spring period. The differences found between sites could be explained with the different origin of the migrants at different migration stopover points. Climatic conditions and vector abundance in the zones of origin are probable reasons for the observed differences between years.

## Introduction

Seasonal bird migration is one of the major ways how avian unicellular haematozoa and other parasites spread (Valkiūnas 1997). Many studies showed that the blood parasites have a wide spectrum of negative influences on their hosts during migration, especially in cases with high infection intensity (Valkiūnas 1983; Møller and Nielsen 2007). Migratory birds often obtain heavy parasite infections during their long flights, and relapses of chronic infections are not rare (Clarabuch et al. 1998; Valkiūnas et al. 2004). Many spring migrants arriving in Europe have high blood parasite infection intensity (Pierce and Mead 1978; personal data) and these prime infections or relapses are part of the cost of migration. Haemosporidian infections may cause delay in the spring returning and territory occupancy, e.g. of barn swallows (*Hirundo rustica*) in Spain (Møller et al. 2004). For understanding the role of blood parasites during spring migration, it is important to have also basic data on spatial and temporal patterns of their prevalence in model bird species. Blood parasites could be used as population markers of the migrant's origin as birds originating from different local breeding populations could host different parasites (Valkiūnas 1997). Considerable spatial and temporal variation in the composition and prevalence of blood parasite lineages was detected among willow warbler (*Phylloscopus trochilus*) populations from Sweden (Bensch and Åkesson 2003). Significant spatial differences in the avian blood parasite prevalence were reported for local breeding populations of many bird species (Merilä et al. 1995; Bennett et al. 1995; Bensch and Åkesson 2003; Shurulinkov and Chakarov 2006). We suppose that such differences could be detected also at stopover sites on the spring migration route of migratory bird species, if separate populations have different routes and timing of migration.

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The present study aims to find answers to the following questions:

- Are there significant spatial differences in the blood parasite fauna and prevalence of infection of model migratory bird species during their spring migration through Bulgaria?
- Are there significant annual fluctuations in the blood parasite prevalence of particular migratory species at a fixed study point?
- Are there any differences in blood parasite fauna and infection prevalence of a migratory species within one spring season at a fixed sampling location?

## Materials and methods

As model species, we chose three species of *Acrocephalus* warblers—great reed warbler (GRW; *Acrocephalus arundinaceus*), reed warbler (RW; *Acrocephalus scirpaceus*) and sedge warbler (SW; *Acrocephalus schoenobaenus*). Between-years comparison was only conducted for GRW; as for the other two species, the sample sizes did not allow splitting between years. For similar reasons, prevalence within one season was compared between sampling sessions only for SW at Petarch in 2006.

Samples were taken during spring migration (April and May 1999–2006) at three freshwater wetlands in Bulgaria—Kalimok fishponds (Kalimok Biological Station), at Nova Cherna, NE Bulgaria (44°00' N; 26°26' E); Dragoman marsh, W Bulgaria (42°56' N; 22°57' E) and Petarch fishponds, W Bulgaria (42°51' N; 23°07' E). The latter two are 15 km apart.

Birds were caught by mist nets in reed habitats. From each bird, three blood smears were prepared, fixed in methanol for 5 min and stained with Giemsa solution for 50 min. Blood was taken by cutting the edge of the longest claw of the studied bird. Smears were examined at different magnifications for scanning, counting and parasite identification ( $\times 200$ ,  $\times 400$  and  $\times 2,000$ ). A sample was accepted

as free of parasites after scanning at least 10 min at  $\times 2,000$  magnification. Identification of the haemoproteids was performed using the descriptions published by Valkiūnas (1997). *Hepatozoon* and *Trypanosoma* parasites were identified using the descriptions in Bennett et al. (1992, 1994), respectively.

The birds recaptured from previous years were excluded from the analyses as they are probably local breeders and not transit migrants. Nevertheless, contamination of the sample by local breeding birds cannot be excluded as their migration over Bulgaria overlaps with the movements of the northern populations. For SW, there is no such problem as the breeding populations at the study sites were too small.

To verify the degree of significance of the differences,  $\chi^2$  test (Essi 1987) was used.

## Results

### Spatial differences

Blood parasite fauna and parasite prevalence for each of the studied bird species at the three study locations are presented in Tables 1, 2 and 3. The results of chi-square tests are presented in Table 4. Significant spatial differences were registered in the blood parasite composition and their prevalence for GRW and RW, whereas for SW, there were no such differences, and the obtained values were uniform between sites. The parasite species *Haemoproteus belopolnyi* was present in GRW migrating only at Kalimok, but it was not detected at all at the other two study sites. *H. belopolnyi* prevalence in RW differed significantly between Kalimok (28.6%) and Dragoman (55.3%) sites and also between Dragoman (55.3%) and Petarch (30.8%) sites.

The other haemoproteid parasites of GRW—*Haemoproteus payevskiyi*, *Plasmodium (Haemamoeba)* sp. and *Plasmodium (Novyella)* sp.—did not show significant spatial changes in their prevalence.

**Table 1** Prevalence of blood parasites in great reed warblers (*A. arundinaceus*) sampled at three stopover sites during spring migration

Locality	Year	Hp	Hb	Pl (H)	Pl (N)	Tr	Total infected	n
Kalimok	1999	3 (16.7%)	1 (5.6%)	0	0	0	4 (22.2%)	18
	2001	3 (27.3%)	1 (9.1%)	1 (9.1%)	0	0	5 (45.5%)	11
	2002	6 (17.6%)	5 (14.7%)	6 (17.6%)	2 (5.9%)	1 (2.9%)	17 (50.0%)	34
	2006	13 (27.7%)	5 (10.6%)	0	0	0	18 (38.3%)	47
	Total	25 (22.7%)	10 (9.1%)	7 (6.4%)	2 (1.8%)	1 (0.9%)	42 (38.2%)	110
Dragoman	2006	10 (25.0%)	0	2 (5.0%)	0	0	12 (30.0%)	40
Petarch	2006	15 (27.3%)	0	1 (1.8%)	0	2 (3.6%)	18 (32.7%)	55
All sites		50 (24.4%)	10 (4.9%)	10 (4.9%)	2 (0.98%)	3 (1.5%)	72 (35.1%)	205

Hp, *H. payevskiyi*; Hb, *H. belopolnyi*; Pl (H), *Plasmodium (Haemamoeba)* sp.; Pl (N), *Plasmodium (Novyella)* sp.; Tr, *Trypanosoma* sp.

**Table 2** Prevalence of blood parasites in reed warblers (*A. scirpaceus*) sampled at three stopover sites during spring migration, 2006

Locality	Hb	Pl (H)	Pl (N)	H.z.s	Tr.a	Total infected	n
Kalimok	6 (28.6%)	0	0	0	0	6 (28.6%)	21
Dragoman	21 (55.3%)	0	0	4 (10.5%)	0	22 (57.9%)	38
Petarch	16 (30.8%)	1 (1.9%)	1 (1.9%)	0	1 (1.9%)	18 (34.6%)	52
All sites	43 (38.7%)	1 (0.9%)	1 (0.9%)	4 (3.6%)	1 (0.9%)	46 (41.4%)	111

Hb, *H. belopolyskyi*; Pl (H), *Plasmodium (Haemamoeba)* sp.; Pl (N), *Plasmodium (Novyella)* sp.; H.z.s, *H. sylvae*; Tr.a, *Trypanosoma avium*

Significant differences were registered also in *Hepatozoon sylvae* prevalence in RW. *H. sylvae* was encountered only at Dragoman marsh.

*Plasmodium* infections were extremely rarely detected in RW, and the differences in their presence were not significant.

#### Annual fluctuations

Significant annual differences in *Plasmodium (Haemamoeba)* sp. infections of GRW caught at Kalimok station were registered between some of the years of the study (Tables 1 and 5). During 2006, these parasites were not recorded even once among 47 GRW.

No significant annual differences were found for the haemoproteids prevalence (Tables 1 and 5). Both haemoproteid species of GRW—*H. belopolyskyi* and *H. payevskyi*—were detected in birds from each of the four nonconsecutive years of sampling. Prevalence of *H. payevskyi* was highest in 2001 and 2006 and lowest in 2002 and 1999. Similarly, prevalence of *H. belopolyskyi* in 2002 was higher compared to 1999 and 2006. But in all these cases, differences were slight and not significant.

#### Within-season patterns in parasite composition and prevalence

Changes in the blood parasite composition and prevalence during the course of a single spring migration period were studied for SW migrating during April–May, 2006, at Petarch fishponds. We made three sampling sessions during the season—at 17–20 April; at 3–5 May; and at 12–14 May (Fig. 1). The results of chi-square tests are presented in Table 6. There was a general decrease of *H. belopolyskyi*

prevalence. On the contrary, *Plasmodium (Haemamoeba)* sp. infections seemed to increase during the season from 0% in the first sampling session to 15.2% in the third sampling session. There was no significant change in the prevalence of *Plasmodium (Novyella)* sp. and *H. sylvae*. Blood parasite composition was uniform during the three periods included in the analysis.

#### Discussion

In general, we found clearer spatial differences and much smaller annual differences in the blood parasite composition and prevalence within the studied bird species. Annual differences were registered only for *Plasmodium* parasites. Within-season interspecific differences in SW were also significant.

The fact that GRW and RW showed marked spatial differences in their parasite fauna could be explained by the different geographic origin of the migrants and separate wintering areas of the populations migrating over each of our study sites. Even closely situated wetlands (like Dragoman and Petarch wetlands) could be used during migration by birds of populations of fairly distant origin. This is also supported by the lack of recoveries of migrating warblers ringed at one of these sites (Dragoman) and recaptured at the other closely situated site (Petarch and Mramor wetlands) in the following years (personal data from the period 2000–2007). At Dragoman for the pointed period during migration, we captured 825 RW and 445 SW, and at Petarch–Mramor, about 200 RW and 400 SW and no cross recaptures were registered. Although from much smaller sample size of breeding RW, we had three cross recaptures between Dragoman and Petarch–Mramor

**Table 3** Prevalence of blood parasites in sedge warblers (*A. schoenobaenus*) sampled at three stopover sites during spring migration, 2006

Locality	Hb	Pl (H)	Pl (N)	H.z.s	Total infected	n
Kalimok	27 (61.4%)	4 (9.1%)	3 (6.8%)	10 (22.7%)	37 (84.1%)	44
Dragoman	10 (62.5%)	0	0	2 (12.5%)	10 (62.5%)	16
Petarch	66 (62.9%)	6 (5.7%)	3 (2.9%)	12 (11.4%)	74 (70.5%)	105
All sites	103 (62.4%)	10 (6.1%)	6 (3.6%)	24 (14.6%)	121 (73.3%)	165

Hb, *H. belopolyskyi*; Pl (H), *Plasmodium (Haemamoeba)* sp.; Pl (N), *Plasmodium (Novyella)* sp.; H.z.s, *H. sylvae*

**Table 4** Chi-square test results for spatial differences in blood parasite prevalence of the studied bird species (data only for 2006)

	Kalimok	Dragoman	Petarch
Great reed warbler ( <i>A. arundinaceus</i> )			
<i>H. payevskyi</i>			
Kalimok	–		
Dragoman	0.079	–	
Petarch	0.002	0.062	–
<i>H. belopolskyi</i>			
Kalimok	–		
Dragoman	4.515*	–	
Petarch	6.147*	–	–
<i>Plasmodium (Haemamoeba) sp.</i>			
Kalimok	–		
Dragoman	2.405	–	
Petarch	0.863	0.767	–
Reed warbler ( <i>A. scirpaceus</i> )			
<i>H. belopolskyi</i>			
Kalimok	–		
Dragoman	3.880*	–	
Petarch	0.034	5.441*	–
<i>H. sylvae</i>			
Kalimok	–		
Dragoman	2.371	–	
Petarch	–	5.728*	–
Sedge warbler ( <i>A. schoenobaenus</i> )			
<i>H. belopolskyi</i>			
Kalimok	–		
Dragoman	0.006	–	
Petarch	0.030	0.001	–
<i>Plasmodium (Haemamoeba) sp.</i>			
Kalimok	–		
Dragoman	1.558	–	
Petarch	0.565	0.962	–
<i>Plasmodium (Novyella) sp.</i>			
Kalimok	–		
Dragoman	1.148	–	
Petarch	1.259	0.469	–
<i>H. sylvae</i>			
Kalimok	–		
Dragoman	0.767	–	
Petarch	3.145	0.016	–

\* $P < 0.05$ 

wetlands for the same period. Unfortunately, apart from solitary cases (two RW and one SW from Hungary and one SW from Finland) we do not have enough ringing recoveries that could show us the origin of the birds migrating over the areas of the study.

Infection prevalence of *H. payevskyi* in migrating GRW (at all three studied points) varied between 22.7% and 27.3%, on average 24.4%, thus being quite similar to the rate of 21% detected on the breeding grounds in a well-studied Swedish population (Hasselquist et al. 2007). Significantly lower rates of infection with *Leucocytozoon* and *Trypanosoma* at spring migration stopover sites

**Table 5** Chi-square test results for annual fluctuations in blood parasite prevalence in great reed warbler (*A. arundinaceus*) at Kalimok Biological Station

	1999	2001	2002	2006
<i>H. payevskyi</i>				
1999	–			
2001	0.468	–		
2002	0.009	0.200	–	
2006	0.848	0.001	0.414	–
<i>H. belopolskyi</i>				
1999	–			
2001	0.133	–		
2002	0.965	0.227	–	
2006	0.401	0.023	0.302	–
<i>Plasmodium (Haemamoeba) sp.</i>				
1999	–			
2001	1.695	–		
2002	3.591	0.463	–	
2006	–	4.348*	8.958**	–

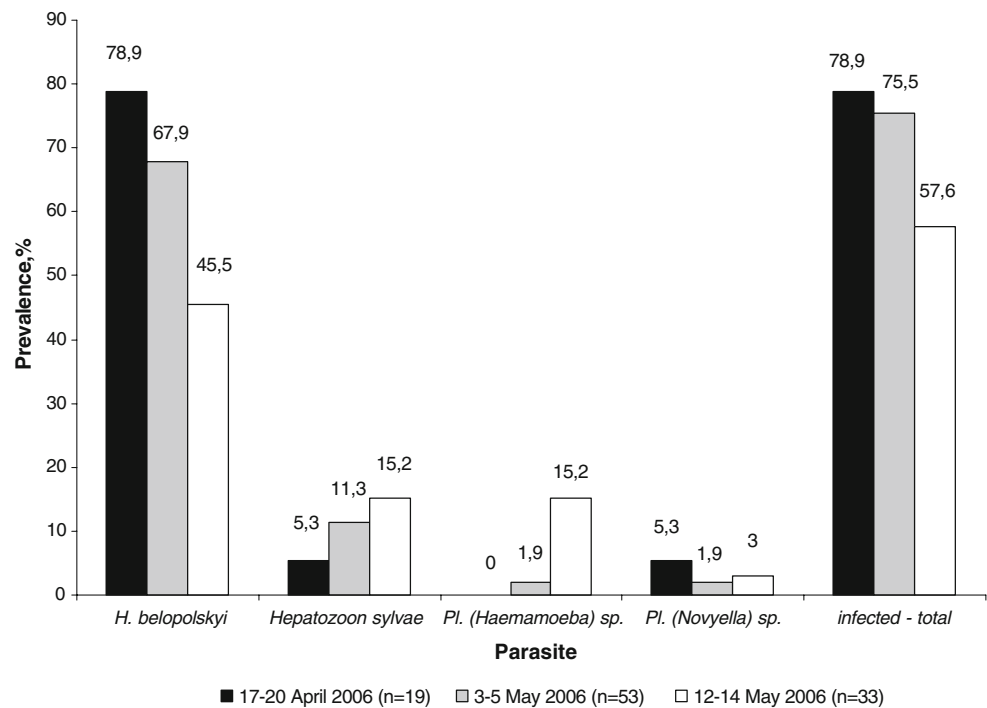
\* $P < 0.05$ ; \*\* $P < 0.01$ 

compared to the breeding areas were detected for redstarts (*Phoenicurus phoenicurus*) in Finland (Rintamäki et al. 1999). These findings lead to the conclusion that haemoproteid transmission takes place mostly on wintering areas and along the migration route of the long distance migrants in contrast to *Leucocytozoon* and *Trypanosoma* that are being transmitted to birds mainly in the breeding areas. This is in accordance with the global trends in the distribution of bird haemosporida in the Northern Hemisphere (Valkiūnas 1997).

The other parasite species of GRW—*H. belopolskyi*, registered by us at one of the three studied stopover sites (Kalimok), was not recorded in the Swedish population at all (Hasselquist et al. 2007). It has been proven that Swedish GRW obtain *H. payevskyi* infections out of their breeding grounds (Hasselquist et al. 2007). Apparently, the birds migrating through Kalimok do not belong to these Scandinavian populations and have different migration routes and wintering areas compared to the Swedish GRW. On the other hand, local transmission of haemoproteids in GRW has been proven to occur at the Kalimok site (Shurulinkov and Chakarov 2006), especially *H. belopolskyi* gametocytes were found in juvenile GRW in July (personal data). It is probable that spring migrants hold parasite infections from previous years gained not only at the wintering areas or during migration but also from their breeding grounds in Europe.

SW showed uniform prevalence and similar blood parasite composition among the study sites. This finding could be caused by a high level of mixing of migrants of different origin in Bulgaria. This mixing process could take place on their wintering grounds or during spring migration and is probably a result of weather and feeding conditions

**Fig. 1** Blood parasite prevalence in different migration waves of sedge warblers (*A. schoenobaenus*) during spring migration at Petarch fishponds



in particular geographic areas. Such specific conditions could attract birds of different origin and cause mixed “migration waves”.

Fluctuations in vector abundances determined by the particular climatic conditions in wintering territories and along the migration route could cause marked differences in parasitic composition and prevalence between years. Annual fluctuations in avian blood parasite prevalence have been detected in other studies and are usually related

to vector abundance (Sol et al. 2000; Ricklefs et al. 2005). Annual fluctuations have been reported for blood parasite prevalence in a blue grouse population (*Dendragapus obscurus*; Forbes et al. 1994) and for *Trypanosoma* prevalence in pied flycatchers (*Ficedula hypoleuca*; Sanz et al. 2002). For Scandinavian great reed warblers, most common blood parasite lineages appear to fluctuate with a periodicity of 3–4 years (Bensch et al. 2007).

There are two most probable explanations for the differences in *H. belopolyskyi* and *Plasmodium (Haemamoeba) sp.* prevalence among the studied migration waves of SW. Firstly, different “waves” probably represent birds of different origin (populations), which is the most popular hypothesis for the composition of the migration waves (Valkiūnas 1997). Such differences have been detected in autumn migrating willow warblers in Finland and have been also attributed to the diverse origin of migrants (Rintamäki et al. 1998). However, an alternative explanation of these results could be the synchronous development of infections in migrating SW. Samples taken at different moments of spring migration would then be snapshots of the same development of an infection. The rise of *Plasmodium* prevalence during the spring migration period could be due to spring relapses or to the increased activity of vectors during May compared to April. It is known that relapses of chronic blood parasite infections are most common during the breeding period of birds which is connected to compromised immune defences and higher vector activity and numbers (Applegate and Beaudoin 1970; Atkinson and Van Riper 1991; Valkiūnas 1997). These mechanisms probably initiate in the pre-breeding migration

**Table 6** Chi-square test results for within spring season differences in blood parasite prevalence in sedge warbler (*A. schoenobaenus*) at Petarch fishponds in 2006

	17–20 April	3–5 May	12–14 May
<i>H. belopolyskyi</i>			
17–20 April	–		
3–5 May	0.823	–	
12–14 May	5.540*	4.255*	–
<i>Plasmodium (Haemamoeba) sp.</i>			
17–20 April	–		
3–5 May	0.364	–	
12–14 May	3.185	5.514*	–
<i>Plasmodium (Novyella) sp.</i>			
17–20 April	–		
3–5 May	0.590	–	
12–14 May	0.163	0.117	–
<i>H. sylvae</i>			
17–20 April	–		
3–5 May	0.585	–	
12–14 May	1.155	0.268	–

\* $P < 0.05$



period and cause relapses already at stopover sites. Moreover, the cost of spring migration also includes weakening of the immune defences (Owen and Moore 2006).

## Conclusions

Blood parasitofauna of sedge warblers did not show any spatial segregation during spring migration in contrast to the blood parasitofauna of the closely related great reed warbler and reed warbler. This could be due to lower consistence in the choice of spring migration routes in sedge warblers. Thus, the level of spatial conservatism of the migration routes could vary substantially even between closely related passerine migratory species (and populations).

Blood parasite fauna, especially *Plasmodium* infections of the migratory birds engaged in spring migration, can show considerable annual fluctuations when sampled at a fixed stopover site.

*Acrocephalus* warblers show high blood parasite prevalence during their spring migration (pre-breeding) period in Southern Europe, reaching up to 70% in sedge warblers.

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