Charles University
Faculty of Science

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Bc. Klára Bystroňová

Spread of Haemosporidia by migratory birds and the influence of climate change

Šíření hemosporidií migratorními ptáky a vliv změny klimatu

Bachelor’s thesis

Supervisor: doc. Mgr. Milena Svobodová, Dr.

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Prohlášení:

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Abstract:

Parasites of the order Haemosporida, including *Plasmodium, Haemoproteus*, and *Leucocytozoon*, are widely distributed among avian populations, with migratory birds serving as key vectors for their dispersal. This thesis examines the role of bird migration in the transmission of these parasites and evaluates the potential effects of climate change on this process. The thesis provides an overview of haemosporidian life cycles, transmission mechanisms, and the ecological conditions necessary for their persistence. Special emphasis is placed on how migratory species introduce these parasites to new environments, where they may pose a threat to immunologically naïve avian populations. By analyzing direct and indirect evidence of transmission during migration, this research identifies key factors influencing the success of parasite dispersal, including vector availability, host susceptibility, and environmental conditions. Additionally, it investigates the ways in which climate change alters migration routes, timing, and vector distributions, potentially reshaping the dynamics of haemosporidian transmission. The findings aim to contribute to a broader understanding of the interplay between avian migration, parasite ecology, and global environmental changes.

Abstrakt:

Tato bakalářská práce se zabývá šířením parazitů z řádu Haemosporida (*Plasmodium*, *Haemoproteus* a *Leucocytozoon*) prostřednictvím migrace ptáků a vlivem klimatické změny na tento proces. Práce popisuje životní cyklus těchto parazitů, způsoby jejich přenosu a ekologické podmínky nezbytné pro jejich úspěšnou reprodukci. Zvláštní pozornost je věnována roli tažných ptáků jako potenciálních přenašečů těchto parazitů do nových oblastí, kde mohou ohrozit naivní ptačí populace. Práce analyzuje nejen přímé i nepřímé důkazy o přenosu během migrace, ale také faktory ovlivňující úspěšnost šíření, jako je dostupnost vektorů, přítomnost hostitelů či enviornmentální podmínky. V závěru se práce zaměřuje na to, jak klimatické změny modifikují migrační trasy, časování tahu a distribuci vektorů, čímž potenciálně ovlivňují dynamiku přenosu hemosporidií. Cílem je poskytnout komplexní přehled o vztahu mezi ptačí migrací, šířením parazitů a měnícím se klimatem.

1. Introduction

Haemosporidia is a group of protozoan parasites within the phylum Apicomplexa, order Haemospororida (Adl et al., 2019). These intracellular parasites have a complex life cycle requiring both vertebrate hosts and blood-feeding dipteran vectors. Birds, reptiles, and mammals can serve as hosts, but avian Haemosporidia—primarily from the genera *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*—have been extensively studied due to their impact on wild bird populations and their relevance in disease ecology (Valkiūnas, 2005). Seasonal bird migration can act as a key driver of parasite dispersal. The area of parasite distribution is linked to dispersal patterns of avian hosts as migratory birds can spread parasites along their migratory journeys (Musa et al., 2024). This can pose a significant ecological risk to naïve bird populations, as they have never come across such pathogens, it could even lead to their extinction as we know that in the past, newly introduced pathogens contributed to extinction of native birds (Atkinson & LaPointe, 2009). Knowledge of parasite distribution plays an important role in assessing infection risk, as in some cases birds have a higher risk of infection in areas with increased parasite diversity.

Climate change is influencing bird migration in multiple ways: routes, destinations and phenology birds travel (Horton et al., 2020; Visser et al., 2009). As a result, migrants might be flying across new areas and potentially introducing parasites to new locations. Global warming might facilitate the spread of parasites to new places and exposure of native populations to those parasites (Short et al., 2017). There is evidence for an increased risk of malaria in birds and *Plasmodium* spread to new locations due to climate change (Garamszegi, 2011; Loiseau et al., 2012). Sites of high prevalence and diversity are predicted to change due to global warming, which would have an impact on bird communities as those shifts would cause native populations to encounter new parasite lineages (Pérez-Rodríguez et al., 2014). The focus of this thesis will be on Haemosporidia, protists which include three genera of avian blood parasites: *Plasmodium*, *Leucocytozoon* and *Haemoproteus*. Haemosporidia are the best studied group of avian blood parasites and are also one of the most prevalent (de Angeli Dutra et al., 2021).

The thesis focuses on the possibilities of parasite transmission during avian migration. The main aims are to investigate the potential of migratory birds in introducing parasites into new regions, alongside an analysis of Haemosporidian transmission patterns and their influencing factors, linked to the role of climate change in shaping Haemosporidian dispersal. Those topics combined are crucial for predicting future parasite distribution and assessing the impact on naïve avian populations. Most importantly, I aim to evaluate whether significant Haemosporidian transmission occurs during migration, and if it leads to introduction into novel areas.

2. Haemosporidia

Haemosporidia are widespread, occurring in nearly all habitats except Antarctica (Quillfeldt et al., 2010). Their transmission dynamics depend on vector availability and presumably on climatic conditions, and bird migration, making them particularly relevant for ecological and epidemiological research (Atkinson et al., 2008; Ciloglu et al., 2020). While avian Haemosporidian infections are sometimes collectively referred to as 'avian malaria,' this term technically applies only to *Plasmodium* species.

2.1. Life Cycle and Transmission

Haemosporidian parasites exhibit a heteroxenous life cycle, alternating between two hosts. Birds serve as intermediate hosts, where asexual reproduction occurs, while the final hosts are blood-sucking Diptera, in which sexual reproduction and sporogony take place (Valkiūnas, 2005).

2.1.1. Development in the Avian Host

Transmission begins when an infected vector injects sporozoites into the bloodstream of a bird while feeding. These sporozoites invade tissues, typically targeting the liver, spleen, or other organs, where they multiply through exoerythrocytic merogony (also called schizogony), forming meronts (or schizonts). Merozoites emerge from these meronts via multiple asexual divisions and enter red blood cells, where they undergo further replication. This cycle of merogony may repeat multiple times. Unlike *Haemoproteus* and *Leucocytozoon*, *Plasmodium* undergoes two stages of merogony with the second one happening in red blood cell (Valkiūnas, 2005). Some merozoites differentiate into gametocytes, the sexual stages of the parasite, which circulate in the blood until ingested by a feeding vector. The severity of infection varies depending on parasite species, host immunity, and environmental factors (Atkinson et al., 2008).

2.1.2. Development in the Vector

Once a vector feeds on an infected bird, it ingests gametocytes, which undergo gametogenesis in its midgut. Gametogenesis is triggered by changes in oxygen and carbon dioxide concentrations upon transition from host to vector. Gametes fuse to form a zygote, which develops into a motile extracellular ookinete. The ookinete crosses the midgut wall and forms an oocyst, where sporozoites are produced by sporogony (Sullivan, 2007). These sporozoites eventually migrate to the salivary glands, from which they are transmitted to another bird during the vector's next blood meal, completing the cycle (Valkiūnas, 2005).

2.2 *Leucocytozoon*

Leucocytozoon species are widespread avian parasites (Garnham, 1966), primarily transmitted by blackflies (Simuliidae, genus *Simulium*), although some species may use biting midges (*Culicoides*) as vectors (Santiago-Alarcon et al., 2012).
The most known *Leucocytozoon* species affecting wild birds mainly include *L. simondi* and the *L. toddi* group, later divided into *L. mathisi, L. buteonis*, and *L. toddi* (Valkiūnas et al., 2010) and in passerines the common ones are *L. fringillinarum,* and *L. dubreuili* (Gutiérrez-Liberato et al.,2025). Transmission depends on temperature, rainfall, and humidity, with running water being crucial for vector development. Passerines host the highest number of *Leucocytozoon* species. Following infection, gametocytes circulate in the blood, eventually forming megalomeronts in organs such as the liver, brain, spleen, and lymph nodes, which rupture to release merozoites (Chagas et al., 2023). Pathogenicity varies, with some species causing severe disease in non-adapted hosts (Santiago-Alarcon et al., 2020). *Leucocytozoon* prevalence can reach 100% in certain duck and raptor species (Mahrt et al., 1991; Valkiūnas, 2005). Interestingly, unlike other Haemosporidia, *Leucocytozoon* prevalence increases at higher latitudes (Fecchio et al., 2023).

2.3 *Plasmodium*

Currently, according to the most recent global assessment of avian *Plasmodium* species there are 55 species recognized (Valkiūnas & Iezhova, 2018), with *P. relictum* being among the most prevalent and widespread (Valkiūnas et al., 2018).

Avian *Plasmodium* species are transmitted by mosquitoes (Culicidae), including genera such as *Culex, Coquillettidia, Aedes, Mansonia, Culiseta, Anopheles*, and *Psorophora* (Atkinson & LaPointe, 2009; Valkiūnas & Iezhova, 2018). While mammalian *Plasmodium* species are mainly transmitted by *Anopheles* (Garnham, 1966), notable avian vectors include *Culex quinquefasciatus, C. tarsalis,* and *C. stigmatosoma* (Atkinson & LaPointe, 2009; Loiseau et al., 2012). *Plasmodium* exhibits low host specificity regarding vectors, and certain lineages complete their life cycle in multiple mosquito species (LaPointe et al., 2012). The latest study from 2020 states that avian *Plasmodium* can develop in 40 mosquito species

(Gutiérrez-López et al., 2020) In experimental conditions, avian *Plasmodium* can develop in over 60 mosquito species (Gutiérrez-López et al., 2020).

The genus *Plasmodium* includes over 250 species, with several adapted specifically to avian hosts ("List of *Plasmodium* Species," 2024). The genus *Plasmodium* has a global distribution except for polar regions, but prevalence in vectors has not been sufficiently studied. Prevalence varies depending on temperature, season, and bird migratory behavior (Loiseau et al., 2012; Valkiūnas, 2005; Ciloglu et al., 2020).

2.4 *Haemoproteus*

The genus *Haemoproteus* belongs to the family *Haemoproteidae* and comprises two subgenera, *Parahaemoproteus* and *Haemoproteus* (Valkiūnas, 2005). The known host range includes 72 bird families with the highest occurrence in passerines, while in seabirds and shorebirds the abundance is significantly lower due to their limited exposure to the vectors. Certain *Haemoproteus* species are highly pathogenic, and infection in avian host can cause myositis (Atkinson, 2008).

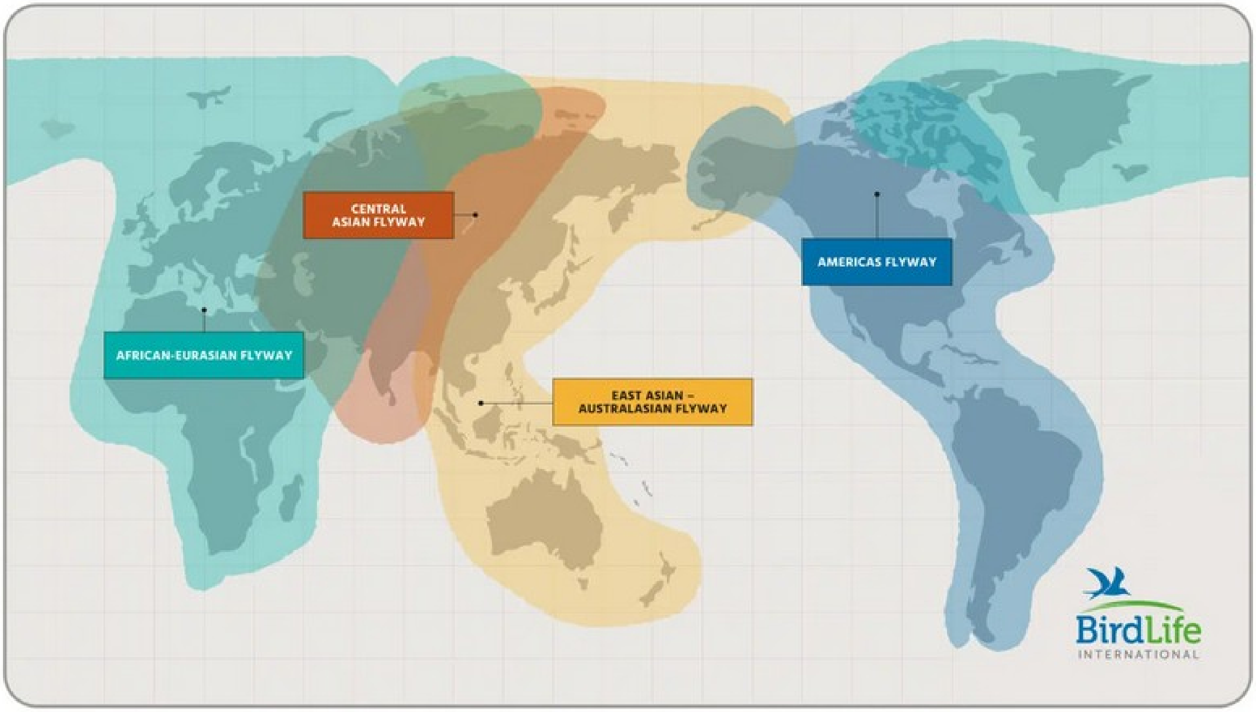
These parasites undergo merogony within tissues (Atkinson et al., 2008) and are often considered less pathogenic than *Plasmodium* species (Santiago-Alarcon & Marzal, 2020). Subegenus *Parahaemoproteus* species are transmitted by biting midges (Ceratopogonidae, genus *Culicoides*) and subgenus *Haemoproteus* is transmitted by louse flies (Hippoboscidae) (Santiago-Alarcon et al., 2012). Vector competence is influenced by climatic conditions, geographic region, and vector population size. In tropical and subtropical regions, transmission is possible year-round (Atkinson et al., 2008; Klei & DeGiusti, 1975).

Host specificity varies among *Haemoproteus* species, with some infecting a broad range of birds while others are highly specialized (Valkiūnas, 2005). In South Africa, *Haemoproteus* prevalence reaches 22% among sampled birds, significantly higher than that of *Plasmodium* which was 3 % (Doussang et al., 2019). This higher prevalence may be linked to efficient vector transmission and broader host compatibility (Fecchio et al., 2023). Molecular studies reveal extensive genetic variation within the genus (Doussang et al., 2019). Certain species, such as *H. columbae*, exhibit strict host specificity due to their dependence on particular vectors (LaPointe et al., 2012).

3. Bird migration

Migration as a form of adaptation is very common and comes in different forms; however, in my work I will focus only on seasonal long-distance migration as a life history trait. Bird migration is a regular seasonal movement and relocation from the breeding grounds, where birds raise their young, to wintering grounds, where they do not reproduce but survive the winter period (Bird migration, 2025). It is an evolutionary adaptation to changing conditions in both areas throughout the year. For migratory birds, it is more advantageous to travel vast distances than to remain in the same place all year round. During their journey, they are capable of flying hundreds of kilometers before stopping for a few days' rest. The main factors influencing bird migration include seasonal changes, which are associated with varying availability of resources that birds can utilize (Berthold, 2001).

3.1. Avian flyways



The global 4 flyways of migratory birds (Birdlife International, 2023)

Migratory flyways are paths of bird migration, primarily determined by geographical conditions between the breeding and wintering grounds. Migration routes are shared or similar among species living in the same regions. Species inhabiting the same area (e.g., Western Europe) tend to follow common or similar migration routes (Berthold, 2001). Birds of the Northern Hemisphere do have longer migration routes than those of the Southern Hemisphere (Gill, 2007).

<u>There are four global flyways for migratory birds (Birdlife International)</u>

- African-Eurasian flyway: contains of three major routes connecting Arctic to Southern Africa. It is used by more than 500 migratory bird species.
- Central Asian flyway: spreads from Siberia to the tropics in Indian ocean. It is used by more than 600 migratory birds.
- East Asian-Australasian flyway: spreads from Alaska through Southeast Asia to Australia and covers over 600 bird migrants.
- Americas flyway: is stretching from Arctic Circle in the North to Southern Argentina and is used by over 2000 bird species which makes it the most species rich flyway out of all four.

The main geographical features shaping the Afro-Eurasian migration route include the Sahara Desert and the Mediterranean Sea and as mentioned above it is divided into three main paths:

- Western route – passing through Western Europe via Spain and Gibraltar to West Africa.
- Central route – crossing Central Europe via Italy, Sicily, then Libya and the Sahara to Central Africa.
- Eastern route – through Eastern Europe, across the Balkans, Turkey, the Middle East, and along the Nile to East Africa

Flyways in America consist of three main routes:

- Pacific Flyway: This migration route extends from Alaska to Patagonia along the Pacific coast of the Americas. It is crucial for many North and South American bird species and features several important stopover sites along the way
- Central Flyway: Primarily used by birds migrating from Canada to the Gulf of Mexico, though some species follow this route all the way from Arctic regions to Patagonia.
- Mississippi Flyway: Extends from central Canada, through the Great Lakes, following the Mississippi and Missouri Rivers down to the Gulf of Mexico.

3.2. Stopover sites

Stopover sites are critical locations along migratory flyways where birds pause to rest, feed, and recover from the physical toll of migration. These sites are essential for the survival of migratory species, providing resources like food and water that are necessary for energy replenishment (Berthold, 2001). Typical stopover sites include islands, which provide crucial resting and feeding spots during sea crossings where no other resources are available. These sites are essential for the survival of migratory birds, and any disruption to them can significantly reduce migration success rates. Stopover sites play an important role in large bird gatherings and as places where huge concentration of birds from different places meet. Example of those in Europe: Curonian Spit, Gibraltar or Bosporus (Busse, 2001). Stopover sites also serve as a place for contact of migratory and residence birds where transmission of parasites might happen. Therefore, stopover sites serve as potential place of Haemosporidia spread through migratory birds onto naïve populations of resident birds or the other way around.

Important stopover sites and bottlenecks:

The Nearctic – Neotropical flyway:

- Gap between Sierra Madre Oriental and the Gulf of Mexico in Veracruz
- Cordillera de Talamanca and Caribbean Sea in Costa Rica
- Western Panama and the Isthmus of Panama
- Darién of Panama and Columbia

African – Eurasian flyway:

- Eilat, Israel
- Spanish coast
- Curonian Spit

3.3. Wintering sites

Wintering sites are areas where birds typically spend the winter period, when their breeding grounds have significantly reduced resource availability and harsh conditions (Ricklefs et al., 2017; Soares et al., 2020). These sites are in warmer climatic zones. Some European birds spend the winter in Mediterranean regions, while others cross the Mediterranean, traverse the

Sahara, and winter in Africa. Most European species use these locations, but some species fly east to India.

In the Americas, birds from northern regions migrate to areas in the Gulf of Mexico, Central America, South America, and as far as Patagonia (Garvin et al., 2006). Some birds from Alaska take migratory routes across the Pacific to Australia and New Zealand.

3.4. Partial migration

Partial migration is the most common form of migration where part of the bird population stays on breeding grounds while the other migrate to wintering grounds (Berthold, 2001). This form of migratory behaviour can be divided into obligatory and facultative, depending on if the ratio of migrants versus resident birds of one species is either constant (certain age or sex cohort ratio) or it’s changing according to environmental condition. An example of such facultative migrants could be the European Robin (Erithacus rubecula) (Newton, 2007). Numbers of resident individuals of partially migratory species are expected to increase due to climate warming (Berthold, 2001).

4. Transmission of Haemosporidia during bird migration

4.1. Indirect evidence of transmission

Transmission of Haemosporidia and the spread on to new locations is hard to prove on its own. The methodology of accessing is based on comparing Haemosporidian diversity and prevalence. Further it is important to distinguish if a certain lineage was newly introduced to the area and to differentiate between actual transmission places and places of occurrence. To do that it is compared if the lineage was found on that location in adults or juveniles and in migrants or residents. Finding the lineage in juveniles or residents is considered evidence that the lineage is transmitted on that location (Musa et al., 2024). A specific example of using such a methodology is demonstrated in the next paragraph. The potential of Haemosporidia spread by migratory birds to novel places is measured by the number of shared lineages between migratory and resident birds as those shared between the two groups have greater geographical range (de Angeli Dutra et al., 2021b). Identifying specific examples of Haemosporidian transmission to novel places is very complicated as the success of transmission depends on various factors and must be measured in multiple ways. The factors and requirements for successful transmission are addressed in the following chapter.

In a study focusing on Haemosporidia in four snipe species (*Gallinago spp.*) during their spring or fall migration in Japan, 18% of tested birds were infected with Haemosporidia but there were significant differences between the species which are presumably caused by ecological factors including different migratory routes. In total seven Haemosporidian lineages were detected and six of them were found in juveniles which means the infection was gained between breeding grounds and the sampling site at migration route as the snipes were caught and tested during their autumn migration and have not been to wintering grounds yet. The seventh lineage found in adult birds is transmitted only in the northernmost areas of Japan meaning it could have been transmitted on to the tested birds only in northernmost areas of Japan or continental areas from Russia to Mongolia and the testing location was only a site of occurrence, not transmission as there is no suitable vector present at the location (Inumaru et al., 2021).

The methodology outlined above was applied in study based on comparing the distribution of parasite lineages shared between migratory and resident birds with those found only in residents. The greater spread of lineages associated with migratory birds led the authors to hypothesize that migration may facilitate parasite transmission (de Angeli Dutra et al., 2021b). This suggests that migrants can carry and transmit Haemosporidian parasites across wider areas as those lineages which infect both migratory and resident birds are more widespread than those infecting just residents (de Angeli Dutra et al., 2021b).

4.2. Conditions and factors influencing transmission

Migratory birds might potentially transmit Haemosporidia to novel places, however the conditions on the new location must be suitable for the parasite to be able to establish and reproduce. The basic conditions for Haemosporidia to complete their life cycle are a suitable vector transmitting the disease and susceptible bird host. The presence of suitable hosts and vectors is largely influenced by parasite specificity as generalists are more likely to succeed at establishing themselves in novel host communities (Ishtiaq & Renner, 2020). For example, Galen et al. (2024) discovered that there is only a limited potential for transmission between migratory and resident birds on stopover sites as there is not a suitable vector overlap.

Year round transmission by migratory birds is conditioned by the presence of gametocytes in their blood (Soares et al., 2020) and the occurrence of suitable vectors which can feed on birds and transmit sporozoites to another avian host (Valkiunas, 2005). Therefore, transmission largely depends on suitable environmental conditions which allow the vectors to survive.

Another important requirement of successful transmission is timing as certain lineages are transmitted only seasonally, during breeding season, and therefore migrants most probably will not carry gametocytes during winter and are not infectious. Transmissions on wintering sites are only feasible for those lineages which do produce gametocyte during winter months (Hellgren et al., 2013; Soares et al., 2020). The possibility of Haemosporidian transmission during migration is limited by seasonal transmission strategies which can strongly influence the chances that Haemosporidian parasites are going to be transported to new places (Hellgren et al., 2013).

Prevalence and diversity of Haemosporidia is essential factor influencing successful transmission as some birds are at higher risk of infection in areas with increased parasite prevalence and diversity (Pulgarín-R et al., 2019). Age plays a role in Haemosporidian prevalence with approximately double prevalence in adult birds than in juveniles. The differences vary among Haemosporidian genera (Musa et al., 2024). Host specificity is another important factor as Haemosporidian lineages are more host specific in locally breeding species than in actively migrating species (Jones et al., 2024).

Haemosporidia which cause milder infection have higher chance of being transmitted for longer distances as they do not affect their hosts ability to fly long distances that much (Santiago-Alarcon & Marzal, 2020). Emmenegger et al. (2018) found that passerines infected with Haemosporidian parasites arrive later at their first main stopover site in the Mediterranean during spring migration, suggesting that infection causes migratory delays. The transmission probably happened before the onset of the migration as they were tested at their first main stopover site and therefore did not have many opportunities to get infected prior to that. This temporal separation—migratory allochrony—may reduce transmission by limiting contact between infected and uninfected birds at key stopover sites and therefore influence transmission dynamics.

4.3 Transmission sites

Transmission of most species of avian Haemosporidia most likely occurs on breeding grounds (Hellgren et al., 2007) but can possibly happen on wintering grounds (Dodge et al., 2013, Hasselquist 2007) and during migratory journey on stopover sites (Ciloglu et al., 2020). As many other migratory animals, migrating passerines represent a spillover source for naive bird populations if environmental conditions for successful parasite reproduction including susceptible vectors are met (Jones et al., 2024).

The potential role of migratory birds in Haemosporidian dispersal was investigated in a study conducted on breeding and migrating shorebirds between April and June — a period when some species breed at the sampling site while others use it only as a stopover during migration. The results indicated that Haemosporidian prevalence was lower in actively migrating birds compared to breeding individuals (Jones et al., 2024). Based on these findings, the authors hypothesized that migratory birds have only a limited potential to act as a source of parasite spillover relative to breeding birds.

Galen et al. (2024) support previous findings and state that stopover sites have limited potential for Haemosporidian transmission between migratory and resident birds, as both groups share a core set of parasite lineages. Although five lineages in the study were transmitted from migrants to residents in the USA, these were already widespread and unlikely to alter local communities. Still, the authors say, migratory birds may introduce these lineages to new regions which have not been tested.

Musa et al. (2024) identified in the Palearctic three transmission areas: breeding grounds in Europe, wintering grounds in Africa and for certain lineages in both breeding and wintering grounds. The study suggest that Europe is transmission area for *Haemoproteus* lineages (hRW2 and hSW3) a *Leucocytozoon* lineage (TUPHI13) with those lineages being specialist which are likely transmitted only during breeding season. *Plasmodium* (pCUCROC01) and *Leucocytozoon* (lANLAT10) lineages are based on the study findings only transmitted in Africa and were detected in adult migratory birds in Europe. *Plasmodium* (pSGS1 and pGRW11), *Haemoproteus* (hRW1) and *Leucocytozoon* (lSFC8) lineages are likely transmitted both in Europe and Africa and are generalists which is making it easier for them to spread (Musa et al., 2024).

5. Influence of climate change on migration

5.1. Changes in migratory routes

Due to climate change, many bird species are shortening their migratory journeys (Visser et al., 2009). Bird species are consequently visiting different wintering sites, exposing themselves to potentially new Haemosporidian lineages. In North America, short distance bird migrants i predominantly shifted winter ranges northward, while breeding range shifts were more variable (Curley et al., 2020). Importantly, the magnitude and direction of these seasonal shifts differed, leading to changes in migration distances for many species, with a general trend towards shorter migrations. The findings suggest that winter and breeding range shifts occur somewhat independently, likely influenced by different environmental pressures.

5.2. Changes in phenology

Climate change influences the phenology of bird migration as significant shifts in migration timing in the past 24 years have been recorded. Those shifts cause trophic mismatches between migrating birds and food resources availability (Horton et al., 2020). This mismatch could not only include food availability but vector and Haemosporidian season as well, possibly impacting the transmission dynamics.

Migratory birds are arriving earlier to their breeding grounds and are prolonging the period spent on breeding grounds. There is a relationship between migration distance and arrival dates, as birds with shorter routes arrive at breeding grounds with bigger date advancement (Koleček et al., 2020). Differences in timing of arrival might influence the spread of Haemosporidia.

6. The impact of climate change on Haemosporidia spread

6.1 The potential risks and importance of predictions

Global warming might cause the spread of parasites to new places and exposure of naive populations to those parasites (Short et al., 2017). Migration seems to lower the prevalence of *Haemoproteus* in Brazilian migratory birds in comparison with resident ones. The authors suggest that migrants have a lower chance of being exposed to local parasite communities and therefore have limited infection risk (Rodrigues et al., 2021). The prevalence of *Plasmodium* in the same study seems to be independent of migration; however, it is positively influenced by higher temperature (Rodrigues et al., 2021). Other study suggests for different genera there might be opposite patterns, as migrants are exposed on their migratory journey to higher diversity of *Leucocytozoon* infections than on both breeding and wintering grounds (Fecchio et al., 2023). Those findings are important for the future understanding of bird migration potential in Haemosporidian spread. *Haemoproteus* and *Leucocytozoon* lineages are expected to suffer from loss of areas with high diversity as their ranges are supposed to shift to the areas with higher elevation, and conversely, *Plasmodium* lineages are expected to undergo gain of high diversity spots which can be explained by expected changes in climate conditions (Pérez-Rodríguez et al., 2014).

In a study conducted by Musa et al. (2024) the scientists detected multiple haemosporidian lineages on location where they are not transmitted. An example is earlier mentioned Leucocytozoon (lANLAT10) which is transmitted in Africa; however, it was detected in adult migratory birds in Europe as well. The transmission doesn't occur in Europe probably because of lack of competent vectors (Musa et al., 2024). Changing climate might lead to more suitable conditions for specific vectors and then the parasite can be passed on from migratory birds.

Plasmodium relictum lineage SGS1 is highly invasive species of plasmodium found in resident birds in Europe as well as in the tropics (Aželytė et al., 2022). Recently it has been found in two resident bird species in North America and is most likely originating in Europe as genetic tests have proven (Theodosopoulos et al., 2021). Authors do hypothesize that the possible explanation of this range expansion is due to infection spillover from the captive birds in zoos. It is likely that further spread is possible to the North America was found in just two chickadee species it is likely to spread onto another bird species (Theodosopoulos et al., 2021).

Possible scenarios of transmission to naive populations are therefore dependent on many variables, and it is important to study the current situation in each of the Haemosporidian genera, together with monitoring specific examples and factors influencing it, to be able to predict future development of Haemosporidia spread and access the risks for prevention or management.

6.2 Mechanisms of influence of climate change on haemosporidia spread

Climate change alters host parasite relationships, creates new opportunities for disease spread and a more suitable environment for the development of vectors and can increase their range (Caminade et al., 2019). Temperature plays an essential role in Haemosporidian distribution as it influences parasite development and vector distribution (Chapa-Vargas et al., 2020). Rise of temperature has a direct impact on avian *Plasmodium* development as its incubation period speed rises with higher temperature and is conditioned by minimum temperature of the environment and the development stops if temperature drops below 13 °C (Lapointe et al., 2009). Global warming consequently leads to prolonging the reproductive window of those pathogens and there is a strong correlation between the increase of global temperatures and increase of *Plasmodium* prevalence over the years (Garamszegi, 2011). Rodrigues et al.

(2021) showed that rising environmental temperatures drive higher Plasmodium prevalence in birds, suggesting that warming climates intensify parasite transmission along migratory routes. Perrin et al. (2025) further revealed that migratory birds function as crucial connectors in global host–parasite networks, dispersing a rich diversity of haemosporidian parasites across major flyways and linking disparate biogeographic realms. However, Garamszegi (2011) also points out that environmental changes can have in some cases negative effect on Haemosporidian distribution as they lower their survival rate due to increased drought and therefore limit the potential of transmission. In general climate change is shifting vector borne parasites such as Haemosporidia further north in the northern hemisphere (Caminade et al., 2019). Together with the insights from Caminade et al. (2019), these studies underscore that climate change not only boosts vector capacity and parasite replication but also interacts with migratory behavior to reshape transmission patterns at both local and global scales.

6.3 Spread of haemosporidia under changing climatic conditions

Hawaii is one of the notorious examples of Haemosporidian distribution into new areas and its serious consequences on naive bird populations. In the case of Hawaii, the epidemic started due to the introduction of a vector which transmits avian malaria to the area (Benning et al., 2002; Derraik et al., 2008, Dulavová, 2023, van Riper.,1986).

The impact of climate change on the distribution of Haemosporidia has been tested on Plasmodium in Alaska. Resident birds including yearlings in the North American Arctic were tested positive for *Plasmodium*, which proves on-site transmission. This is the first time that avian *Plasmodium* transmission has been recorded in the North American Arctic with the most northern occurrence of 64°N. Those findings are important for future predictions of Haemosporidian transmission under the conditions of changing climate (Loiseau et al., 2012). Another evidence for spread above the polar circle are high prevalence levels (76%) of Haemosporidia found in passerine birds in northwestern Siberia which is higher than any results from other northern regions (Yusupova et al., 2023). However, there is no evidence of prevalence in previous periods from the same location.

7. Conclusion

This thesis explored the relationship between bird migration, the transmission of haemosporidian parasites, and the influence of climate change on these dynamics. Haemosporidia—particularly *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*—rely on complex life cycles involving both avian hosts and insect vectors, with successful transmission requiring a convergence of biological, ecological, and environmental conditions. Migratory birds, by traversing vast and ecologically diverse regions, play a pivotal role in connecting parasite populations across continents. However, the actual transmission of haemosporidia along migratory routes remains difficult to confirm directly, due to numerous interacting factors such as parasite diversity, vector availability, timing of reproduction, and ecological barriers. While some evidence suggests that migratory journeys increase exposure to parasites, other findings highlight the constraints that limit effective spread.

Climate change introduces an additional layer of complexity. By altering migration phenology, shifting routes, and modifying the distribution and development rates of vectors, it has the potential to reshape transmission dynamics. Warmer temperatures, for instance, may accelerate parasite replication within vectors, increasing infection rates in avian hosts. Yet, these effects are not uniform—some regions may become more suitable for transmission, while others may become less hospitable.

To conclude, climate change is a popular mainstream topic that many studies mention but there is no robust evidence on the combined influence of bird migration and climate change on haemosporidia spread and the impacts on naïve bird populations remain insufficient. Nevertheless, the potential ecological consequences, especially for naive or endangered bird populations, underscore the urgency for continued investigation. A more integrated and longitudinal research approach is needed to clarify these complex interactions and better predict how global change will shape host–parasite networks in the future.

References:

Adl, S. M., Bass, D., Lane, C. E., Lukeš, J., Schoch, C. L., Smirnov, A., Agatha, S., Berney, C., Brown, M. W., Burki, F., Cárdenas, P., Čepička, I., Chistyakova, L., del Campo, J., Dunthorn, M., Edvardsen, B., Eglit, Y., Guillou, L., Hampl, V., … Zhang, Q. (2019). Revisions to the classification, nomenclature, and diversity of eukaryotes. *Journal of Eukaryotic Microbiology, 66*(1), 4–119. https://doi.org/10.1111/jeu.12691

Atkinson, C. T. (2008). Avian malaria. In C. T. Atkinson, N. J. Thomas, & D. B. Hunter (Eds.), *Parasitic diseases of wild birds* (pp. 35–53). Wiley. https://doi.org/10.1002/9780813804620.ch3

Atkinson, C. T., & LaPointe, D. A. (2009). Introduced avian diseases, climate change, and the future of Hawaiian honeycreepers. *Journal of Avian Medicine and Surgery, 23*(1), 53–63.

Aželytė, J., Platonova, E., Bensch, S., Hellgren, O., & Palinauskas, V. (2022). A comparative analysis of the dynamics of *Plasmodium relictum* (GRW4) development in the blood during single and co-infections. *Acta Tropica, 226*, 106247. https://doi.org/10.1016/j.actatropica.2021.106247

Benning, T. L., LaPointe, D., Atkinson, C. T., & Vitousek, P. M. (2002). Interactions of climate change with biological invasions and land use in the Hawaiian Islands: Modeling the fate of endemic birds using a geographic information system. *Proceedings of the National Academy of Sciences, 99*(22), 14246–14249. https://doi.org/10.1073/pnas.162372399

Berthold, P. (2001). *Bird migration: A general survey*. Oxford University Press.

BirdLife International. (2024, October 11). Flyways. https://www.birdlife.org/europe-and-central-asia/our-work/flyways/

Busse, P. (2001). European passerine migration system – what is known and what is lacking. *Ring, 23*.

Caminade, C., McIntyre, K. M., & Jones, A. E. (2019). Impact of recent and future climate change on vector-borne diseases. *Annals of the New York Academy of Sciences, 1436*(1), 157–173. https://doi.org/10.1111/nyas.13950

Chapa-Vargas, L., Matta, N. E., & Merino, S. (2020). Effects of ecological gradients on tropical avian hemoparasites. In D. Santiago-Alarcon & A. Marzal (Eds.), *Avian malaria and related parasites in the tropics* (1st ed., pp. 349–377). Springer. https://doi.org/10.1007/978-3-030-40070-1_14

Ciloglu, A., Ergen, A. G., Inci, A., Dik, B., Duzlu, O., Onder, Z., Yetismis, G., Bensch, S., Valkiūnas, G., & Yildirim, A. (2020). Prevalence and genetic diversity of avian Haemosporidian parasites at an intersection point of bird migration routes: Sultan Marshes National Park, Turkey. *Acta Tropica, 210*, 105465. https://doi.org/10.1016/j.actatropica.2020.105465

Curley, S. R., Manne, L. L., & Veit, R. R. (2020). Differential winter and breeding range shifts: Implications for avian migration distances. *Diversity and Distributions, 26*(4), 415–425. https://doi.org/10.1111/ddi.13036

de Angeli Dutra, D., Fecchio, A., Martins Braga, É., & Poulin, R. (2021a). Migratory birds have higher prevalence and richness of avian Haemosporidian parasites than residents. *International Journal for Parasitology, 51*(10), 877–882. https://doi.org/10.1016/j.ijpara.2021.03.001

de Angeli Dutra, D., Filion, A., Fecchio, A., Braga, É. M., & Poulin, R. (2021b). Migrant birds disperse Haemosporidian parasites and affect their transmission in avian communities. *Oikos, 130*(6), 979–988. https://doi.org/10.1111/oik.08199

Derraik, J., Tompkins, D., Alley, M., Holder, P., & Atkinson, T. (2008). Epidemiology of an avian malaria outbreak in a native bird species (*Mohoua ochrocephala*) in New Zealand. *Journal of the Royal Society of New Zealand, 38*, 237–242. https://doi.org/10.1080/03014220809510558

Dodge, M., Guers, S. L., Sekercioğlu, Ç. H., & Sehgal, R. N. M. (2013). North American transmission of Haemosporidian parasites in the Swainson’s thrush (*Catharus ustulatus*), a migratory songbird. *Journal of Parasitology, 99*(3), 548–553. https://doi.org/10.1645/GE-3134.1

Dulavová, K. (2023). *Ptačí plasmodia a jejich vliv na hostitele* [Bakalářská práce, Univerzita Karlova, Přírodovědecká fakulta]. Digitální repozitář Univerzity Karlovy. https://dspace.cuni.cz/bitstream/handle/20.500.11956/181324/130357830.pdf

Doussang, D., González-Acuña, D., Torres-Fuentes, L. G., Lougheed, S. C., Clemente-Carvalho, R. B., Greene, K. C., & Vianna, J. A. (2019). Spatial distribution, prevalence and diversity of Haemosporidia in the rufous-collared sparrow, *Zonotrichia capensis*. *Parasites & Vectors, 12*(1), 2. https://doi.org/10.1186/s13071-018-3243-4

Emmenegger, T., Bauer, S., Hahn, S., Müller, S. B., Spina, F., & Jenni, L. (2018). Blood parasites prevalence of migrating passerines increases over the spring passage period. *Journal of Zoology, 306*(1), 23–27. https://doi.org/10.1111/jzo.12565

Fecchio, A., Bell, J. A., Williams, E. J., Dispoto, J. H., Weckstein, J. D., & Dutra, D. de A. (2023). Co-infection with *Leucocytozoon* and other Haemosporidian parasites increases with latitude and altitude in New World bird communities. *Microbial Ecology*. https://doi.org/10.1007/s00248-023-02283-x

Galen, S. C., Ostrow, E., Ray, S., Henry, M., Dispoto, J., Fetterman, A., Kiziuk, L., & Weckstein, J. D. (2024). Migratory birds have a distinct Haemosporidian community and are temporally decoupled from vector abundance at a stopover site. *Parasitology, 1*–10. https://doi.org/10.1017/S0031182024001239

Garnham, P. C. C. (1966). *Malaria parasites and other* Haemosporidia.

Garamszegi, L. Z. (2011). Climate change increases the risk of malaria in birds. *Global Change Biology, 17*(5), 1751–1759. https://doi.org/10.1111/j.1365-2486.2010.02346.x

Garvin, M. C., Szell, C. C., & Moore, F. R. (2006). Blood parasites of Nearctic–Neotropical migrant passerine birds during spring trans-Gulf migration: Impact on host body condition. *Journal of Parasitology, 92*(5), 990–996. https://doi.org/10.1645/GE-758R.1

Gill, F. B. (2007). *Ornithology*. W. H. Freeman.

Gutiérrez-Liberato, G. A., Duc, M., Eigirdas, V., & Chagas, C. R. F. (n.d.). Leucocytozoon infections in tits (Aves, Paridae): Blood and tissue stages investigated using an integrative approach. *Parasite*, *32*, 13. https://doi.org/10.1051/parasite/2025007

Gutiérrez-López, R., Bourret, V., & Loiseau, C. (2020). Is Host Selection by Mosquitoes Driving Vector Specificity of Parasites? A Review on the Avian Malaria Model. *Frontiers in Ecology and Evolution*, *8*. https://doi.org/10.3389/fevo.2020.569230

Hasselquist, D., Östman, Ö., Waldenström, J., & Bensch, S. (2007). Temporal patterns of occurrence and transmission of the blood parasite *Haemoproteus payevskyi* in the great reed warbler *Acrocephalus arundinaceus*. *Journal of Ornithology, 148*(4), 401–409. https://doi.org/10.1007/s10336-007-0144-2

Hellgren, O., Waldenström, J., Peréz-Tris, J., Szöll, E., Si, Ö., Hasselquist, D., Krizanauskiene, A., Ottosson, U., & Bensch, S. (2007). Detecting shifts of transmission areas in avian blood parasites—A phylogenetic approach. *Molecular Ecology, 16*(6), 1281–1290. https://doi.org/10.1111/j.1365-294X.2007.03227.x

Hellgren, O., Wood, M. J., Waldenström, J., Hasselquist, D., Ottosson, U., Stervander, M., & Bensch, S. (2013). Circannual variation in blood parasitism in a sub-Saharan migrant passerine bird, the garden warbler. *Journal of Evolutionary Biology, 26*(5), 1047–1059. https://doi.org/10.1111/jeb.12129

Horton, K. G., La Sorte, F. A., Sheldon, D., Lin, T.-Y., Winner, K., Bernstein, G., Maji, S., Hochachka, W. M., & Farnsworth, A. (2020). Phenology of nocturnal avian migration has shifted at the continental scale. *Nature Climate Change, 10*(1), 63–68. https://doi.org/10.1038/s41558-019-0648-9

Inumaru, M., Odaya, Y., Sato, Y., & Marzal, A. (2021). First records of prevalence and diversity of avian Haemosporidia in snipe species (genus *Gallinago*) of Japan. *International Journal for Parasitology: Parasites and Wildlife, 16*, 5–17. https://doi.org/10.1016/j.ijppaw.2021.07.007

Ishtiaq, F., & Renner, S. C. (2020). Bird migration and vector-borne parasite transmission. In D. Santiago-Alarcon & A. Marzal (Eds.), *Avian malaria and related parasites in the tropics: Ecology, evolution and systematics* (pp. 513–526). Springer. https://doi.org/10.1007/978-3-030-51633-8_16

Jones, W., Tóth, Z., Khursanov, V., Kisliakova, N., Krüger, O., Székely, T., Karlionova, N., Pinchuk, P., & Chakarov, N. (2024). Haemosporidian infections are more common in breeding shorebirds than in migrating shorebirds. *Ibis, 166*(4), 1354–1367. https://doi.org/10.1111/ibi.13318

Klei, T. R., & DeGiusti, D. L. (1975). Seasonal occurrence of *Haemoproteus columbae* Kruse and its vector *Pseudolynchia canariensis* Bequaert. *Journal of Wildlife Diseases, 11*(1), 130–135. https://doi.org/10.7589/0090-3558-11.1.130

Koleček, J., Adamík, P., & Reif, J. (2020). Shifts in migration phenology under climate change: Temperature vs. abundance effects in birds. *Climatic Change, 159*(2), 177–194. https://doi.org/10.1007/s10584-020-02668-8

LaPointe, D. A., Atkinson, C. T., & Samuel, M. D. (2012). Ecology and conservation biology of avian malaria. *Annals of the New York Academy of Sciences, 1249*(1), 211–226. https://doi.org/10.1111/j.1749-6632.2011.06431.x

Lapointe, D., Goff, M., & Atkinson, C. (2009). Thermal Constraints to the Sporogonic Development and Altitudinal Distribution of Avian Malaria Plasmodium relictum in Hawai'i. *The Journal of Parasitology*, *96*, 318–324. https://doi.org/10.1645/GE-2290.1

List of *Plasmodium* species. (2024). In *Wikipedia*. https://en.wikipedia.org/w/index.php?title=List_of_*Plasmodium*_species&oldid=1259172008

Loiseau, C., Harrigan, R. J., Cornel, A. J., Guers, S. L., Dodge, M., Marzec, T., Carlson, J. S., Seppi, B., & Sehgal, R. N. M. (2012). First evidence and predictions of *Plasmodium* transmission in Alaskan bird populations. *PLOS ONE, 7*(9), e44729. https://doi.org/10.1371/journal.pone.0044729

Mahrt, J. L., Zwickel, F. C., & Tessier, T. G. (1991). Blood parasites of blue grouse (*Dendragapus obscurus*) in western North America. *Journal of Wildlife Diseases, 27*(3), 482–485. https://doi.org/10.7589/0090-3558-27.3.482

Musa, S., Altenburger, C., Vázquez, R. M., Woog, F., & Mackenstedt, U. (2024). Parasite airlines: Mapping the distribution and transmission of avian blood parasites in migratory birds. *International Journal for Parasitology, 54*(12), 635–648. https://doi.org/10.1016/j.ijpara.2024.06.004

New £3 million partnership will help bolster the protection of the African-Eurasian Flyway. (2023, June 2). BirdLife International. https://www.birdlife.org/news/2023/06/02/new-3-million-partnership-will-help-bolster-the-protection-of-the-african-eurasian-flyway/

Newton, I. (2007). *The migration ecology of birds* (1st ed.). Academic Press.

Patz, J. A., Graczyk, T. K., Geller, N., & Vittor, A. Y. (2000). Effects of environmental change on emerging parasitic diseases. *International Journal for Parasitology, 30*(12), 1395–1405. https://doi.org/10.1016/S0020-7519(00)00141-7

Perrin, A., Glaizot, O., & Christe, P. (n.d.). Migratory birds spread their Haemosporidian parasites along the world's major migratory flyways. *Oikos, e11012*. https://doi.org/10.1111/oik.11012

Pérez-Rodríguez, A., de la Hera, I., Fernández-González, S., & Pérez-Tris, J. (2014). Global warming will reshuffle the areas of high prevalence and richness of three genera of avian blood parasites. *Global Change Biology, 20*(8), 2406–2416. https://doi.org/10.1111/gcb.12542

Pulgarín-R, P. C., Gómez, C., Bayly, N. J., Bensch, S., FitzGerald, A. M., Starkloff, N., Kirchman, J. J., González-Prieto, A. M., Hobson, K. A., Ungvari-Martin, J., Skeen, H., Quillfeldt, P., Martinez, J., Hennicke, J., Ludynia, K., Gladbach, A., Masello, J., Riou, S., & Merino, S. (2010). Hemosporidian blood parasites in seabirds—A comparative genetic study of species from Antarctic to tropical habitats. *Die Naturwissenschaften, 97*, 809–817. https://doi.org/10.1007/s00114-010-0698-3

Ricklefs, R. E., Medeiros, M., Ellis, V. A., Svensson-Coelho, M., Blake, J. G., Loiselle, B. A., Soares, L., Fecchio, A., Outlaw, D., Marra, P. P., Latta, S. C., Valkiūnas, G., Hellgren, O., & Bensch, S. (2017). Avian migration and the distribution of malaria parasites in New World passerine birds. *Journal of Biogeography, 44*(5), 1113–1123. https://doi.org/10.1111/jbi.12928

Rodrigues, R. A., Felix, G. M. F., Pichorim, M., Moreira, P. A., & Braga, E. M. (2021). Host migration and environmental temperature influence avian Haemosporidia prevalence: A molecular survey in a Brazilian Atlantic rainforest. *PeerJ, 9*, e11555. https://doi.org/10.7717/peerj.11555

Santiago-Alarcon, D., & Marzal, A. (Eds.). (2020). *Avian malaria and related parasites in the tropics: Ecology, evolution and systematics*. Springer. https://doi.org/10.1007/978-3-030-51633-8

Santiago-Alarcon, D., Palinauskas, V., & Schaefer, H. M. (2012). Diptera vectors of avian Haemosporidian parasites: Untangling parasite life cycles and their taxonomy. *Biological Reviews, 87*(4), 928–964. https://doi.org/10.1111/j.1469-185X.2012.00234.x

Short, E. E., Caminade, C., & Thomas, B. N. (2017). Climate change contribution to the emergence or re-emergence of parasitic diseases. *Infectious Diseases, 10*, 1178633617732296. https://doi.org/10.1177/1178633617732296

Soares, L., Young, E. I., & Ricklefs, R. E. (2020). Haemosporidian parasites of resident and wintering migratory birds in The Bahamas. *Parasitology Research, 119*(5), 1563–1572. https://doi.org/10.1007/s00436-020-06646-y

Sullivan, J. T. (2007). *A color atlas of parasitology.* (6th ed.). University of San Francisco

Theodosopoulos, A. N., Grabenstein, K. C., Bensch, S., & Taylor, S. A. (2021). A highly invasive malaria parasite has expanded its range to non-migratory birds in North America. *Biology Letters, 17*(9), 20210271. https://doi.org/10.1098/rsbl.2021.0271

Valkiunas, G. (2005). *Avian malaria parasites and other* Haemosporidia. CRC Press. https://doi.org/10.1201/9780203643792

Valkiūnas, G., & Iezhova, T. A. (2018). Keys to the avian malaria parasites. *Malaria Journal, 17*(1), 212. https://doi.org/10.1186/s12936-018-2359-5

Valkiūnas, G., Ilgūnas, M., Bukauskaitė, D., Fragner, K., Weissenböck, H., Atkinson, C. T., & Iezhova, T. A. (2018). Characterization of *Plasmodium relictum*, a cosmopolitan agent of avian malaria. *Malaria Journal, 17*(1), 184. https://doi.org/10.1186/s12936-018-2325-2

Valkiūnas, G., Sehgal, R. N. M., Iezhova, T. A., & Hull, A. C. (2010). Identification of *Leucocytozoon toddi* group (Haemosporida: Leucocytozoidae), with remarks on the species taxonomy of leucocytozoids. *The Journal of Parasitology, 96*(1), 170–177. https://doi.org/10.1645/GE-2109.1

van Riper, C., van Riper, S. G., Goff, M. L., & Laird, M. (1986). The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecological Monographs, 56*(4), 327–344. https://doi.org/10.2307/1942550

Visser, M. E., Perdeck, A. C., Van Balen, J. H., & Both, C. (2009). Climate change leads to decreasing bird migration distances. *Global Change Biology, 15*(8), 1859–1865. https://doi.org/10.1111/j.1365-2486.2009.01865.x

Wikipedia contributors. (2025, April 17). Bird migration. In *Wikipedia, The Free Encyclopedia*. https://en.wikipedia.org/wiki/Bird_migration

Yusupova, D. A., Schumm, Y. R., Sokolov, A. A., & Quillfeldt, P. (2023). Haemosporidian blood parasites of passerine birds in north-western Siberia. *Polar Biology, 46*(6), 497–511. https://doi.org/10.1007/s00300-023-03130-y