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Prevalence of Avian Haemosporidian Parasites: A Comparative Study between Resident and Migratory Birds of Iraq

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Abstract

Haemosporidians are a diverse group of vector-borne parasitic protozoa that have a global distribution and some of them live in the avian body as a benign parasite, with no symptoms. Avian Haemosporidians, include three main genera, *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*. These blood parasites are transmitted across different regions through migratory birds. We studied the prevalence of avian haemosporidian parasites in both resident and migratory birds in the central and southern regions of Iraq. Our study represents pioneering research on Haemosporidian parasites in a wide range of avian species, including 248 samples from 47 species of both resident and migratory birds, collected from five cities in central and southern Iraq. We identified and determined the prevalence of three distinct haemosporidian genera, *Haemoproteus* spp., *Leucocytozoon* spp., and *Plasmodium* spp. Overall parasite infection was higher in resident hosts than in migrants. The prevalence of *Plasmodium* spp. was found to be highest among resident birds, with a rate of 20.1%, while the highest rate of *Leucocytozoon* spp. was observed in migratory birds, with a rate of 8.2%. Our study holds promising opportunities for understanding the impact of migratory and resident hosts on the dynamics of infectious diseases in wildlife.

Key words: Haemosporidian, Haemoproteus spp., Plasmodium spp., Leucocytozoon spp., Resident birds, Migratory birds, microscopic examination.

INTRODUCTION

Birds exhibit the highest diversity of haemosporidian parasites, with more than 250 species classified into three genera: *Plasmodium* spp., *Haemoproteus* spp., and *Leucocytozoon* spp. (Harl et al., 2020). These parasites are commonly transmitted by dipterans and are commonly referred to as "avian malaria" parasites due to their ability to cause malaria-like symptoms in infected birds. Haemosporidian infections are widespread among bird populations globally, affecting a significant number of bird species each year (Clark et al., 2014).

Numerous studies have demonstrated that haemosporidian infections can impose different costs on life-history traits, including impaired body condition (Valkiūnas et al., 2006), reduced reproductive success (Marzal et al., 2005; Knowles et al., 2010), and decreased survival rates (Sol et al., 2003; Bunbury et al., 2007; Lachish et al., 2011). The consequences and symptoms of infection may vary



depending on factors such as the avian species, the age and immunity of the bird, and the parasite species and lineage, ranging from asymptomatic to severe and potentially fatal disease. Severe outbreaks of infection can lead to significant declines in wild bird populations and, in some cases, even the extinction of bird species (Meister et al., 2021). The roles of migratory and resident hosts in infectious disease dynamics have been hypothesized to be distinct, but the contribution of these hosts to wildlife infectious disease has largely remained unstudied.



FIGURE 1. The study area.

The geological diversity of Iraq plays a crucial role in supporting its rich biodiversity, with bird diversity being a prime example. Furthermore, Iraq's privileged location between the hemispheres makes it a vital stopover site for waterbird migration between Eurasia and Africa (Boere & Stroud, 2006). The diversity of habitats and landscapes represents an added value in harboring large numbers of migratory birds during each migration season, in addition to resident breeding bird species (Salim et al., 2006). The marshes located in central and southern Iraq are considered wintering and resting areas for migratory water birds and other migratory birds, and are well-known for their biodiversity. These marshes also serve as a permanent habitat for millions of birds and as a flight path for millions of other birds migrating between Siberia and Africa, and numerous bird species depend on these wetlands for feeding, resting, and nesting purposes (Salim & Porter, 2009). According to recent studies, a total of 395 bird species, including 130 resident species and 265 migratory species have been recorded (Salim & Porter (2009); Salim et al., 2010).

Despite the high diversity of habitats, a limited number of studies have been conducted on the prevalence of bird infection in Iraq (Shamsuddin & Mohammad 1980; Mohammad, 1990; Al-Hiyali et al., 1998). Interestingly, no studies have focused specifically on the role of resident and migratory hosts in the

dynamics of infection. Furthermore, in most of these studies, no distinction was made between resident and migratory host birds. However, many bird species are composed of resident and migratory individuals, known as partial migrants (Lack, 1943). These Individuals that belong to the same species but use distinct migratory strategies, may differ in morphology and behavior (e.g. body size, dominance; Chapman et al., 2011). As a result, it leads to potential differences in their contribution to local and global blood infection dynamics. The few existing studies conducted on individual species or groups of different species in Iraq (e.g. Shamsuddin & Mohammad, 1980; Mohammad, 1990, 2002; Al-Hiyali et al., 1998), have reported a low rate of blood parasite infection, less than 10%. However, domestic birds such as pigeons or doves, which are considered resident birds, have shown a higher infection rate with *Haemoproteus* spp. (Wahhab et al., 2017).

Previous studies conducted in other regions have investigated the roles of migratory and resident hosts in the dynamics of blood parasite infections, revealing differences in the prevalence of these infections between migratory and resident populations (Waldenstro et al., 2002; Altizer, 2011; Altizer, 2011). Migratory birds are often considered potential introducers of blood parasites from their breeding areas to their wintering grounds, while resident birds may serve as reservoirs, facilitating the year-round circulation of these infections (Altizer, 2011). However, the specific roles of migratory and resident hosts and their contributions to local and global blood infection dynamics have not been extensively studied.

Therefore, the objective of this study is to assess the prevalence, infection rate, and distribution of blood parasites among birds in Iraq, with a particular focus on the central and southern regions. Additionally, we aim to investigate the contributions of migratory and resident hosts to the local dynamics of blood parasite infections.

MATERIAL AND METHODS

Sampling

This study was performed in the Sedimentary Plain Area of southern and central Iraq (Figure 1) which is characterized by great geodiversity, as it contains semi-desert lands, and vast areas of agricultural land, in addition to the existence of marshes that made it a suitable environment for most of the resident and migratory birds. After determining the appropriate localities in Najaf, Karbala, Qadisiyah, Babel, and Basra, (Table 1), the necessary permits for sampling were obtained from the relevant organizations. All birds were caught with mist nets from January to December 2021.

The blood sample was taken from the brachial vein using an insulin syringe and capillary tube based on bioethical methods, and the bird was returned to the natural environment unharmed. From each bird, 1 or 2 blood films were prepared on microscope glass slides. The residential status of the bird species was determined according to BirdLife International (2023), and Salim et al., (2010).

Study area	Longitude	Latitude	Total	Resident	Migratory	Time	
				birds	birds		
Najaf	44° 19' 48"	32° 00' 00"	60	45	15	FebruaryJanuary	
Karbala	44°01'30"	32° 36' 50"	43	41	2	May -April	
Qadisiyah	45° 04' 59.99"	31° 55' 0.01"	69	28	41	October -September	
Babel	44°37'0.01"	32° 31' 59.99"	32	23	9	August -July -June	
Basra	47° 48' 59"	30° 30' 03"	44	39	5	December November -March	

TABLE 1. Longitude, latitude, and number of migratory and resident captured species in each study area.

Preparation and examination of blood smears

The blood films were air-dried and fixed in absolute methanol for 1 minute in the field. In the laboratory, blood smears were stained in a 10% working solution of a stock solution of Giemsa's stain, pH 7.0–7.2, for 20-25 minutes, as described by Valkiūnas, Iezhova et al. (2008). A light microscope equipped with a

digital camera was used to examine blood films and prepare illustrations. Finally, about 100 fields were studied at high magnification (1000 x). Morphological identification of parasite species in blood smears was performed according to the method presented by Valkiūnas (2005).

Statistical Analysis

A blood sample was categorized as 'positive' if at least one endoparasite species was found. Prevalence was calculated as the number of individuals infected out of the total sample size, along with the corresponding 95% confidence intervals (95% CI). The normality of the data was tested using one-sample Kolmogorov-Smirnov test. Differences between types of endoparasites were compared using the chi-square test. P values <0.050 were considered significant. Differences between resident and migratory bird groups were compared using an ANOVA test.

RESULTS

In this study, we examined the prevalence of haemosporidian infections in 248 birds belonging to 47 species, 27 families, and 14 orders. Among the sampled birds, 23 species were migratory, while the remaining 24 species were resident birds. We found that Passeriformes species had the highest rate of haemosporidian infections, accounting for 23.3 % of all infections observed. Other orders, such as Anseriformes (18%), Charadriiformes (9%), Coraciiformes (6.5%), Gruiformes (5%), Pelecaniformes (3.3%), and Columbiformes (2%), exhibited lower infection rates compared to Passeriformes. The remaining orders showed even lower infection rates, accounting for less than 1% of the total analyzed samples. Specifically, Galliformes and Phoenicopteriformes had an infection rate of 1.25%, Pterocliformes, and Carimulgiformes had an infection rate of 0.8%, and orders Bucerotiformes, Accipitriformes, and Suliformes had an infection rate of 0.4% (Figure 2).

Microscopic examination

We prepared a total of 294 thin blood smears from 248 birds from south and central Iraq to detect avian blood parasites from three genera *Haemoproteus* spp, *Plasmodium* spp. and *Leucocytozoon spp*. Our finding revealed the presence of haemosporidian parasites which were only identified by microscopy in

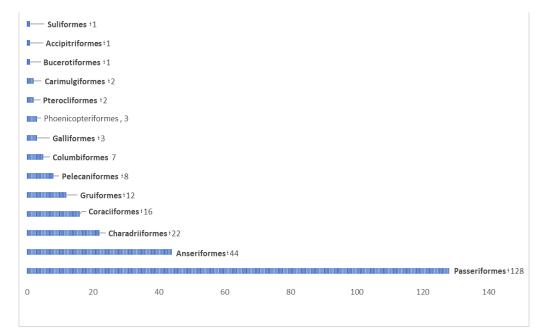


FIGURE 2. The number of birds examined in each order to determine the prevalence of haemosporidian infections.

TABLE 2. The prevalence of blood parasites in wild passerine birds was shown separately for each geneus: H: *Haemoproteus* spp., L: *Leucocytozoon* spp., and P: *Plasmodium* spp.

Order-Family	Genus	State	Positive/	Blood	Prevalence (%)			
Of det - raining	Genus		examined	parasite infection	н	Р	L	(H+L) OR (P+L)
Passeriformes- Alaudidae	Calandrella brachydactyla	Migratory	7/14	0.50	14.2	21.4	7.1	(H+L) 7.1
Passeriformes- Alaudidae	Emberiza calandra	Migratory	0/3	0.0	0.0	0.0	0.0	0.0
Passeriformes- Alaudidae	Eremophila alpestris	Migratory	0/6	0.0	0.0	0.0	0.0	0.0
Passeriformes- Alaudidae	Galerida cristata	Resident	12/21	57.1	4.7	52.3	0.0	0.0
Passeriformes- Cisticolidae	Prinia gracilis	Resident	0/1	0.0	0.0	0.0	0.0	0.0
Passeriformes- Corvidae	Corvus corone	Resident	0/1	0.0	0.0	0.0	0.0	0.0
Passeriformes- Corvidae	Pica pica	Resident	0/6	0.0	0.0	0.0	0.0	0.0
Passeriformes- Fringillidae	Carduelis carduelis	Resident	0/2	0.0	0.0	0.0	0.0	0.0
Passeriformes- Motacillidae	Motacilla alba	Migratory	1/6	16.6	0.0	16.6	0.0	0.0
Passeriformes- Muscicapidae	Erithacus rubicola	Migratory	1/10	10	0.0	10	0.0	0.0
Passeriformes- Muscicapidae	Oenanthe isabellina	Migratory	1/3	33.3	0.0	33.3	0.0	0.0
Passeriformes- Passeridae	Passer domesticus	Resident	15/23	78.2	60.8	8.6	0.0	(P+L) 4.3
Passeriformes- Phylloscopidae	Phylloscopus collybita	Migratory	0/1	0.0	0.0	0.0	0.0	0.0
Passeriformes- Prunellidae	Prunella modularis	Migratory	1/6	16.6	0.0	16.6	0.0	0.0
Passeriformes- Pycnonotidae	Argya altirstris	Resident	3/12	25	16.6	0.0	0.0	(P+L) 16.6
Passeriformes- Pycnonotidae	Pycnonotus leucotis	Resident	1/6	16.6	0.0	0.0	16.6	0.0
Passeriformes- Sturnidae	Acridotheres tristis	Resident	0/1	0.0	0.0	0.0	0.0	0.0
Passeriformes-Sturnidae	Sturnus vulgaris	Migratory	1/5	20.0	0.0	0.0	20.0	0.0
Anseriformes- Anatidae	Anas acuta	Migratory	0/3	0.0	0.0	0.0	0.0	0.0
Anseriformes- Anatidae	Anas clypeata	Migratory	2/6	33.3	0.0	16.6	16.6	(P+L) 16.6
Anseriformes- Anatidae	Anas crecca	Migratory	0/3	0.0	0.0	0.0	0.0	0.0
Anseriformes- Anatidae	Anas platyrhynchos	Migratory	0/5 0/9	0.0 0.0	0.0	0.0 0.0	0.0	0.0 0.0
Anseriformes- Anatidae Anseriformes- Anatidae	A. p. domesticus	Resident		28.5	0.0	14.2	0.0 14.2	0.0
	Aythya ferina	Migratory	2/7 0/1	28.5 0.0	$\begin{array}{c} 0.0 \\ 0.0 \end{array}$	14.2 0.0	14.2 0.0	0.0
Anseriformes- Anatidae Anseriformes- Anatidae	Netta rufina Tadorna ferruginea	Migratory	0/1 0/5	0.0	0.0	0.0	0.0	0.0
Anseriformes- Anatidae	Tadorna jerruginea Tadorna tadorna	Migratory Migratory	0/5	0.0	0.0	0.0	0.0	0.0
Charadriiformes- Charadriidae	Vanellus indic	Migratory Resident	0/3 1/6	0.0 16.6	0.0	16.6	0.0	0.0
Charadriiformes- Charadriidae	Vanellus leucurus	Resident	0/8	0.0	0.0	0.0	0.0	0.0
Charadriiformes- Recurvirostridae	Himantopus himantopus	Resident	0/8	0.0	0.0	0.0	0.0	0.0
Coraciiformes- Alcedinidae	Alcedo atthis	Resident	1/2	50	0.0	50	0.0	0.0
Coraciiformes- Alcedinidae	Ceryle rudis	Resident	2/3	66.6	0.0	33.3	0.0	(P+L)33.3
Coraciiformes- Alcedinidae	Halcyon smyrnensis	Resident	0/1	0.0	0.0	0.0	0.0	0.0
Coraciiformes- Coraciidae	Coracias benghalensis	Resident	1/3	33.3	0.0	0.0	33.3	0.0
Coraciiformes-Meropidae	Merops persicus	Resident	0/6	0.0	0.0	0.0	0.0	0.0
Gruiformes- Rallidae	Fulica atra	Migratory	0/5	0.0	0.0	0.0	0.0	0.0
Gruiformes- Rallidae	Gallinula chloropus	Resident	1/7	14.2	0.0	0.0	0.0	(p+L)14.2
Pelecaniformes- Ardeidae	Ardea alba	Migratory	0/8	0.0	0.0	0.0	0.0	0.0
Columbiformes- Columbidae	Streptopelia turtur	Resident	0/5	0.0	0.0	0.0	0.0	0.0
Columbiformes- Columbidae	Streptopelia risoria	Resident	0/2	0.0	0.0	0.0	0.0	0.0
Galliformes- Phasianidae	Francolinus francolinus	Resident	1/3	33.3	0.0	33.3	0.0	0.0
Phoenicopteriformes- Phoenicopteridae	Phoenicopterus roseus	Migratory	0/3	0.0	0.0	0.0	0.0	0.0
Pterocliformes- Pteroclidae	Pterocles exustus	Resident	1/2	50	50	0.0	0.0	0.0
Carimulgiformes- Caprimulgidae	Caprimulgus aegyptius	Migratory	2/2	100	50	50	0.0	0.0
Bucerotiformes- Upupidae	Upupa epops	Resident	0/1	0.0	0.0	0.0	0.0	0.0
Accipitriformes- Accipitridae	Hieraaetus pennatus	Migratory	0/1	0.0	0.0	0.0	0.0	0.0
Suliformes- Phalacrocoracidae	Phalacrocorax nigrogulari	Migratory	0/1	0.0	0.0	0.0	0.0	0.0
Fotal			58/248	23.3%	7.2%	12.9%	3.2%	4%

			Prevalence (%)			
	Positive / examined	Blood parasites infection				
			Η	Р	L	
Resident birds	40/139	28.7%	14.2%	20.1%	2.4%	
Migratory birds	18/109	16.5%	2.1%	6.2%	8.2%	

TABLE 3. The number of migratory and resident birds, along with the corresponding percentage of infection by blood parasites (H: *Haemoproteus* spp., L: *Leucocytozoon* spp., P: *Plasmodium* spp.).

58 birds. Of which, 27 were infected with *Plasmodium* spp., 18 with *Haemoproteus* spp., six with *Leucocytozoon* spp. and 7 showed mixed infection. Among the mixed infections, one bird was infected with both *Haemoproteus* spp. and *Leucocytozoon* spp., while six birds were infected with both *Plasmodium* spp. and *Leucocytozoon* spp. Observed differences in terms of parasite species were statistically significant. (P = 0.003).

Gametocytes of haemosporidians have sexually dimorphic characteristics, which can be easily distinguished using a light microscope. Haemosporidian macrogametocytes possess compact nuclei and bluish-stained cytoplasm, whereas microgametocyte nuclei are diffuse and the cytoplasm stains appear paler than macrogametocytes. It is important to note that in the Plasmodiidae family, merogony occurs within blood cells, and blood stages contain malarial pigment, also known as hemozoin. On the other hand, in the family Haemoproteidae, merogony does not take place within blood cells.

Statistical analysis showed a significant difference (P = 0.007) between resident and migratory bird groups in terms of overall infection (28.7% vs. 16.5%). Our study revealed that out of 27 individuals that were infected with *Plasmodium* (Figure 3 A-B), 18 samples belonging to six species of resident host birds including *Passer domesticus*, *Galerida cristata*, *Francolinus francolinus*, *Alcedo atthis*, *Vanellus indic and Ceryle rudis*. Furthermore, 9 samples were obtained from migratory host birds, representing 6 different species including *Oenanthe isabellina*, *Erithacus rubicola*, *Prunella modularis*, *Calandrella brachydactyla*, *Aythya ferina*, and *Caprimulgus aegyptius*.

The infection with *Haemoproteus* spp, was also relatively severe (Figure 3 C-D), and was observed in 14 samples from resident host birds belonging to 4 species; *P. domesticus, G. cristata, Pterocles alchata, and Argya altirstris*) and four samples from migratory host birds in two species, *C. brachydactyla* and *C.* aegyptius. In contrast, fewer infections with *Leucocytozoon* spp., (Figure 3 E-F) were recorded in migratory host birds, four samples from four migratory species host birds including *C. brachydactyla*, Anas *acuta, A. clypeata* and Ardea *alba* were infected, and two samples from resident host birds, *Gallinula chloropus* and *Pycnonotus leucotis*.

Leucocytozoon spp. was recorded in all seven cases of mixed infections, among these, one mixed infection involving Haemoproteus spp. and Leucocytozoon spp. was recorded in the migratory host bird (C. brachydactyla). While six mixed infection including Plasmodium spp. and Leucocytozoon spp. were observed in four samples obtained from resident host birds belonging to three species (P. domesticus, A. altirstris and, C. rudis), and four samples from migratory host birds representing 4 species (A. ferina, C. aegyptius, Anas clypeata, and, Motacilla alba).

The results of examining the blood of the studied birds are summarized in Table 2. It was found that 58 out of 248 (23.3 %) of examined birds were infected with Haemosporidians. Among these, *Plasmodium* spp., *Haemoproteus spp.*, and *Leucocytozoon* spp. were detected in 12.9%, 7.2%, and 3.2% of the birds, respectively. Mixed infections were also observed, with 4% of the birds showing a co-infection of *Plasmodium* spp. and *Leucocytozoon* spp., while 3.2% and 0.8% of the birds had mixed infections of *Haemoproteus* spp. and *Leucocytozoon* spp., respectively. The total numbers of positive samples, prevalence values, and 95% CI are summarized in Table 2.

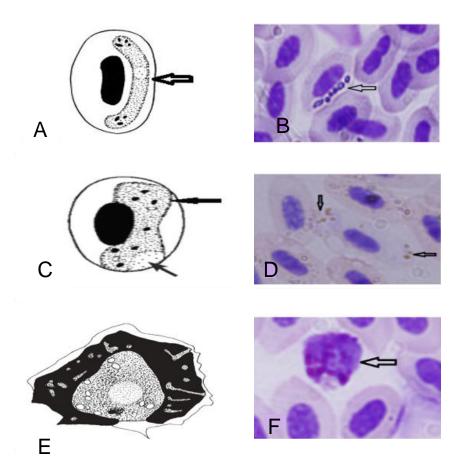


FIGURE 3. Avian haemosporidian parasite, A-B: *Plasmodium* of *Galerida cristata*, C-D: *Haemoproteus* spp. of *Passer domesticus*, and E-F: *Leucocytozoon* of *Anas acuta*.

DISCUSSION

In this study, we report the prevalence and distribution of avian haemosporidian infections in both resident and migratory bird species. Our study reveals an increase in the level of infection within Iraqi birds compared to previous studies that recorded a lower prevalence of blood parasites in the past years.

This could be due to the high vector population (biting mites) in Iraq as well as the limited use of insecticides. Alternatively, it could be due to the more extensive sampling conducted in the present study compared to previous ones.

Initially, we expected a higher prevalence of infections in migratory birds since they are exposed to a larger variety of vector and parasite species during their annual cycle (Waldenstro et al., 2002). However, our results were different with high levels of parasitemia recorded in resident birds, indicating a prevalence of nearly 36.6%. Among the blood parasites, *Plasmodium* spp. demonstrated the highest infection rate at 20.1%, followed by *Leucocytozoon* spp. at 8.2%. (Table 3, Figure 3) This observation could potentially be attributed to the heavy contamination of the study area with dipteran insect vectors, especially black flies (Simuliidae), which are active during summer (Greiner, 1991). Furthermore, we know that birds migrate to Iraq during the spring and winter seasons when temperatures decrease, inhibiting the emergence of suitable vector insects. This reduced exposure to vectors could explain the lower prevalence of blood parasites in migratory birds (Johnston&Janiga,1995). The low prevalence in migratory birds may also be due to migration, which may have a protective effect as migratory behavior allows the host to escape from environments with a high risk of infection (Altizer, 2011, Poulin, 2012; Satterfield, 2015; Fecchio et al., 2020).

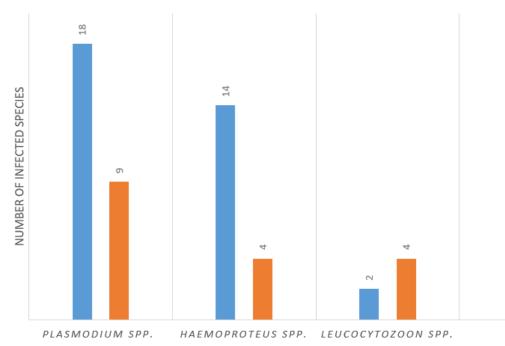


FIGURE 4. Comparisons between the number of resident (blue) and migratory (orange) bird species infected with each genus of blood parasites.

Our research results align with the overall infection rate reported in a study conducted in Turkey, which examined 565 specimens of migratory and resident birds and recorded 34.2% infection rate (Ciloglu et al., 2020). However, they found that overall parasite prevalence was higher in migratory birds compared to resident birds which is contrary to what we found here. In contrast, a study in Brazil examining birds from the Atlantic Forest reported higher infection prevalence in migratory species compared to resident ones (24% vs. 9%) (Anjos et al., 2021). Similarly, our research differs from a study conducted in eastern Tennessee, United States, which reported an overall prevalence of 44% in resident and migratory bird species. Similarly, our research differs from a study conducted in eastern Tennessee, United States, which reported and migratory bird species (Matthews et al., 2016).

Previous studies have consistently demonstrated that *Leucocytozoon* species have a wide range of avian host species and are commonly found in wild birds (Bensch et al., 2009; Clark et al., 2014; Valkiūnas & Iezhova, 2017). In our study, we observed a lower prevalence of *Leucocytozoon* species in resident birds compared to migratory birds, which is consistent with previous studies (Anjos, et al., 2021) suggesting a higher prevalence of this parasite in higher latitudes and colder area. Accordingly, it is reasonable that birds living in the tropical regions of Iraq show a lower *Leucocytozoon* prevalence than migratory birds that come from higher altitudes. This finding is also in agreement with what Ciloglu et al., 2020 reported from Sultan Marshes National Park, Turkey, which suggested insufficient habitat conditions for active transmission of *Leucocytozoon* species.

Another explanation for these observations can be resulted from studies conducted on vector species. Several studies have shown that black fly species are distinguishable as either mammalophilic or ornithophilic, in which ornithophilic black fly species preferentially choose large and abundant host species for feeding. (Malmqvist et al., 2004. Chakarov et al., 2021). In this context our results are reasonable, as most migratory birds in our study are large waterfowl. This result is also consistent with the results reported by Anjos et al. (2021) from Brazil, where all positive samples for *Leucocytozoon* were detected in *Elaenia albiceps*.

Plasmodium, on the other hand, has a global distribution and infects various bird hosts (Meister et al., 2021). In our study, microscopic examination revealed a higher prevalence of *Plasmodium* infection compared to the other two parasite genera, with resident birds exhibiting a higher prevalence than migratory birds (20.1% vs 6.2%). In contrast, several studies conducted in Iran on wild passerines have consistently identified *Haemoproteus* as the most common parasite among birds (Nourani et al., 2017a, 2017b, 2018a, 2018b; Djadid, 2019; Noorani et al., 2020a, 2020b). This difference in parasite prevalence may be attributed to favorable environmental conditions that support both the vector and the parasite in the Iranian region.

It is worth mentioning that the current study is the first large-scale description of avian haemosporidian infections in Iraq providing insights into the infection rates of blood parasites between migratory and resident birds in central and southern regions of the country. The high infection rate observed in resident Iraqi birds is significant, as these birds serve as reservoirs for blood parasites that can immediately infect migrant birds upon their arrival in Iraqi migration areas.

However, it is important to note that in morphological studies like the present study, rely on the identification of blood parasites mainly based on morphology and morphometry and, which can be challenging in certain stages of their life cycle (Anjos, et al., 2021). Therefore, further examination of these parasites with advanced methods such as molecular tools is necessary to clarify their taxonomic status and infection rate more accurately (Fallon et al., 2003). Host-parasitic relationships vary widely depending on host species or the geographical regions, and therefore detailed analyses which reflect these dynamics are promising.

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