

Determinants of blood parasite infections in birds

Scientific background

Birds are exposed to avian malaria (*Haemoproteus* and *Plasmodium* spp.) infections all over the world, because insect vectors (*Haemoproteus*: *Hippoboscidae*, *Ceratopogonidae*; *Plasmodium*: *Culicidae*) transmitting these parasites are widely distributed in all continents except the Antarctic (Valkiūnas 2005). As a result, both migratory and resident birds may show moderate to very high prevalence of Haemosporidian infections depending on habitat characteristics (MalAvi database, <http://mbio-serv2.mbioekol.lu.se/Malavi/>; Bensch et al. 2009, Szöllősi et al. 2011, 2016). Acute and in some cases chronic infections may have a strong impact on the birds' health (Atkinson and van Riper 1991, Valkiūnas 2005), infected birds experience behavioural changes and lower reproductive success (e.g. van Riper et al. 1993, Sanz et al. 2001, Marzal et al. 2005). However, the effects of chronic infections may only be detected on the long-term and may result in lower life-time reproductive success and reduced lifespan of the infected birds (Asghar et al. 2015).

Parasite prevalence and virulence may vary between different populations of the same host species (Marzal et al. 2011, Szöllősi et al. 2011) and because geographic distances often correlate with genetic distances of the host populations (Verheyen et al. 1995) geographically closer host populations may show similar host-parasite coevolutionary patterns resulting in more similar parasite fauna (Szöllősi et al. 2011). However, because in different habitats parasites face different competitors and host species to which parasites are adapted to, this may cause variation in parasite prevalence between populations.

Though the prevalence and the effects of Haemosporidian parasites may differ also within a population, e.g. between different years (see e.g. Knowles et al. 2011) due to different climatic conditions and thus vector populations, or even within a season due to seasonal dependent activity of vectors and parasites (Szöllősi et al. 2016), only a few studies have examined the long-term effects of infections on hosts' fitness (but see Asghar et al. 2015). Furthermore, there is little information on the early life conditions, genetic quality of the individuals or climatic conditions on the variation of parasite prevalence (but see e.g. Møller et al. 2013), even though early life conditions that nestlings experience have been shown to have long-term fitness consequences (see e.g. Szász et al. 2017) and they may also contribute to the sensitivity of the individuals to different type of infections. In addition, females may mate with a male other than their social partner to improve the genetic quality of their nestlings (Hasselquist et al. 1996, Kempenaers et al. 1997) and may also increase the resistance of their offspring to various type of infections.

Little is known about the physiological factors that mediate between early life conditions and sensitivity to infections. Recent research emphasizes the importance of the insulin-like growth factor (IGF-1) in the relationship between life-history traits and the susceptibility of individuals to infections in different vertebrate taxa (reviewed in Dantzer and Swanson 2001). Human malaria research suggests that IGF-1 may have a role in resistance against malaria also in birds (e.g. Luckhart et al. 2015).

In our projects we aimed to reveal what causes differences in the blood parasite prevalence patterns of different populations of two bird species (project I/1, I/2). As there is little information on the parasite prevalence in birds during autumn migration and the effects of the parasites on their hosts, we also wanted to study these questions on various other passerine species (project II/1, II/2). In addition the long-term effects of these parasites on host fitness were also investigated (project III/1, III/2 and III/3). We also aimed to develop a quick and cheap parasite detection method that can be used under field conditions (project IV/1).

Research output

I. Differences in avian malaria prevalence between populations of a bird species

I.1. Avian malaria in bearded reedling (*Panurus biarmicus*) populations

In the first part of the study, two populations of bearded reedlings were studied and blood samples were collected to investigate the role of IGF-1 in malaria resistance. The prevalence was extremely low in the studied populations (0,0% and 3,9% in the Hortobágy and the Lake Fertő populations, respectively), even though the prevalence of vectors transmitting avian malaria was high in both populations. Due to the high vector densities, such a low malaria prevalence is extremely unusual in reed dwelling passerines, where malaria prevalence generally ranges between 23,2% to 55,0% on average, depending on bird species. We have compared our findings with data found in the literature and published a paper discussing these results (*Szöllősi et al. 2020*).

Bearded reedlings are the only species in the family *Panuridae*, living exclusively in wetlands: they forage, breed and overwinter in extensive reedbeds over a distribution range spanning from Scotland to the Yellow Sea in China. They are characterized by an extremely fast pace of life (one of the few species in the northern hemisphere with two generations in a single breeding season), strong fluctuations in population densities, including sudden local extinction events and the establishment of new populations in other areas. These unique traits suggest a rapid evolution and the extraordinary low malaria prevalence we found indicates strong selection pressure for resistance genes.

Due to the consistently low parasite prevalence in the two studied bearded reedling populations we were not able to perform the originally planned antimalarial drug experiment. However, the surprisingly low prevalence made us start a collaborative study to examine blood parasite prevalence in other bearded reedling populations across the distribution range of the species to detect the environmental factors that possibly influence malaria resistance in these birds. Due to the Covid pandemic, the collection of the samples was delayed, and the last samples arrived in 2023. The analyses of the samples for blood parasites are finishing by the PI and her students (Dorottya Sára Pásti, Milán Gábor Berki).

Our preliminary results show extremely low prevalence of blood parasites also in the new 8 populations included in this project (Sweden, Mongolia, Bulgaria, Lithuania, Romania, Poland and two populations from Spain). The prevalence ranges between 0% and 7.5% in these populations and we found only two very generalist blood parasite lineages and another one that is probably specific to the species as this will be the first description of the lineage. We are currently finishing the data analysis and **writing up the manuscript** on these results.

I.2. Avian malaria in mosquitoes and great tit (*Parus major*) populations

The effects and distribution of malaria parasites in different bird species have long been studied, however, much less is known about the vectors transmitting these parasites. Previous studies found various malaria parasites also in Hungarian resident birds (in blue tits, bearded reedlings and tree-sparrows; Szöllősi et al. 2011, 2020, unpublished), which prove that blood parasite transmission does occur also in Hungary. Therefore, we aimed to sample both the potential vectors of avian malaria parasites and resident bird populations breeding in different habitats.

We have started to collect mosquitoes (family Culicidae) from different parts of Hungary in 2020 and 2021. Mosquito samples were identified to species level and we started to screen them for blood parasites. In parallel we blood sampled great tit populations breeding in different parks of Budapest, in nature protection areas around Budapest, and in different urban and natural habitats around Veszprém. We screened the samples for blood parasites and found that avian malaria prevalence varied between 30% to

100% in the seven populations investigated. We found 8 parasite lineages out of which some are very generalists, while others are specialists to the *Parus* genus. We are starting the statistical analyses to investigate what environmental factors affect prevalence and whether there is a difference in prevalence and parasite species composition between populations breeding in urban and natural habitats. This project will serve the basis of *Milán Gábor Berki's MSc thesis* and we aim to publish it in a *peer-reviewed scientific journal*.

II. Avian malaria during autumn migration

II.1. Malaria infection status of European robins (*Erithacus rubecula*) in relation to timing of autumn migration

Though avian malaria parasites may negatively affect many aspects of the life of the passerines, previous studies on avian malaria focused mainly on the spring migration and the breeding period of the birds but the effects of these parasites during autumn migration of the hosts are under investigated. We have therefore aimed to investigate avian malaria prevalence and the effects of infections in European robins during autumn migration. We have found that parasitized individuals arrived later at the Hungarian stopover site. This could either be because avian malaria infections adversely affect the migration patterns of the birds, or because later arriving individuals come from more distant populations with higher blood parasite prevalence (*Ágh et al. 2019*).

We have also identified the parasite lineages infecting the individuals of migrating European robins and analysed the effects of different lineages on the fat accumulation probability and migration timing of the individuals. We found that individuals infected with a certain *Plasmodium* lineage (P-TURDUS1) were heavier on average and juveniles infected with this lineage had higher probability of having a visible fat. On the other hand, adult birds infected with a *Haemoproteus* lineage (H-ROBIN1) had lower probability of having a visible fat. The presence of these parasite lineages correlated with the timing of migration too. Our results emphasize that different lineages may have different effects, therefore it is very important to examine the effects of the different parasite lineages separately on the health of the birds (*Ágh et al. 2022*).

II.2. Malaria in different reed-dwelling passerines during autumn migration

The low blood parasite prevalence detected in bearded reedlings and the interesting results we got for European robins made us curious to analyse the blood samples of other reed-dwelling passerines during autumn migration. We have screened altogether 650 DNA samples collected from two consecutive years from sedge warblers (*Acrocephalus schoenobaenus*), marsh warblers (*Acrocephalus palustris*) and Eurasian reed warblers (*Acrocephalus scirpaceus*) for the prevalence of avian malaria.

We found age-related differences in the prevalence of blood parasites in the studied species. The prevalence of *Haemoproteus* species was higher in adult birds, while in juvenile birds we found almost exclusively *Plasmodium* species. Furthermore, we found that parasite prevalence increased during autumn migration in juveniles of one of the three study species, in the sedge warbler. However, there was no significant relationship between actual body condition and infection status in any of the studied bird species (*Ágh et al. 2025*).

III. Long-term effects of avian malaria infections

III.1. *Consequences of early life, environmental conditions and extra-pair paternity on Haemosporidian infection patterns and reproductive success*

In a collared flycatcher (*Ficedula albicollis*) population breeding in the Pilis-Visegrád mountains, we previously found that male nestlings can grow faster under good conditions, but are more sensitive to adverse conditions. Assuming that sensitivity of the male nestlings results from their larger energy requirement, we predicted increased costs in broods with male-biased experimental brood sex ratios. However, nestling growth was related only to background variables, namely brood size and hatching rank. Nestling mortality was related only to hatching asynchrony (Szász *et al.* 2023). We also expected higher feeding and survival rate by parents that originally had more sons, however, contrary to our prediction: males with female-biased original brood sex ratio fed their foster chicks more frequently (Gyarmathy *et al.* 2024). We found that 63.6% of the broods contained extra-pair young, and 23% of the nestlings were sired by extra-pair fathers and neither the prevalence nor the proportion of extra-pair young was related to male feeding rate (Gyarmathy *et al.* 2025).

We also measured reproductive success and collected blood samples for Haemosporidian parasite identification from recruiting adult individuals since 2002 to investigate the early environmental effects (such as rearing conditions, relatedness and nestling sex) on parasite prevalence, because in another long-term study related to our project we found that climatic conditions affected the breeding phenology of collared flycatchers (Laczi *et al.* 2024). We have found that temperature in the preceding breeding season affects prevalence of parasites transmitted in the breeding ground. We are now finishing the analysis of the dataset and writing up the *manuscript*.

III.2. *The effects of climatic conditions on the prevalence and intensity of different parasites of European bird species*

In a collaborative study, we compared the abundance and prevalence of parasites and reproductive parameters of fourteen bird populations in two different periods separated by about ten years in the Western Palearctic. Overall, 9 different bird species and 62 different host-parasite interactions were studied. We found non-significant trends over the ten-year-period in terms of advanced laying date, reduced clutch and brood size, and decreased population sizes of the birds. Feather parasites and non-dipteran parasites tended to decrease in both prevalence and abundance, while prevalence of blood parasites showed a non-significant increase over time. Importantly, the magnitude and even the sign of the temporal changes in parasitism experienced by the different host species in different populations depended on latitude. These results suggest that climate change potentially affect the incidence of parasitic diseases, but with a variable intensity across a latitudinal gradient in Europe (Møller *et al.* *under review*).

III.3. *Malaria infection status of barn swallows (*Hirundo rustica*) in relation to morphological and physiological characters of the individuals during breeding*

We also aimed to investigate malaria parasites in relation to different physiological and morphological characters of the individuals in a barn swallow population. We collected reproductive effort and survival data and blood samples for physiological parameters from approximately 70 breeding pairs each year between 2015 and 2017. We predicted that ageing is affected by oxidative physiology, however the rate of senescence is modified by parasitism.

Unfortunately the parasite prevalence was very low in this bird species (only 14,8%) and the birds were infected with so many different lineages so that we were not able to analyse the effects of parasites even though we screened 492 samples in total.

IV. Avian malaria detection method development

IV.1. *Adapting a new magneto-optical detection method in avian malaria field studies: the first steps*

We have also started a collaboration with István Kézsmárki and his research group to adapt a magneto-optical method they developed to the diagnosis of human malaria also to the field diagnosis of avian malaria. We have simultaneously collected blood samples for the magneto-optical measurements and for PCR analyses of malaria parasites from collared flycatchers (*Ficedula albicollis*), blue tits (*Cyanistes caeruleus*) and great tits to validate the magneto-optical method also in birds. The samples collected for the magneto-optical measurements were transported into the Genome Metabolism and Biostruct Laboratory of Beáta G. Vértessy and the samples collected to PCR analyses into our laboratory at the Eötvös Loránd University.

We have finished the magneto-optical analyses and the molecular analyses of the samples collected from 2021 and 2022. The initial results were promising as the results of the PCR and the magneto-optical analyses showed a very good match. However, because of the different characteristics of the human and avian blood we had to optimize and test the method further. In 2022/2023 we tested an additional 101 blood samples. Unfortunately, there was a relatively high mismatch between the positive samples detected by PCR and by the magneto-optical method, so that we still cannot publish the results. To solve this problem, we are going to test further reagents and buffers for the optimization of the magneto-optical analyses.

Student training

Four BSc students of the Eötvös Loránd University have joined and worked in the research project: Dóra Szalai, Eszter Plankó, Milán Gábor Berki, Dorottya Sára Pásti. Dóra Szalai, Eszter Plankó and Milán Gábor Berki have already defended their thesis successfully. Milán Gábor Berki has been continuing his work as a MSc student. Eszter Plankó got a special award at the *Scientific Student Conference of Eötvös Loránd University* and a 3rd price at the *Scientific Student Video Conference of Eötvös Loránd University*.

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Publications

Published papers:

- Ágh, N. Pásztory-Kovács, Sz., Prohászka, V., Csörgő, T., Szöllősi, E. (2025) Different age, different blood parasites - *Acrocephalus* species and their Haemosporidian parasites during autumn migration in Central Europe. *International Journal for Parasitology: Parasites and Wildlife*. 27, 101085.
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Manuscripts prepared:

- Møller, A.P., Merino, S., Soler, J.J., Adriaensen, F. Cantarero, A., Eeva T., Figuerola, J., García-del Río, M., Garrido-Bautista, J., Ruiz-Rodríguez, M., Heylen, D., Marzal, A., Matthysen, E., Matyjasiak, P., Norte, A.C., Svobodova, M., Szöllősi, E., Török, J., Valera, F., Veiga J., Ziane, N. (under review) Temporal changes in intensity of bird parasite infections are dependent of latitude in the Western Palearctic. *PlosOne*

Published papers that utilized data obtained partly during the project:

- Szabó, G., Boross, N., Hegyi, G., Herényi, M., Jablonszky, M., Kötél, D., Krenhardt, K., Markó, G., Nagy, G., Rosivall, B., Szász, E., Szöllősi, E., Zsebők, S., Török J., Laczi, M. (in revision). Sex-dependent carry-over effects between physiological state and reproduction in a passerine species. *Ecology and Evolution*
- Laczi, M., Sarkadi, F., Herényi, M., Nagy, G., Hegyi, G., Jablonszky, M., Könczey, R., Krenhardt, K., Markó, G., Rosivall, B., Szász, E., Szöllősi, E., Tóth, L., Zsebők, S., Török, T. (2024) Responses in the breeding parameters of the collared flycatcher to the changing climate. *Science of the Total Environment*. 20:926:171945.
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Conference contributions:

- Ágh, N., Csörgő, T., Szöllősi, E. (2023) Haemosporidian parasites and European Robins: lineage specific correlations during autumn migration. Poster at the 14th European Ornithologists' Union Congress, Lund, Sweden
- Hegyi, G., Herényi, M., Laczi, M., Markó, G., Nagy, G., Rosivall, B., Szöllősi, E., Török, J. (2023) Long-term inverse fluctuations of sexual ornament size and population density. Poster at the 14th European Ornithologists' Union Congress, Lund, Sweden
- Ferraguti, M., Magallanes, S., Jiménez-Peñuela, J., Martínez-de la Puente, J., Garcia-Longoria, L., Figuerola, J., Muriel, J., Albayrak, T., Bensch, S., Bonneaud, C., Clarke, R.H., Cziráj, G.Á., Dimitrov, D., Espinoza, K., Ewen, J.G., Ishtiaq, F., Flores-Saavedra, W., Garamszegi L.Z., Hellgren, O., Horakova, D., Huyvaert, K.P., Jensen, H., Križanauskienė, A., Lima, M.R., Lujan-Vega, C., Magnussen, E., Martin, L.B., Matson, K.D., Møller, A.P., Munclinger, P., Palinauskas, V., Pap, P.L., Pérez-Tris, J., Renner, S.C., Ricklefs, R., Scebba, S., Sehgal, R.N.M., Soler, M., Szöllősi, E., Valkiūnas, G., Westerdahl, H., Zehindjiev, P., Marzal, A. (2023) Human and time-related impacts on avian malaria infections in native and introduced populations of house sparrows (*Passer domesticus*). Talk at the 14th European Ornithologists' Union Congress, Lund, Sweden
- Rosivall, B., Gyarmathy, H., Kopena, R., Sarkadi, F., Szöllősi, E., Szász, E., Török, J. (2023) Do males penalize unfaithful females in a population with high level of extra-pair paternity? Poster at the 14th European Ornithologists' Union Congress, Lund, Sweden
- Ágh, N., Csörgő, T., Szöllősi, E. (2022) Linkage-specific influence of Haemosporidian parasites on European Robin's autumn migration. Poster at the Congress of the European Society for Evolutionary Biology, Prague, Czech Republic
- Gyarmathy, H., Kopena, R., Szöllősi, E., Sarkadi, F., Szász, E., Török, J., Rosivall, B. (2022) Is brood sex ratio related to parental feeding rate? An experimental study on collared flycatchers. Poster at the Congress of the European Society for Evolutionary Biology, Prague, Czech Republic
- Plankó Eszter (2021) A madármalária vizsgálata hazánkban előforduló csípőszúnyogokban. ELTE Biológus Tudományos Diákköri Konferencia. Special prize
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