Integrative Zoology

ORIGINAL ARTICLE OPEN ACCESS

Unraveling Occurrence Patterns and Diversity of Avian Malaria Parasites in Iberian Obligate and Facultative Scavenger Birds

Pilar Oliva-Vidal[1,2,3] | Jaime Muriel[4,5] | Alfonso Marzal[6,7] | Grethell Mabel López del Aguila[7] | José María Martínez[8] | Antoni Margalida[1,3]

[1]Institute for Game and Wildlife Research (CSIC-UCLM-JCCM) Ronda de Toledo, Ciudad Real, Spain | [2]Department of Animal Science, ETSEA, University of Lleida, Lleida, Spain | [3]Pyrenean Institute of Ecology (IPE-CSIC), Jaca, Spain | [4]Department of Zoology, University of Córdoba, Córdoba, Spain | [5]Department of Biology, University of Turku, Turku, Finland | [6]Department of Anatomy, Cell Biology and Zoology, Faculty of Biology, University of Extremadura, Badajoz, Spain | [7]Wildlife Research Group, Universidad Nacional de San Martín, Tarapoto, Perú | [8]Unidad de Conservación del Medio Natural, Departamento Medio Ambiente, Subdirección General de Desarrollo Rural y Sostenibilidad, Gobierno de Aragón, Huesca, Spain

Correspondence: Pilar Oliva-Vidal (pilaroliva@ipecsic.es)

Received: 7 June 2025 | **Revised:** 18 August 2025 | **Accepted:** 2 October 2025

Funding: This study was supported by the Ministry of Science and Innovation (project PID2022-142328OB-I00) and by line of action LA4 (R + D + I program in the Biodiversity Area financed with the funds of the FEDER Extremadura 2021–2027 Operational Program of the Recovery, Transformation and Resilience Plan).

Keywords: avian haemosporidians | *Leucocytozoon* | *Plasmodium* | SGS1 | vultures

ABSTRACT

Avian malaria is a globally distributed vector-borne infectious disease caused by haemosporidian parasites capable of driving population declines and even species extinctions, posing major challenges for conservation biology. However, its occurrence in scavenger birds, particularly vulture species, remains poorly understood. We conducted active monitoring in northeastern and central Spain, collecting 383 blood samples from free-living birds of all age classes, including obligate (all European vultures) and facultative (red and black kites) scavenger species, to assess the occurrence of avian malaria parasites and identify their lineages using a nested-PCR protocol. Overall haemosporidian prevalence was 3.4% (13/383), with *Leucocytozoon* and *Plasmodium* detected at values of 2.3% and 1.6%, respectively. Among positive birds, *Leucocytozoon* spp. (69.2%) were more common than *Plasmodium* spp. (46.1%), including two co-infected individuals. Red kites, cinereous, bearded, and Egyptian vultures harbored both *Plasmodium* and *Leucocytozoon*, while black kites and griffon vultures only showed *Plasmodium* and *Leucocytozoon*, respectively. Black kites exhibited the highest haemosporidian prevalence (8.3%), followed by cinereous vultures (5.3%), red kites (4.8%), Egyptian (4.6%), bearded (1.9%), and griffon vultures (1.3%). Interestingly, we report 10 new *host–parasite* interactions and describe a novel *Leucocytozoon* lineage (lGYPBAR01) infecting all European vultures except the griffon vulture. We also detected *Plasmodium relictum* pSGS1 in an adult red kite, the first confirmed occurrence of this lineage in adults of the species. Our findings highlight a previously overlooked threat to avian scavengers and suggest that global warming may further facilitate the spread of haemosporidian-infected vectors, underscoring the urgent need for targeted conservation measures and further research into parasite dynamics in vulnerable wild populations.

Pilar Oliva-Vidal and Jaime Muriel contributed equally to this work.

Integrative Zoology, 2026; 0:1–13
https://doi.org/10.1111/1749-4877.70032

1 | Introduction

Infectious diseases play a profound role in shaping wildlife populations and ecosystems, influencing survival, reproductive success, and the evolutionary dynamics of host species (Dobson and Foufopoulos 2001; Tompkins et al. 2015; Valenzuela-Sánchez et al. 2021). Among birds, infectious agents are of particular concern due to the diverse habitats they occupy and their global mobility, both of which can facilitate the spread of pathogens across ecosystems and even continents (Viana et al. 2016; Owen et al. 2021; Moraga-Fernández et al. 2023). Haemosporidian infections in birds, such as avian malaria, caused by parasites in the genera *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*, represent a significant threat with well-documented impacts on bird populations worldwide (Santiago-Alarcon and Marzal 2020). Diptera vectors, including several species of mosquitoes (Culicidae), simuliid flies, as well as several species of hippoboscid and ceratopogonid flies, are the main route of infection and transmission of avian malaria parasites (Santiago-Alarcon et al. 2012; Valkiūnas and Atkinson 2020). This parasitic infection has been linked to declines in native bird species, especially in isolated regions like Hawaii, where non-native mosquito vectors introduced avian malaria to immunologically naive populations, leading to severe declines or extinction of various native species (van Riper et al. 1986; Atkinson and LaPointe 2009). Beyond direct impacts on mortality, avian malaria can alter survival, behavior, and reproductive success (Merino et al. 2000; Navarro et al. 2004; Marzal et al. 2005; Puente et al. 2010), imposing selective pressures that shape avian life histories and physiological adaptations (Asghar et al. 2018; Schoenle et al. 2018; Muriel 2020). Additionally, birds infected with haemosporidians often require longer rehabilitation treatments in rescue centers (Cruz et al. 2024), which may further impair their survival prospects.

Haemosporidian infections are well documented in many passerine species; however, other bird orders, such as *Accipitriformes*, and in particular avian scavenger species, have been comparatively understudied. Obligate (species that depend almost totally on carrion, i.e., vultures) and facultative scavenger birds (species that scavenge opportunistically, e.g., eagles, kites, and corvids) provide crucial ecosystem services, primarily by regulating carcass removal (Santangeli et al. 2024). Although the scavenging diet of this guild may expose birds to numerous pathogens, including bacteria and other mycotic microorganisms (Roggenbuck et al. 2014; Blumstein et al. 2017; Pitarch et al. 2020; Plaza et al. 2020), current knowledge on how this feeding behavior may be related to haemosporidian infection susceptibility or to the risk of being bitten by a blood-sucking vector remains poor. Concerning Western European obligate scavengers, studies carried out by microscopic examination found no haemosporidian-infected individuals (Blanco et al. 1998; Tella et al. 1999), and the prevalence was low (or no infection evidence was found) when using molecular detection techniques by nested-PCR (<10%) (Chakarov and Blanco 2021; Moraga-Fernández et al. 2023). In contrast, in African vultures, reported prevalence values are considerably higher (>30%), reaching values >70% in some adult individuals (Greiner and Mundy 1979). This suggests that diet alone is not the primary driver of haemosporidian infections, and that other factors—such as environmental and climatic conditions—may play a more important role in shaping malaria distribution in wild populations (Fecchio et al. 2019). By contrast, studies on facultative avian scavengers, such as kite species in Western Europe, have also reported lower prevalence values (Pérez-Rodríguez et al. 2013).

Most Old and New World vultures are nowadays threatened, and their populations are in serious decline, mainly due to anthropogenic pressures (McClure et al. 2018). Iberian trends, however, are stable or even increasing, playing a key role in the future viability of European vulture populations (i.e., griffon *Gyps fulvus*, cinereous *Aegypius monachus*, bearded *Gypaetus barbatus*, and Egyptian vultures *Neophron percnopterus*; Safford et al. 2019). Spain is playing a crucial role in the conservation of obligate and other facultative avian scavenger species, hosting >90% of European vulture populations (Margalida et al. 2010) as well as the majority of the entire population of the globally threatened Spanish imperial eagle (*Aquila adalberti*) and significant numbers of red (*Milvus milvus*) and black kites (*Milvus migrans*). Nevertheless, globally, a myriad of non-natural mortality factors persist: the illegal use of poisons (Margalida and Mateo 2019), ingestion of veterinary drugs and other environmental pollutants present in human-dominated environments (Margalida and Oliva-Vidal 2017; Oliva-Vidal et al. 2022a; Herrero-Villar et al. 2023), lead contamination (Monclús et al. 2020), habitat loss/transformation (e.g., increase of energy infrastructures; Serrano et al. 2020), changes in landscape configuration (Oliva-Vidal et al. 2022b) and in health policies (Donázar et al. 2009), and human–wildlife conflicts related to vulture attacks toward livestock (Lambertucci et al. 2021; Oliva-Vidal et al. 2022c), further threatening this guild and its functional roles. Other factors, such as climate change and the spread of infectious diseases, remain poorly understood (but see Moraga-Fernández et al. 2023; Loureiro et al. 2024), highlighting the need for further research to inform effective management and conservation measures.

Global warming plays a significant role in reshaping the distribution and prevalence of vector-borne diseases, including those caused by haemosporidian parasites (Garamszegi 2011; Ferraguti et al. 2020). Rising global temperatures can influence the range and activity of vectors like mosquitoes, enabling them to thrive at higher altitudes and latitudes previously unsuitable due to colder conditions (LaPointe et al. 2012). In this regard, climate change may alter *host–parasite* dynamics by favoring generalist haemosporidian parasites over specialists (Fecchio et al. 2019) and lead to a homogenization of parasite diversity (Pérez-Rodríguez et al. 2014). For bird communities inhabiting mountain regions, this shift could mean increased exposure to haemosporidian-infected vectors in areas that were historically free of these diseases. This could expose scavenger birds to novel disease pressures, potentially leading to declines in species that are vital for ecosystem health and scavenger guild functioning (Sebastián-González et al. 2021; Oliva-Vidal et al. 2024). For instance, the impact of climate change on haemosporidian distribution has been underscored by the detection of these parasites in the endangered Pyrenean capercaillie (*Tetrao urogallus aquitanicus*) (Nicolás de Francisco et al. 2023), a species inhabiting high-altitude forests. This finding highlights a potential emerging vulnerability to malaria in birds inhabiting mountain ecosystems and colder environments and raises concerns about the increased threats that climate change poses to biodiversity conservation.

Despite growing research on avian malaria and related parasites (Order: *Haemosporida*) across different bird species and populations, studies focusing on avian scavengers remain scarce and have largely concentrated on nestlings (Chakarov and Blanco 2021; Bukauskaitė et al. 2024; but see Pérez-Rodríguez et al. 2013). Indeed, the MalAvi database, which compiles global records of haemosporidian parasite diversity across bird species worldwide, includes data for only 56.5% of the world's 23 vulture species (Bensch et al. 2009; Table S1). This gap in knowledge is concerning, particularly as global warming and habitat alterations may heighten the exposure of this guild to haemosporidian parasites (LaPointe et al. 2012). In this regard, we investigated the prevalence of haemosporidians responsible for causing avian malaria and identified their lineages in free-living obligate (all four European vultures) and other facultative avian scavengers (red and black kites) of all age classes inhabiting a mountain region in northeastern and central Spain. We predicted that (1) the prevalence of avian malaria (*Plasmodium* spp.) and malaria-like parasites (*Haemoproteus* and *Leucocytozoon* spp.) in this guild would be low (Pérez-Rodríguez et al. 2013), and (2) individuals would be infected exclusively by *Leucocytozoon* parasites as previously suggested (Chakarov and Blanco 2021). Our findings provide novel and valuable insights into the parasite ecology in this globally endangered functional guild and contribute to future efforts to conserve these species and the pivotal ecosystem services they provide.

2 | Material and Methods

2.1 | Study Area

This study was carried out essentially in the Pyrenees and adjacent regions (NE Iberian Peninsula), except for three non-nestling cinereous vultures that were captured in the "Finca El Castañar" (Toledo, Central Spain). The Pyrenees is a 430-km long and 65–150-km wide continuous mountainous barrier running from the Atlantic to the Mediterranean, covering around 50 000 km^2, becoming a natural boundary between France and Spain. Its geographical position between the Mediterranean Sea and the Atlantic Ocean, together with its range of altitudinal gradients from sea level to >3000 m a.s.l., explains its heterogeneous meteorology. Further details regarding climatic conditions of the study area are provided in Oliva-Vidal (2023). This region holds breeding populations of the four obligate European avian scavengers and a rich community of facultative avian (e.g., eagles, kites, and corvids) and mammal species, which provide pivotal cultural and regulatory ecosystem services (García-Jiménez et al. 2022; Oliva-Vidal et al. 2022b). This area is characterized by extensively and semi-extensively grazed livestock and holds important populations of wild ungulates, which provide most of the biomass for the scavenger guild (Margalida et al. 2018). Moreover, a network of supplementary feeding stations ("vulture restaurants") for scavenging birds is present throughout this region (Moreno-Opo et al. 2015), and this guild frequently also exploits anthropogenic food resources at the urban open-air landfills as well as domestic carcasses from intensive farms that occur throughout the study area (Tauler-Ametller et al. 2018; Fernández-Gómez et al. 2022).

2.2 | Study Species and Field Sampling

Over a 6-year period (from 2017 to 2022), we performed active monitoring, collecting blood samples from 383 free-living scavenging birds (Table S2). We focused this study on the four European obligate (i.e., the griffon, cinereous, bearded, and Egyptian vultures) and other facultative avian scavengers (red and black kites). Blood samples were collected when birds were handled to be ringed and marked with patagial tags or fitted with satellite transmitters. Our sampling included individuals of all age classes: nestlings (birds sampled in the nest), juveniles (birds in their first year), subadults, and adults (Table S3). Age classes were identified according to plumage characteristics and molt pattern (Forsman 2016). Non-nestling individuals were captured using a variety of methods (e.g., baited traps), according to the species concerned. Further details on the capture systems used for sampling each species and regarding the days of age of each species are provided in Oliva-Vidal et al. (2022a). All individuals were handled by trained and authorized personnel. Whole-blood samples (3–5 mL, never exceeding 1% of the body weight of the bird) were collected from the brachial vein and were immediately placed into EDTA or heparinized tubes and stored at −80°C until laboratory analysis. DNA was extracted from approximately 0.10 mL of blood preserved in 100% ethanol and used for sex determination (following a previously established protocol; Griffiths et al. 1998) and haemosporidian parasite screening (see details below). All fieldwork was conducted in accordance with national permits and guidelines.

2.3 | Molecular Parasite Screening

Genomic DNA was extracted from all blood samples collected in this study using GeneJET Genomic DNA Purification Kit (Thermo Scientific Inc., reference #K0722) according to the manufacturer's instructions. Haemosporidian infections were detected from blood samples using molecular methods targeting conserved regions of the haemosporidian cytochrome *b* gene (cyt b) (Hellgren et al. 2004). We conducted nested PCR assays to detect haemosporidian parasites using diluted genomic DNA (25 ng/µL) as the template, following the protocols outlined by Hellgren et al. (2004). The process began with a primary PCR consisting of 20 cycles, using outer primers (HaemNFI and HaemNR3) flanking the target region. Subsequently, 2 µL of the primary PCR product was used in two separate nested reactions (35 cycles each) to selectively amplify either *Plasmodium/Haemoproteus* or *Leucocytozoon* lineages. For *Leucocytozoon* detection, the primers HaemFL and HaemR2L were used, while HaemF and HaemR2 targeted *Plasmodium* and *Haemoproteus*. PCR success was verified by electrophoresis of 2.5 µL of the final product on a 2% agarose gel. Each PCR run included negative controls (one for every 8 samples) and positive controls (two for every 24 samples). Positive amplifications were sequenced using methods described by Hellgren et al. (2004), with sequencing performed from the 5′ end using the forward primers HaemF and HaemFL. The obtained sequences of 478 bp of the cyt b were edited, aligned, and compared in a sequence identity matrix by BLAST (Basic Local Alignment Search Tool) implemented in MalAvi database (Bensch et al. 2009) to identify parasite lineage. New lineages (sequences not previously published in GenBank) were also sequenced from the reverse end using the primer

HaemR2. Parasites with sequences differing by one nucleotide substitution were considered to represent evolutionary independent lineages (Bensch et al. 2004, 2009). The new *Leucocytozoon* lineage (lGYPBAR01) was coded following the nomenclature of the MalAvi database (Bensch et al. 2009) and deposited in GenBank under the accession number PV037200 (Table 1).

2.4 | Phylogenetic Analyses

The genetic relationship between the parasites was investigated by analyzing the avian haemosporidian cytochrome b sequence divergence using a maximum likelihood method with 1000 bootstrap replicates in the program Geneious version 6.1.6 (Kearse et al. 2012). We used *Theileria annulata* (GenBank #PP465045) from Piroplasmida, the sister group to the Haemosporida, as the outgroup (Kuo and Kissinger 2008). We used a relative substitution rate model in order to define the rate at which each of the transitions and transversions occurs in an evolving sequence. The phylogenetic tree was edited by using R version 3.6.1 (R Core Team 2019) and libraries ggplot (Wilkinson 2011) and ggtree (Yu et al. 2017).

3 | Results

3.1 | Prevalence of Haemosporidian Parasites in Iberian Scavenger Birds

We analyzed 383 blood samples from six European avian scavenger species, including the four obligate scavengers: griffon (*n* = 76), cinereous (*n* = 19), Egyptian (*n* = 109), and bearded vultures (*n* = 104), and two facultative species: red (*n* = 63) and black kites (*n* = 12) (Table 2). Individuals of all age classes (Table S2) were screened for *Plasmodium*, *Haemoproteus*, and *Leucocytozoon* parasites. Haemosporidian parasites were detected in all six species sampled, but only from two of the three targeted genera—*Plasmodium* and *Leucocytozoon*—while *Haemoproteus* was not found (Table 2; Figure 1). Overall prevalence across all species was 3.4% (13/383), with the highest infection rate observed in black kites (8.3%; 1/12), followed by cinereous vultures (5.3%; 1/19), red kites (4.8%; 3/63), and Egyptian (4.6%; 5/109), bearded (1.9%; 2/104), and griffon vultures (1.3%; 1/76) (Figure 1; Table 2). Because of the low overall prevalence found, we were unable to statistically test the influence of bird species, age class, and sex on haemosporidian occurrence patterns.

At the parasite genus level, prevalence was 2.3% for *Leucocytozoon* and 1.6% for *Plasmodium*. Among the 13 infected birds, 46.1% (6/13) carried *Plasmodium*, 69.2% (9/13) harbored *Leucocytozoon*, while 15.4% (2/13) were co-infected with both genera (Table 1). At the interspecific level, the highest prevalence of *Plasmodium* was observed in black kites (8.3%), followed by cinereous vultures (5.3%), red kites (3.2%), and bearded (1.0%) and Egyptian vultures (0.9%), while infection by this genus was not detected in griffon vultures (Figure 1; Table 2). Regarding *Leucocytozoon* infections, the highest prevalence was found in cinereous vultures (5.3%), followed by Egyptian vultures (3.7%), red kites (3.2%), and griffon (1.3%) and bearded vultures (1.0%), while infection by this genus was not observed in black kites (Figure 1; Table 2).

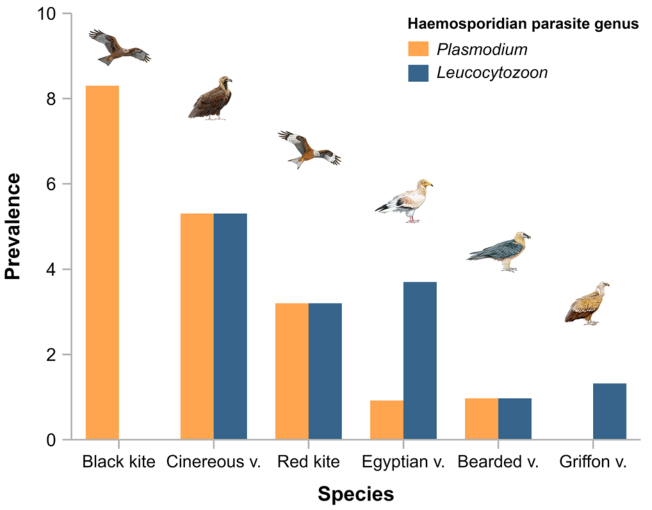

FIGURE 1 | Interspecific prevalence (in percentage) of haemosporidian parasites including the three genera tested (*Plasmodium*, *Haemoproteus*, and *Leucocytozoon*) found in free-living obligate: griffon (adult female); cinereous (subadult female); bearded (juvenile and subadult male); and Egyptian (two adult female and three nestlings involving two female and one male) vultures and other facultative avian scavengers: red (adult male and two nestlings of both sexes) and black (adult female) kites sampled in NE (Pyrenees, Pre-Pyrenees) and central Spain (Toledo) during the period 2017–2022. *Source:* Illustrations by Juan Varela.

3.2 | Genetic Diversity of Haemosporidians in Iberian Scavenger Birds

We detected only two (*Plasmodium* and *Leucocytozoon*) of the three haemosporidian parasite genera tested (Figure 1), identifying three unique lineages of *Plasmodium* and five of *Leucocytozoon*; one of them was described for the first time (lGYPBAR01) (Table 1; Figure 2). Multiple infections involving different lineages of *Plasmodium*, *Haemoproteus*, or *Leucocytozoon* were not observed, as indicated by the absence of double peaks in the same DNA sequencing chromatogram. However, we detected co-infection in two individuals: one cinereous vulture (subadult female) and one red kite (adult male). The cinereous vulture was infected with a combination of a new *Leucocytozoon* lineage (lGYPBAR01) and the *Plasmodium* pRTSR1—revealing new host records for both lineages—while the red kite was infected with a combination of the *Plasmodium* pSGS1 and the *Leucocytozoon* lASOT1 lineages, evidencing a new host record concerning lASOT1 lineage (Table 1; Figure 2). No co-infections were detected in all other species sampled.

Except for lineages pMILANS05, pSGS1, and lCIAE02 that had previously been found, respectively, on black kites, red kites, and griffon vultures, we could identify 10 new *host–parasite* interactions (six for *Leucocytozoon* and four for *Plasmodium*; Table 1; Figure 2). Regarding *Leucocytozoon* spp., we found four lineages infecting different species for the first time: lGYPBAR01 in bearded (*n* = 1; juvenile male), Egyptian (*n* = 3; two nestlings of both sexes and one adult female), and cinereous vultures (*n* = 1; subadult female; the last one species being also co-infected with pRTSR1); lFIEB-L6 in Egyptian vultures (*n* = 1; nestling female); and lASOT1 (*n* = 1; adult male also co-infected

TABLE 1 | Overall haemosporidian prevalence (%) observed according to the avian scavenger species, age class ("N": Nestling; "J": Juvenile; "S": Subadult; "Ad": Adult), and sex ("F": Female; "M": Male). The parasite genus ("P": *Plasmodium*; "L": *Leucocytozoon*) detected as well as the corresponding lineage names, GenBank accession numbers, alternative hosts ("Alt. hosts"), and study reference in which the parasite lineages were previously recorded are shown.

Species	Overall prevalence	Age	Sex	Genus_Lineage	GenBank Acc. N	Alt. host	Reference
Griffon vulture	1.3 (1/76)	Ad	F	L_CIAE02	HF543631	*N. percnopterus* *A. monachus*	Chakarov and Blanco (2021)
Cinereous vulture	5.3 (1/19)	S	F	**L_GYPBAR01**§ + P_RTSR1§	PV037200 + AF495568	— *M. migrans*	Undocumented Pérez-Rodríguez et al. (2013); Zerek et al. (2023)
Bearded vulture†	1.9 (2/104)	J	M	**L_GYPBAR01**§	PV037200	—	Undocumented
		S	M	P_RTSR1§	AF495568	*M. migrans*	Pérez-Rodríguez et al. (2013); Zerek et al. (2023)
Egyptian vulture	4.6 (5/109)	N	F	L_FIEB-L6§	MT577565	*Tyto alba*	García-del-Río et al. (2021)
		N	M	**L_GYPBAR01**§	PV037200	—	Undocumented
		N	F	**L_GYPBAR01**§	PV037200	—	Undocumented
		Ad	F	P_RTSR1§	AF495568	*M. migrans*	Pérez-Rodríguez et al. (2013); Zerek et al. (2023)
		Ad	F	**L_GYPBAR01**§	PV037200	—	Undocumented
Red kite	4.8 (3/63)	N	F	P_MILANS05§	HM179149	*M. migrans*	Pérez-Rodríguez et al. (2013)
		N	M	L_ASOT06§	EU627822	*Asio otus*	Ishak et al. (2008)
		Ad	M	P_SGS1 + L_ASOT1§	KJ488565 + EF607286	*Athene noctua* *Asio otus*	Mata et al. (2015); Coeurdassier et al. (2021) Ishak et al. (2008)
Black kite	8.3 (1/12)	Ad	F	P_MILANS05	HM179149	*Philomachus pugnax*	Mendes et al. (2013)

Note: New parasite lineages are indicated by bold letters (MalAvi; Bensch et al. 2009). † denotes that the bird species was not previously documented infected by haemosporidians, and § represents a new host record for this haemosporidian lineage.

TABLE 2 | Prevalence values (%) of each tested haemosporidian parasite genus (*Plasmodium*, *Haemoproteus*, and *Leucocytozoon*) and total haemosporidian occurrence found in free-living obligate (i.e., griffon, cinereous, bearded, and Egyptian vultures) and facultative (red and black kite) avian scavengers sampled in NE (Pyrenees, Pre-Pyrenees) and central (Toledo) Spain during the period 2017–2022.

		Plasmodium		***Leucocytozoon***		**Total**	
	N	***N+***	**%**	***N+***	**%**	***N+***	**(%)**
Obligate							
Cinereous v.‡	19	1	5.3	1	5.3	1	5.3
Egyptian v.	109	1	0.9	4	3.7	5	4.6
Bearded v.	104	1	1.0	1	1.0	2	1.9
Griffon v.	76	—	—	1	1.3	1	1.3
Facultative							
Red kite‡	63	2	3.2	2	3.2	3	4.8
Black kite	12	1	8.3	—	—	1	8.3

Note: ‡ indicates co-infections.

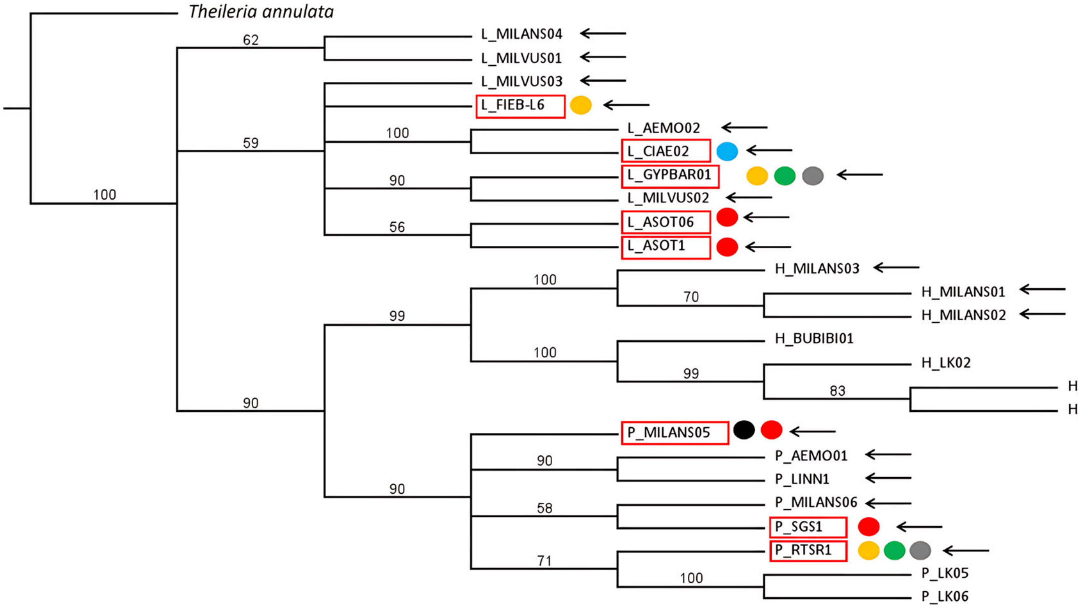

FIGURE 2 | Consensus phylogenetic tree based on *cyt b* sequences from haemosporidian lineages previously detected in Spanish Falconiformes, including those found in scavenger birds. Lineages detected in the present study are highlighted with red frames and colored dots representing host species: griffon vulture (blue), cinereous vulture (gray), bearded vulture (green), Egyptian vulture (yellow), red kite (red), and black kite (black). Node tips are labeled with an abbreviation for parasite genus ("L_" = *Leucocytozoon*, "P" = *Plasmodium*, and "H" = *Haemoproteus*), followed by the lineage name. *Theileria annulata* (GenBank accession #PP465045) was used as an outgroup. Lineages detected in scavenger birds are marked with a black arrow.

with pSGS1) and lASOT06 (*n* = 1; nestling male) in red kites (Table 1; Figure 2). Concerning *Plasmodium* spp., we discovered the following four new *host–parasite* interactions involving two lineages: pRTSR1 in cinereous (*n* = 1; subadult female also co-infected with lGYPBAR01), bearded (*n* = 1; subadult male), and Egyptian vultures (*n* = 1; adult female), and pMILANS05 in the red kite (*n* = 1; nestling female); the last individual also being co-infected with lASOT1 (Table 1; Figure 2).

Considering all 13 haemosporidian-infected birds (reporting 15 host interactions as two individuals exhibited co-infection), the most prevalent (33.3%) lineage was *Leucocytozoon* lGYPBAR01, detected in cinereous (*n* = 1), bearded (*n* = 1), and Egyptian (*n* = 3) vultures; followed by the *Plasmodium* pRTSR1 (20%), found in cinereous (*n* = 1), bearded (*n* = 1), and Egyptian (*n* = 1) vultures; and the *Plasmodium* pMILANS05 (13.3%) found in red (*n* = 1) and black kites (*n* = 1). The other five lineages were detected once: lCIAE02 in griffon vultures; lFIEB-L6 in Egyptian vultures; and lASOT06, lASOT1, and pSGS1 in red kites (Table 1). At the interspecific level, red kites exhibited the greatest diversity of lineages (pMILANS05, pSGS1, lASOT1, and lASOT06), followed by Egyptian vultures (pRTSR1, lGYPBAR01, and lFIEB-L6; Figure 3). Bearded and cinereous vultures exhibited one lineage of each parasite genus (lGYPBAR01 and pRTSR1), and the remaining species (griffon vultures and black kites) were infected only with lCIAE02 and pMILANS05, respectively (Table 1; Figures 2 and 3).

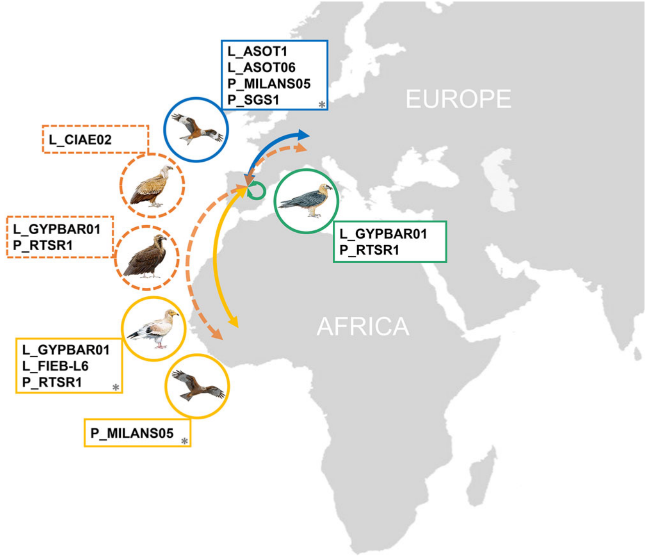

FIGURE 3 | Potential intra and inter-continental avian haemosporidian infection/transmission routes among European scavenging birds. All species considered here are migratory except the bearded vulture (see Oliva-Vidal et al. 2022a). Cinereous and griffon vultures are partial migrants across the trans-Saharan Africa (only by juveniles; Ramírez et al. 2022; García-Macía et al. 2023; Moraga-Fernández et al. 2023) but both juveniles and adults can perform intercontinental movements or even move to Mediterranean islands (Tobajas et al. 2024). *Species with small sedentary Spanish populations.

4 | Discussion

Our study provides the first molecular evidence of haemosporidian infections across the entire European obligate scavenger guild (griffon, cinereous, bearded, and Egyptian vultures) and other facultative avian scavengers (red and black kites), revealing unexpected parasite diversity and previously undocumented *host–parasite* interactions in these globally threatened species (McClure et al. 2018; Safford et al. 2019). Despite their major ecological roles, both the prevalence and diversity of haemosporidian parasites in scavenging birds—particularly vultures—remain poorly understood. This knowledge gap partly stems from early studies relying on microscopy, which failed to detect infections in large samples of griffon vulture nestlings from Spain, reinforcing the assumption of low susceptibility in this guild (Blanco et al. 1998; Tella et al. 1999). However, the advent of molecular tools has revealed a more complex *host–parasite* landscape across birds (Bensch et al. 2009), though data for obligate avian scavengers remain scarce (but see Yabsley et al. 2018; Chakarov and Blanco 2021).

Using a nested-PCR approach, we document haemosporidian infections in all six European avian scavenger species examined—including both obligate and facultative species—across all age classes of free-ranging individuals. Notably, we detected *Plasmodium* and *Leucocytozoon* infections in both endangered bearded and Egyptian vultures, uncovered a high lineage diversity—including a novel *Leucocytozoon* lineage (lGYPBAR01) found in all European vultures but the griffon vulture—and identified several new *host–parasite* associations. In contrast, no *Haemoproteus* spp. were detected. These findings are of major conservation relevance, as previous molecular studies in Iberian vultures have focused exclusively on nestlings and reported only *Leucocytozoon* spp. (Chakarov and Blanco 2021), suggesting a narrower *host–parasite* spectrum than our results reveal. Most haemosporidian research in raptors has been limited to nestlings or rehabilitation center admissions (Krone et al. 2008) due to the difficulty of sampling free-living adults. Our study therefore establishes a critical baseline for haemosporidian disease ecology in this globally endangered functional guild with clear implications for conservation management.

Although overall prevalence was low (3.4%), this value is consistent with those reported for other raptor populations (e.g., Chakarov and Blanco 2021; Zerek et al. 2023; Subaneg et al. 2024) and may reflect biological traits specific to avian scavengers. One possible explanation is the limited presence of competent vectors in the study area, as vector availability is a key constraint on haemosporidian transmission (Santiago-Alarcon et al. 2012). Host-related factors may also play a significant role; for example, genetic resistance or acquired immunity could reduce infection rates, particularly in populations with historical exposure to these parasites (Atkinson et al. 2001; Muriel 2020). Behavioral traits might further reduce infection risk—such as cavity-roosting, high perching sites, or strictly diurnal activity patterns—that limit contact with crepuscular or nocturnal mosquito vectors (Darbro and Harrington 2007; Clayton et al. 2010). Some birds may even move to higher altitudes to avoid vector-rich environments (Atkinson and LaPointe 2009), which is consistent with observations by Chakarov and Blanco (2021), who found higher haemosporidian prevalence in nestling griffon vultures raised in tree nests compared to those in cliff nests. Regarding facultative avian scavengers, we observed an overall prevalence of 8.3% in black and 4.8% in red kites—figures in line with previous reports from Spain (Pérez-Rodríguez et al. 2013) and slightly higher than those observed in obligate scavenger species. Alternatively, these low prevalence values may also result from infections in closely related breeding raptor species that do not complete their full life cycle in these new hosts, leading to abortive development of haemosporidians and rendering them dead-end hosts (Dimitrov et al. 2015). In this context, PCR amplification of DNA does not necessarily indicate that the host is fully susceptible or capable of supporting the development of infective stages that can be transmitted to a new host (Valkiūnas and Atkinson 2020). Therefore, further studies examining the presence of infective stages, such as gametocytes circulating in the peripheral blood, are essential to demonstrate the true competence of these avian hosts.

We found the highest overall haemosporidian prevalence in black kites, followed by cinereous vultures, red kites, and Egyptian, bearded, and griffon vultures. This pattern supports the idea that tree-nesting species (e.g., kites and cinereous vultures) are generally more susceptible to infection than cliff-breeders (e.g., griffon, bearded, and Egyptian vultures) (Chakarov and Blanco 2021). This highlights the ecological heterogeneity within the scavenger guild, as differences in habitat preferences (trees vs. cliffs) and characteristics (e.g., breeding altitude) may strongly influence exposure to vectors. However, the absence of infection in cinereous vulture nestlings from a Pre-Pyrenean colony suggests that species-specific traits can modulate infection risk even among tree-breeders (Bukauskaitė et al. 2024). Beyond breeding habitat, other ecological traits—such as trophic behavior, use of anthropogenic food sources (e.g., landfills and supplementary feeding stations), or other predictable aggregation sites—could further shape exposure to infected vectors, particularly in highly mobile or gregarious species (Pérez-Rodríguez et al. 2013; van Overveld et al. 2020). Such sites, regardless of their level of "cleanliness," may facilitate parasite transmission if birds remain there for a sufficient time, and repeated or consistent use of the same location could further enhance transmission effectiveness by attracting vectors over time. Scavenging birds frequently exploit landfills and supplementary feeding stations (Tauler-Ametller et al. 2017, Tauler-Ametlller et al. 2019; Arévalo-Ayala et al. 2023), which often attract large mixed-species flocks and competent vectors and are linked to increased risk of pathogen exposure and contact with emerging environmental pollutants (Qasim et al. 2020; Oliva-Vidal et al. 2022a; Sangkachai et al. 2024). Such aggregation sites could facilitate cross-species malaria transmission and therefore warrant further investigation (Ricklefs and Fallon 2002; Križanauskienė et al. 2006). Similarly, social structure (gregarious vs. solitary) may be a key factor affecting exposure and transmission rates, while the role of communal roosts, bathing water points, and migratory stopover sites—potential hubs for parasite exchange—remains largely unexplored. Overall, this ecological heterogeneity, spanning breeding habitats, feeding behaviors, and sociality, may be critical for understanding the variation in haemosporidian prevalence and diversity among scavenger birds.

Migration behavior and long-distance movements, both traits intrinsic to all species studied but the bearded vulture (see details in Oliva-Vidal et al. 2022a), could significantly affect the distribution and patterns of vector-borne diseases. One of the most important factors in the transmission of haemosporidians is the presence of suitable vectors; thus migratory—or highly mobile—species are exposed to a wider variety of vectors than non-migratory ones, increasing the possibility of finding a suitable vector (Valkiūnas 2005). This idea is in line with our results, since we found the greatest lineage diversity in red kites and Egyptian vultures (see Table 1 and Figure 3). In contrast, although black kites are also migratory and tree-nesting, we detected only a single haemosporidian lineage (pMILANS05) in this species. This low diversity may reflect the limited sample size for black kites in our study ($n = 12$), together with the fact that only one individual tested positive, despite this species showing the highest overall prevalence in our dataset. Migratory birds play a critical role in the emergence of new sources of infection at great distances from their original (or endemic) areas and can expose host populations to novel parasites or introduce them into new geographic areas (Koprivnikar and Leung 2015). This scenario is particularly critical for isolated bird populations that have not co-evolved with certain pathogens, such as those inhabiting high-altitude mountainous/alpine environments (e.g., the bearded vulture), as these species often lack an evolved immune defense and are thus highly susceptible to infections from novel parasites, which could significantly affect their survival or reproduction (Schmid-Hempel 2021).

Regarding nestlings, we also observed a low haemosporidian prevalence (4.7%; 5/106), and only involving the Egyptian vulture (5.8%; 3/52) and the red kite (10%; 2/20). Chakarov and Blanco (2021) found a lower haemosporidian prevalence in nestlings of griffon (3.1%) and Egyptian (5.3%) vultures than in cinereous vultures (10.3%)—a tree-breeding species—identifying exclusively *Leucocytozoon* spp. Bukauskaitė et al. (2024) investigated haemosporidians in nestlings of three tree-breeding raptors in temperate forests of Lithuania and found an overall prevalence of 30.5% and, similar to Chakarov and Blanco (2021), only detected *Leucocytozoon* spp. Differences in haemosporidian occurrence and diversity we found in contrast to those reported in vulture nestlings from central Spain could potentially be related to different environmental and landscape characteristics (Tamayo-Quintero et al. 2025) that can drive different distributions of suitable vectors at breeding sites and parasite richness in the area (Valkiūnas and Atkinson 2020; Bukauskaitė et al. 2024). Otherwise, the prevalence we found in red kite nestlings is lower than that observed by Wiegmann et al. (2021) in Eastern Westphalia, Germany (32.6%) and by Coeurdassier et al. (2021) in France (28%). These findings support the idea that haemosporidian prevalence in Spanish red kites is lower than that reported in northern European areas, which could be explained by the dryness of the Iberian environment, making it "apparently" unsuitable for the main suitable vectors (Tella et al. 1999). However, importantly, it is possible that some infections were missed, as our nested-PCR protocol may underestimate the prevalence of *Leucocytozoon* infections due to its reduced sensitivity for certain raptor-specific strains (Chakarov and Blanco 2021). Future research combining the approach we used with optimized protocols (e.g., Pérez-Rodríguez et al. [2013] would be therefore valuable for gaining a more accurate understanding of the true prevalence and diversity of haemosporidian parasites in raptors.

Interestingly, we identified *Leucocytozoon* spp. in 80% (4/5) of the infected nestlings—comprising three different lineages, including one newly discovered (lGYPBAR01). Specifically, lineages lFIEB-L6 and lGYPBAR01 were found in one and two Egyptian vultures, respectively, while lineage lASOT06 was detected in one red kite. An unexpected finding was that one red kite harbored the lineage pMILANS05 (see Table 1). To our knowledge, this represents the first record of a nestling infected with this parasite lineage within the European avian scavenger guild to date, evidencing the presence of suitable vectors in the study area. This fact is remarkable since pMILANS05 has only been found in adult black kites from Spain (Pérez-Rodríguez et al. 2013) and in a single Western marsh harrier (*Circus aeruginosus*) (parasite spp.: *P.* aff. *elongatum*) from Austria (Harl et al. 2022). Second, pMILANS05 was also found in the ruddy quail-dove (*Geotrygon montana*) in Jamaica (Santiago-Alarcon et al. 2010), cattle egret (*Bubulcus ibis*) in Africa (Villar Couto et al. 2019), ruff (*Philomachus pugnax*) in Malawi and the Netherlands (Mendes et al. 2013), and *Culex neavei* from Cameroon (Njabo et al. 2011), while *Plasmodium*—and *Haemoproteus*—genera were never reported in red kites. Conversely, several haplotypes of *Plasmodium* have been reported in black kites, thus supporting that its transmission occurs in African wintering grounds (Pérez-Rodríguez et al. 2013; Nourani et al. 2020). This idea is in line with our findings, since we found pMILANS05 in one adult black kite, and reported for the first time pRTSR1 in one adult Egyptian vulture (which has also recently been detected in black kites from Turkey; Zerek et al. 2023). Our findings therefore partially agree with the hypothesis that transmission of many haplotypes of *Plasmodium* and *Haemoproteus* takes place exclusively in African wintering grounds and apparently not in Europe, possibly due to the lack of suitable vectors (Valkiūnas 2005; Pérez-Rodríguez et al. 2013). At the same time, our results indicate that transmission of both *Leucocytozoon* and *Plasmodium* spp. may also occur at European breeding sites, suggesting the presence of suitable vectors in Spain.

Investigating blood parasite occurrence and richness in nestlings provides valuable information on local parasite transmission, which is crucial for understanding the dynamics of avian malaria and other emerging vector-borne infectious diseases (e.g., Moraga-Fernández et al. 2023). Monitoring haemosporidians in nestlings of different species and populations can therefore help track changes in parasite prevalence patterns and diversity over time in breeding areas (Bukauskaitė et al. 2024). For instance, we found the same lineage (lGYPBAR01) in two Egyptian vulture nestlings from nests that are ≈40 km apart, while the remaining nestlings (one Egyptian and two red kites) were infected with different *Leucocytozoon* lineages and one *Plasmodium* lineage (see above), and nests were also located several kilometers away. Concerning non-nestlings, we also found pRTSR1 in one subadult Pyrenean bearded vulture male and in one subadult cinereous vulture female from Central Spain. In addition, we found co-infection—which is known to increase virulence (Palinauskas et al. 2011; Dimitrov et al. 2015)—with *Plasmodium relictum* (lineage SGS1) and lASOT1 in one adult red kite male. This finding is also of concern because, to our knowledge, it represents the first record of an adult red kite harboring *P. relictum*. This parasite was only previously found in one red kite nestling in France, which also exhibited co-occurrence with *Leucocytozoon* sp. (lMILVUS1) (Coeurdassier et al. 2021).

Our report may have conservation relevance, as *P. relictum* is the most prevalent and widely distributed haemosporidian parasite, commonly associated with virulent disease (Garnham 1966; Remple 2004). Among its different haplotypes/lineages, we found pSGS1, which has been frequently reported in Spanish birds (Garcia-Longoria et al. 2019; Ferraguti et al. 2018; Muriel et al. 2018) and in local vectors (Martínez-de la Puente et al. 2021). This cosmopolitan parasite is considered a serious bird pathogen because of its well-known invasive behavior and fatal outcomes (van Riper et al. 1986; Marzal et al. 2015; Meister et al. 2021) that depend on the host species and its adaptability to infection (Valkiūnas et al. 2018). Although its effects in raptors appear less severe than in other avian hosts (Remple 2004; Coeurdassier et al. 2021), its detection in an adult red kite is noteworthy. The red kite is one of the few migratory raptor species believed to breed exclusively in Europe. Spain plays a critical role in preserving this species (hosting ≈50 000 individuals in winter, roughly 80% of the European population; BirdLife International 2021), but its populations are still declining, which led to updating its conservation status as "Endangered" on the Red List of Spanish birds (López-Jiménez 2021) and on the Spanish Catalogue of Species of Concern (RD 139/2011). Several threats dominated by anthropogenic pressures have contributed to its decline, but the potential population consequences of avian malaria remain unknown. In fact, only Pérez-Rodríguez et al. (2013) assessed haemosporidian patterns and diversity in Spanish red kites. The fact that *P. relictum* is now shown to infect this species raises speculation about its potential impacts on vulnerable populations that are not recovering.

In Spain, the bearded vulture is designated as "Endangered" and both Egyptian and cinereous vultures as "Vulnerable" (RD 139/2011). Because they are priority species of concern, policymakers and technicians are required to design conservation measures to improve their habitat and populations. Within the framework of national law 42/2007 (Directive 92/43/CEE and 2009/147/CE), negative population trends reported in these species have led to the implementation of Recovery Plans (bearded vulture and red kite) or Conservation Plans (Egyptian and cinereous vultures), which should diagnose and assess the main threats for each species, including health status. Anthropogenic pressures at multiple threat levels have driven the obligate scavenger guild to a critical global state (Margalida and Ogada 2018; McClure et al. 2018). However, the potential impact and population consequences avian malaria may cause in these populations remain unknown, despite the notorious devastating precedents observed in some wild populations and European zoo-kept birds—including lethal disease of captive birds (Olias et al. 2011; Meister et al. 2021). This knowledge gap clearly points to the urgent need for further research on parasite ecology to better understand avian malaria patterns and parasite/vector richness and distribution in this critically endangered guild.

In the Pyrenees, weather conditions have traditionally been considered suboptimal for the presence of suitable vectors. However, both *Haemoproteus* and *Leucocytozoon* spp. infections have recently been reported in the endangered Pyrenean capercaillie, a species with restricted habitat in high-altitude (e.g., from >2000 m a.s.l.) forests (Nicolás de Francisco et al. 2023). In fact, altitudes around 2000 m may still provide favorable summer conditions for some vector groups, such as blackflies and biting midges, particularly when forest desiccation is not an issue and low temperatures do not limit insect development—as is likely the case in much of Spain. Although *Haemoproteus* spp. are cosmopolitan and often occur in high prevalence (Valkiūnas 2005; Clark et al. 2014), we did not detect infection by this genus. Further, preliminary research suggests the presence of vectors (e.g., sand flies and *Culex* mosquitoes) in bearded vulture territories located at >2000 m a.s.l., and especially in higher abundance at lower altitudes in the Pre-Pyrenees, infected with *P. relictum* and *P. vaughani* and other emerging pathogens such as the West Nile Virus (González-Serrano et al. 2019). This demonstrates the presence of suitable vectors (including common mosquitoes) in mountain environments that are often assumed to be less favorable for these insects (but see Loureiro et al. 2024), particularly during the chick-rearing period. Our outcomes, therefore, highlight that suitable *Leucocytozoon* and *Plasmodium* vectors may be present even at high altitudes, potentially facilitated by current environmental conditions, including rapid climate changes and global warming (Chapa-Vargas et al. 2020).

5 | Conclusions

Our first assessment of molecular prevalence and genetic diversity of avian malaria parasites in European scavenger birds provides novel findings of significant conservation interest, showing (i) infection across all six avian scavenger species examined, (ii) several new *host–parasite* interactions (e.g., 10 new records of lineages in different avian scavenger species apart from their documented hosts to date), as well as (iii) a new *Leucocytozoon* lineage (lGYPBAR01) infecting all European vultures except the griffon vulture. Our investigation is also the first to report the presence of pMILANS05 in a red kite nestling, pRTSR1 in an adult Egyptian vulture, and, notably, *P. relictum* (lineage pSGS1)—a cosmopolitan malaria parasite listed by the IUCN as one of the 100 worst invasive species worldwide due to its devastating effects on native avifauna when established outside its natural range—in an adult red kite. Although we detected different haemosporidian lineages among obligate and facultative species, our results suggest that a scavenging diet alone is unlikely to determine infection risk. Instead, other species-specific ecological traits—such as feeding site use, degree of aggregation, social versus solitary behavior, or migratory habits—may modulate the likelihood of infection in this guild. We highlight that rising temperatures may increase the occurrence, distribution, and intensity of avian malaria and its vectors. Our findings will contribute to the understanding of avian malaria in European obligate and facultative scavenger birds and encourage further research on parasite ecology and dynamics in this endangered guild in the current scenario of global warming.

Acknowledgments

We are especially grateful to the Government of Aragón (M. Alcántara), Generalitat of Catalonia (R. Casanovas and D. García), and Diputación Foral de Gipuzkoa (I. Mendiola and A. Lekuona) for providing support and permissions. We are also indebted to J. L. Rivas, J. Sanz, J. C. Albero, J. A. Sesé, A. Giménez, Paquito, O. Boneta, Tonet, J. M. Martínez, M. Olano, J. Vázquez, J. Ugarte, I. Artola, I. Zubeldia, E. Iriarte, and forest rangers in Aragon, Catalonia, and Basque Country for cooperating and contributing during fieldwork and helping with the capture of the birds. We also thank GREFA, TRENCA, and GACO institutions, who partially contributed to the collection of samples. P.O.-V. was supported by a postdoctoral project (PID2022-142328OB-I00). J.M. was supported by a postdoctoral grant from the Juan de la Cierva Subprogram (FJCI 2017-34109), with the financial sponsorship of the MICINN. J.M. was also supported during later analytical and write-up phases by a Marie Skłodowska-Curie Actions Postdoctoral Fellowship (grant agreement no. 101063149). This study was supported by the Ministry of Science and Innovation (project PID2022-142328OB-I00) and by line of action LA4 (R + D + I program in the Biodiversity Area financed with the funds of the FEDER Extremadura 2021–2027 Operational Program of the Recovery, Transformation and Resilience Plan). We also thank the technical and human support provided by the Facility of Bioscience Applied Techniques of SAIUEx (financed by UEX, Junta de Extremadura, MICINN, FEDER and FSE). Nayden Chakarov and an anonymous reviewer made helpful comments on earlier versions of the manuscript.

References

Arévalo-Ayala, D. J., J. Real, C. Durà, J. Aymerich, and A. Hernández-Matías. 2023. "Reduction of Organic Waste in a Landfill Lowers the Visitation Probability but Not the Local Abundance of a Long-Lived Scavenger Species." *Bird Conservation International* 33: e15.

Asghar, M., V. Yman, M. V. Homann, et al. 2018. "Cellular Aging Dynamics After Acute Malaria Infection: A 12-Month Longitudinal Study." *Aging Cell* 17: e12702.

Atkinson, C. T., R. J. Dusek, and J. K. Lease. 2001. "Serological Responses and Immunity to Superinfection with Avian Malaria in Experimentally-Infected Hawaii Amakihi." *Journal of Wildlife Diseases* 37: 20–27.

Atkinson, C. T., and D. A. LaPointe. 2009. "Introduced Avian Diseases, Climate Change, and the Future of Hawaiian Honeycreepers." *Journal of Avian Medicine and Surgery* 23: 53–63.

BirdLife International. 2021. *European Red List of Birds*. Publications Office of the European Union.

Beasley, J. C., Z. H. Olson, N. Selva, and T. L. DeVault. 2019. "Ecological Functions of Vertebrate Scavenging." In *Carrion Ecology and Management*, edited by P. Olea, P. Mateo-Tomás, and J. A. Sánchez-Zapata, 125–157. Wildlife Research Monographs. Springer.

Bensch, S., O. Hellgren, and J. Pérez-Tris. 2009. "MalAvi: A Public Database of Malaria Parasites and Related Haemosporidians in Avian Hosts Based on Mitochondrial Cytochrome *b* Lineages." *Molecular Ecology Resources* 9: 1353–1358.

Bensch, S., J. Pérez-Tris, J. Waldenström, and O. Hellgren. 2004. "Linkage Between Nuclear and Mitochondrial DNA Sequences in Avian Malaria Parasites: Multiple Cases of Cryptic Speciation?" *Evolution* 58: 1617–1621.

Blanco, G., A. Gajón, G. Doval, and F. Martínez. 1998. "Absence of Blood Parasites in Griffon Vultures from Spain." *Journal of Wildlife Diseases* 34: 640–643.

Blumstein, D. T., T. N. Rangchi, T. Briggs, F. S. De Andrade, and B. Natterson-Horowitz. 2017. "A Systematic Review of Carrion Eaters' Adaptations to Avoid Sickness." *Journal of Wildlife Diseases* 53: 577–581.

Bukauskaitė, D., C. R. F. Chagas, M. Duc, M. Kazak, and R. Treinys. 2024. "Prevalence and Local Transmission of Haemosporidian (Haemosporida) Parasites in Nestlings of Birds of Prey (Aves, Accipitriformes) in the Temperate Forests in Lithuania." *International Journal for Parasitology: Parasites and Wildlife* 25: 101013.

Chakarov, N., and G. Blanco. 2021. "Blood Parasites in Sympatric Vultures: Role of Nesting Habits and Effects on Body Condition." *International Journal of Environmental Research and Public Health* 18: 2431.

Clayton, D. H., J. A. H. Koop, C. W. Harbison, B. R. Moyer, and S. E. Bush. 2010. "How Birds Combat Ectoparasites." *The Open Ornithology Journal* 3: 41–71.

Clark, N. J., S. M. Clegg, and M. R. Lima. 2014. "A Review of Global Diversity in Avian Haemosporidians (*Plasmodium* and *Haemoproteus:* Haemosporida): New Insights from Molecular Data." *International Journal for Parasitology* 44: 329–338.

Coeurdassier, M., N. Bassin, T. Powolny, C. Morin, and E. Afonso. 2021. "Prevalence of Hematozoan Parasites in Red Kite Nestlings from France." *Journal of Ornithology* 162: 521–527.

Cruz, J. T., L. M. de Carvalho, M. R. Ferreira, C. Nunes, M. Casero, and A. Marzal. 2024. "Avian Haemosporidian Infection in Wildlife Rehabilitation Centres of Portugal: Causes, Consequences, and Genetic Diversity." *Animals* 14: 1216.

Darbro, J. M., and L. C. Harrington. 2007. "Avian Defensive Behavior and Blood-Feeding Success of the West Nile Vector Mosquito, *Culex pipiens*." *Behavioral Ecology* 18: 750–757.

Dimitrov, D., V. Palinauskas, T. A. Iezhova, et al. 2015. "*Plasmodium* spp.: An Experimental Study on Vertebrate Host Susceptibility to Avian Malaria." *Experimental Parasitology* 148: 1–16.

Dobson, A., and J. Foufopoulos. 2001. "Emerging Infectious Pathogens of Wildlife." *Philosophical Transactions of the Royal Society B: Biological Sciences* 356: 1001–1012.

Donázar, J. A., A. Margalida, M. Carrete, and J. A. Sánchez-Zapata. 2009. "Too Sanitary for Vultures." *Science* 326: 664–664.

Fecchio, A., K. Wells, J. A. Bell, et al. 2019. "Climate Variation Influences Host Specificity in Avian Malaria Parasites." *Ecology Letters* 22: 547–557.

Fernández-Gómez, L., A. Cortés-Avizanda, E. Arrondo, et al. 2022. "Vultures Feeding on the Dark Side: Current Sanitary Regulations May Not be Enough." *Bird Conservation International* 32: 590–608.

Ferraguti, M., C. Hernández-Lara, R. Sehgal, and D. Santiago-Alarcon. 2020. "Anthropogenic Effects on Avian Haemosporidians and Their vectors." In *Malaria and Related Parasites in the Tropics*., 451–485. Springer International Publishing.

Forsman, D. 2016. "*Flight Identification of Raptors of Europe, North Africa and the Middle East: A Handbook of Field Identification*." Bloomsbury Publishing PLC.

Garamszegi, L. Z. 2011. "Climate Change Increases the Risk of Malaria in Birds." *Global Change Biology* 17: 1751–1759.

García-del-Río, M., R. Sancho, J. Martínez, and S. Merino. 2021. "Blood Parasite Infections in Strigiformes and Psittaciformes Species in Captivity with a New Record of Potential Fatal Blood Parasite Transmission to Parrots." *Journal of Zoo and Wildlife Medicine* 51: 799–813.

García-Jiménez, R., J. M. Pérez-García, A. Margalida, and Z. Morales-Reyes. 2022. "Avian Scavengers' Contributions to People: The Cultural Dimension of Wildlife-Based Tourism." *Science of the Total Environment* 806: 150419.

Garcia-Longoria, L., A. Marzal, F. De Lope, and L. Garamszegi. 2019. "*Host–Parasite* Interaction Explains Variation in the Prevalence of Avian Haemosporidians at the Community Level." *PLoS ONE* 14: e0205624.

García-Macía, J., M. Gálvez, G. Plana, et al. 2023. "Analysis of the Trans-Saharan Migration and Wintering Areas of GPS-Tagged Cinereous Vultures *Aegypius monachus*." *Bird Study* 70: 289–294.

Chapa-Vargas, L., N. E. Matta, and S. Merino. 2020. "Effects of Ecological Gradients on Tropical Avian Hemoparasites." In *Avian Malaria and Related Parasites in the Tropics: Ecology, Evolution and Systematics*, edited by D. Santiago-Alarcon and A. Marzal, 349–377. Springer.

Ferraguti, M., J. Martínez-de la Puente, S. Bensch, et al. 2018. "Ecological determinants of avian malaria infections: An integrative analysis at landscape, mosquito and vertebrate community levels." *Journal of Animal Ecology* 87: 727–740. https://doi.org/10.1111/1365-2656.12805.

Garnham, P. C. C. 1966. "*Malaria Parasites and Other Haemosporidia*." Blackwell Scientific Publications.

González-Serrano, P., I. G. Fernández de Mera, S. Delacour, et al. 2019. "Mosquito Vectors and Mosquito Transmitted Pathogens in Bearded Vulture (*Gypaetus barbatus*) Breeding Territories." European Vulture Conference, Algarve, Portugal, Spain, October 1–4.

Greiner, E. C., and P. J. Mundy. 1979. "Hematozoa from Southern African Vultures, with a Description of *Haemoproteus janovyi* sp. n." *The Journal of Parasitology* 65: 147–153.

Griffiths, R., M. C. Double, K. Orr, and R. J. Dawson. 1998. "A DNA Test to Sex Most Birds." *Molecular Ecology* 7: 1071–1075.

Harl, J., T. Himmel, G. Valkiūnas, et al. 2022. "Avian Haemosporidian Parasites of Accipitriform Raptors." *Malaria Journal* 21: 14.

Hellgren, O., J. Waldenström, and S. Bensch. 2004. "A New PCR Assay for Simultaneous Studies of *Leucocytozoon*, *Plasmodium*, and *Haemoproteus* from Avian Blood." *Journal of Parasitology* 90: 797–802.

Herrero-Villar, M., M. A. Taggart, and R. Mateo. 2023. "Medicated Livestock Carcasses and Landfill Sites: Sources of Highly Toxic Veterinary Pharmaceuticals and Caffeine for Avian Scavengers." *Journal of Hazardous Materials* 459: 132195.

Ishak, H. D., J. P. Dumbacher, N. L. Anderson, et al. 2008. "Blood Parasites in Owls with Conservation Implications for the Spotted Owl (*Strix occidentalis*)." *PLoS ONE* 3: e2304.

Kearse, M., R. Moir, A. Wilson, et al. 2012. "Geneious Basic: An Integrated and Extendable Desktop Software Platform for the Organization and Analysis of Sequence Data." *Bioinformatics* 28: 1647–1649.

Križanauskienė, A., O. Hellgren, V. Kosarev, L. Sokolov, S. Bensch, and G. Valkiūnas. 2006. "Variation in Host Specificity Between Species of Avian Hemosporidian Parasites: Evidence from Parasite Morphology and Cytochrome *B* Gene Sequences." *Journal of Parasitology* 92: 1319–1324.

Koprivnikar, J., and T. L. Leung. 2015. "Flying with Diverse Passengers: Greater Richness of Parasitic Nematodes in Migratory Birds." *Oikos* 124: 399–405.

Krone, O., J. Waldenström, G. Valkiūnas, et al. 2008. "Haemosporidian Blood Parasites in European Birds of Prey and Owls." *Journal of Parasitology* 94: 709–715.

Kuo, C. H., and J. C. Kissinger. 2008. "Consistent and Contrasting Properties of Lineage-Specific Genes in the Apicomplexan Parasites *Plasmodium* and *Theileria*." *BMC Evolutionary Biology* 8: 108.

Lambertucci, S. A., A. Margalida, K. L. Speziale, et al. 2021. "Presumed Killers? Vultures, Stakeholders, Misperceptions and Fake News." *Conservation Science and Practice* 3: e415.

LaPointe, D. A., C. T. Atkinson, and M. D. Samuel. 2012. "Ecology and Conservation Biology of Avian Malaria." *Annals of the New York Academy of Sciences* 1249: 211–226.

López-Jiménez, N. 2021. *Libro Rojo de las Aves de España*. SEO/BirdLife.

Loureiro, F., L. Cardoso, A. Matos, M. Matos, and A. C. Coelho. 2024. "West Nile Virus in Vultures from Europe—A Sight Among Other Raptors." *Slovenian Veterinary Research/Slovenski Veterinarski Zbornik* 61: 233–244.

Margalida, A., J. A. Donázar, M. Carrete, and J. A. Sánchez-Zapata. 2010. "Sanitary Versus Environmental Policies: Fitting Together Two Pieces of the Puzzle of European Vulture Conservation." *Journal of Applied Ecology* 47: 931–935.

Margalida, A., and R. Mateo. 2019. "Illegal Killing of Birds in Europe Continues." *Science* 363: 1161–1161.

Margalida, A., and D. Ogada. 2018. "Old World Vultures in a Changing Environment." In *Raptor Ecology and Conservation*, edited by J. H. Sarasola, J. M. Grande, and J. J. Negro, pp. 457–471. Springer.

Margalida, A., and P. Oliva-Vidal. 2017. "The Shadow of Diclofenac Hangs Over European Vultures." *Nature Ecology & Evolution* 1: 1050–1050.

Margalida, A., P. Oliva-Vidal, A. Llamas, and M. À. Colomer. 2018. "Bioinspired Models for Assessing the Importance of Transhumance and Transboundary Management in the Conservation of European Avian Scavengers." *Biological Conservation* 228: 321–330.

Martínez de la Puente, J., S. Merino, G. Tomás, et al. 2010. "The Blood Parasite *Haemoproteus* Reduces Survival in a Wild Bird: A Medication Experiment." *Biology Letters* 6: 663–665.

Martínez-de la Puente, J., D. Santiago-Alarcon, V. Palinauskas, and S. Bensch. 2021. "Plasmodium relictum." *Trends in Parasitology* 37: 355–356.

Marzal, A., F. D. Lope, C. Navarro, and A. P. Møller. 2005. "Malarial Parasites Decrease Reproductive Success: An Experimental Study in a Passerine Bird." *Oecologia* 142: 541–545.

Marzal, A., L. García-Longoria, J. M. Cárdenas Callirgos, and R. N. M. Sehgal. 2015. "Invasive Avian Malaria as an Emerging Parasitic Disease in Native Birds of Peru." *Biological Invasions* 17: 39–45.

Mata, V. A., L. P. da Silva, R. J. Lopes, and S. V. Drovetski. 2015. "The Strait of Gibraltar Poses an Effective Barrier to Host-Specialised but Not to Host-Generalised Lineages of Avian Haemosporidia." *International Journal for Parasitology* 45: 711–719.

McClure, C. J. W., J. R. S. Westrip, J. A. Johnson, et al. 2018. "State of the World's Raptors: Distributions, Threats, and Conservation Recommendations." *Biological Conservation* 227: 390–402.

Meister, S. L., O. K. Richard, S. Hoby, C. Gurtner, and W. U. Basso. 2021. "Fatal Avian Malaria in Captive Atlantic Puffins (*Fratercula arctica*) in Switzerland." *International Journal for Parasitology: Parasites and Wildlife* 14: 97–106.

Mendes, L., S. Pardal, J. Morais, et al. 2013. "Hidden Haemosporidian Infections in Ruffs (*Philomachus pugnax*) Staging in Northwest Europe en Route From Africa to Arctic Europe." *Parasitology Research* 112: 2037–2043.

Merino, S., J. Moreno, J. José Sanz, and E. Arriero. 2000. "Are Avian Blood Parasites Pathogenic in the Wild? A Medication Experiment in Blue Tits

(*Parus caeruleus*).” *Proceedings of the Royal Society of London Series B: Biological Sciences* 267: 2507–2510.

Monclús, L., R. F. Shore, and O. Krone. 2020. “Lead Contamination in Raptors in Europe: A Systematic Review and Meta-Analysis.” *Science of the Total Environment* 748: 141437.

Moraga-Fernández, A., P. Oliva-Vidal, M. Sánchez-Sánchez, et al. 2023. “Health Risks Associated with Argasid Ticks, Transmitted Pathogens, and Blood Parasites in Pyrenean Griffon Vulture (*Gyps fulvus*) Nestlings.” *European Journal of Wildlife Research* 69: 112.

Moreno-Opo, R., A. Trujillano, and A. Margalida. 2015. “Optimization of Supplementary Feeding Programs for European Vultures Depends on Environmental and Management Factors.” *Ecosphere* 6, no. 7: 1–15.

Muriel, J. 2020. “Ecophysiological Assessment of Blood Haemosporidian Infections in Birds.” *Ecosistemas* 29: 1979.

Muriel, J., J. A. Graves, D. Gil, et al. 2018. “Molecular Characterization of Avian Malaria in the Spotless Starling (*Sturnus unicolor*).” *Parasitology Research* 117: 919–928.

Njabo, K. Y., A. J. Cornel, C. Bonneaud, et al. 2011. “Nonspecific Patterns of Vector, Host and Avian Malaria Parasite Associations in a Central African Rainforest.” *Molecular Ecology* 20: 1049–1061.

Navarro, C. 2004. “Predation Risk, Host Immune Response, and Parasitism.” *Behavioral Ecology* 15: 629–635.

Nicolás de Francisco, O., I. Sacristán, A. C. Ewbank, et al. 2023. “First Detection of Herpesvirus and Hemosporidians in the Endangered Pyrenean Capercaillie (*Tetrao urogallus aquitanicus*).” *Scientific Reports* 13: 21936.

Nourani, L., S. Zakeri, and N. Dinparast Djadid. 2020. “Dynamics of Prevalence and Distribution Pattern of Avian *Plasmodium* Species and Its Vectors in Diverse Zoogeographical Areas—A Review.” *Infection, Genetics and Evolution* 81: 104244.

Olias, P., M. Wegelin, W. Zenker, S. Freter, A. D. Gruber, and R. Klopfleisch. 2011. “Avian Malaria Deaths in Parrots, Europe.” *Emerging Infectious Diseases* 17: 950.

Oliva-Vidal, P. 2023. “Avian Scavengers in a Changing World: A Multidisciplinary Conservation Approach in the Pyrenees.” PhD thesis, University of Lleida.

Oliva-Vidal, P., A. Hernández-Matías, D. García, M. À. Colomer, J. Real, and A. Margalida. 2022c. “Griffon Vultures, Livestock and Farmers: Unraveling a Complex Socio-economic Ecological Conflict From a Conservation Perspective.” *Biological Conservation* 272: 109664.

Oliva-Vidal, P., J. M. Martínez, I. S. Sánchez-Barbudo, et al. 2022a. “Second-Generation Anticoagulant Rodenticides in the Blood of Obligate and Facultative European Avian Scavengers.” *Environmental Pollution* 315: 120385.

Oliva-Vidal, P., E. Sebastián-González, and A. Margalida. 2022b. “Scavenging in Changing Environments: Woody Encroachment Shapes Rural Scavenger Assemblages in Europe.” *Oikos* 2022: e09310.

Oliva-Vidal, P., D. Villalba, M. À. Colomer, and A. Margalida. 2024. “Heterospecific Visual Cues and Trophic Facilitation Processes Used by a Solitary Bone-eating Vulture.” *Ecosphere* 15: e4941.

Owen, J. C., D. M. Hawley, and K. P. Huyvaert. 2021. “Infectious Disease Ecology of Wild Birds.” In *Infectious Disease Ecology of Wild Birds*. Oxford University Press.

Palinauskas, V., G. Valkiūnas, C. V. Bolshakov, and S. Bensch. 2011. “*Plasmodium relictum* (lineage SGS1) and *Plasmodium ashfordi* (lineage GRW2): The Effects of the Co-Infection on Experimentally Infected Passerine Birds.” *Experimental Parasitology* 127: 527–533.

Pérez-Rodríguez, A., I. de la Hera, S. Fernández-González, and J. Pérez-Tris. 2014. “Global Warming Will Reshuffle the Areas of High Prevalence and Richness of Three Genera of Avian Blood Parasites.” *Global Change Biology* 20: 2406–2416.

Pérez-Rodríguez, A., J. de la Puente, A. Onrubia, and J. Pérez-Tris. 2013. “Molecular Characterization of Haemosporidian Parasites from Kites of the Genus *Milvus* (Aves: Accipitridae).” *International Journal for Parasitology* 43: 381–387.

Pitarch, A., C. Gil, and G. Blanco. 2020. “Vultures From Different Trophic Guilds Show Distinct Oral Pathogenic Yeast Signatures and Co-Occurrence Networks.” *Science of the Total Environment* 723: 138166.

Plaza, P. I., G. Blanco, and S. A. Lambertucci. 2020. “Implications of Bacterial, Viral and Mycotic Microorganisms in Vultures for Wildlife Conservation, Ecosystem Services and Public Health.” *Ibis* 162: 1109–1124.

Qasim, M., H. Xiao, K. He, et al. 2020. “Impact of Landfill Garbage on Insect Ecology and Human Health.” *Acta Tropica* 211: 105630.

R Core Team. 2019. “*R: A Language and Environment for Statistical Computing*.” R Foundation for Statistical Computing.

Ramírez, J., J. Elorriaga, and A. de la Cruz. 2022. “Cinereous Vulture *Aegypius monachus* Movements Between Europe and Africa Show a Pattern Across the Strait of Gibraltar.” *Ostrich* 93: 151–156.

Remple, J. D. 2004. “Intracellular Hematozoa of Raptors: A Review and Update.” *Journal of Avian Medicine and Surgery* 18: 75–88.

Ricklefs, R. E., and S. M. Fallon. 2002. “Diversification and Host Switching in Avian Malaria Parasites.” *Proceedings of the Royal Society of London Series B: Biological Sciences* 269: 885–892.

Roggenbuck, M., I. Bærholm Schnell, N. Blom, et al. 2014. “The Microbiome of New World Vultures.” *Nature Communications* 5: 5498.

Safford, R., J. Andevski, A. Botha, et al. 2019. “Vulture Conservation: The Case for Urgent Action.” *Bird Conservation International* 29: 1–9.

Sangkachai, N., B. Gummow, O. Hayakijkosol, S. Suwanpakdee, and A. Wiratsudakul. 2024. “A Review of Risk Factors at the Human-Animal-Environmental Interface of Garbage Dumps That Are Driving Current and Emerging Zoonotic Diseases.” *One Health* 19: 100915.

Santangeli, A., S. A. Lambertucci, A. Margalida, et al. 2024. “The Global Contribution of Vultures Towards Ecosystem Services and Sustainability: An Experts’ Perspective.” *iScience* 27: 109925.

Santiago-Alarcon, D., and A. Marzal. 2020. *Avian Malaria and Related Parasites in the Tropics: Ecology, Evolution and Systematics*.Springer.

Santiago-Alarcon, D., D. C. Outlaw, R. E. Ricklefs, and P. G. Parker. 2010. “Phylogenetic Relationships of Haemosporidian Parasites in New World Columbiformes, with Emphasis on the Endemic Galapagos Dove.” *International Journal for Parasitology* 40: 463–470.

Santiago-Alarcon, D., V. Palinauskas, and H. M. Schaefer. 2012. “Diptera Vectors of Avian Haemosporidian Parasites: Untangling Parasite Life Cycles and Their Taxonomy.” *Biological Reviews* 87: 928–964.

Schmid-Hempel, P. 2021. *Evolutionary Parasitology: The Integrated Study of Infections, Immunology, Ecology, and Genetics*. 2nd ed. Oxford University Press.

Schoenle, L. A., I. Schoepf, N. M. Weinstein, I. T. Moore, and F. Bonier. 2018. “Higher Plasma Corticosterone Is Associated with Reduced Costs of Infection in Red-Winged Blackbirds.” *General and Comparative Endocrinology* 256: 89–98.

Sebastián-González, E., Z. Morales-Reyes, F. Botella, et al. 2021. “Functional Traits Driving Species Role in the Structure of Terrestrial Vertebrate Scavenger Networks.” *Ecology* 102: e03519.

Serrano, D., A. Margalida, J. M. Pérez-García, et al. 2020. “Renewables in Spain Threaten Biodiversity.” *Science* 370: 1282–1283.

Subaneg, S., R. Sitdhibutr, P. Pornpanom, et al. 2024. “Molecular Prevalence and Haematological Assessments of Avian Malaria in Wild Raptors of Thailand.” *Birds* 5: 428–439.

Tamayo-Quintero, J., M. San-José, J. Martínez-de la Puente, C. González-Quevedo, and H. F. Rivera-Gutierrez. 2025. “It’s All About Scale: The Landscape Effect on Avian Haemosporidians.” *Science of the Total Environment* 962: 178426.

Tauler-Ametller, H., A. Hernández-Matías, F. Parés, J. L. Pretus, and J. Real. 2018. "Assessing the Applicability of Stable Isotope Analysis to Determine the Contribution of Landfills to Vultures' Diet." *PLoS ONE* 13: e0196044.

Tauler-Ametller, H., A. Hernández-Matías, J. L. Pretus, and J. Real. 2017. "Landfills Determine the Distribution of an Expanding Breeding Population of the Endangered Egyptian Vulture *Neophron percnopterus*." *Ibis* 159: 757–768.

Tauler-Ametlller, H., J. L. Pretus, A. Hernández-Matías, M. E. Ortiz-Santaliestra, R. Mateo, and J. Real. 2019. "Domestic Waste Disposal Sites Secure Food Availability but Diminish Plasma Antioxidants in Egyptian Vulture." *Science of the Total Environment* 650: 1382–1391.

Tella, J. L., G. Blanco, M. G. Forero, Á. Gajón, J. A. Donázar, and F. Hiraldo. 1999. "Habitat, World Geographic Range, and Embryonic Development of Hosts Explain the Prevalence of Avian Hematozoa at Small Spatial and Phylogenetic Scales." *Proceedings of the National Academy of Sciences* 96: 1785–1789.

Tobajas, J., J. J. Iglesias-Lebrija, É. Delepoulle, E. Álvarez, P. Oliva-Vidal, and A. Margalida. 2024. "Movement Ecology of Pre-Adult Cinereous Vultures *Aegypius monachus:* Insights from a Reintroduced Population." *Bird Conservation International* 34: e17.

Tompkins, D. M., S. Carver, M. E. Jones, M. Krkošek, and L. F. Skerratt. 2015. "Emerging Infectious Diseases of Wildlife: A Critical Perspective." *Trends in Parasitology* 31: 149–159.

Valenzuela-Sánchez, A., M. Q. Wilber, S. Canessa, et al. 2021. "Why Disease Ecology Needs Life-History Theory: A Host Perspective." *Ecology Letters* 24: 876–890.

Valkiunas, G. 2005. *Avian Malaria Parasites and Other Haemosporidia*. CRC Press.

Valkiūnas, G., and C. T. Atkinson. 2020. "Introduction to Life Cycles, Taxonomy, Distribution, and Basic Research Techniques." In *Avian Malaria and Related Parasites in the Tropics: Ecology, Evolution and Systematics*, edited by D. Santiago-Alarcon, and A. Marzal, 45–80. Springer.

Valkiūnas, G., M. Ilgūnas, D. Bukauskaitė, et al. 2018. "Characterization of *Plasmodium relictum*, a Cosmopolitan Agent of Avian Malaria." *Malaria Journal* 17: 184.

van Overveld, T., G. Blanco, M. Moleón, et al. 2020. "Integrating Vulture Social Behavior into Conservation Practice." *The Condor* 122: duaa035.

van Riper, C., S. G. van Riper, M. L. Goff, and M. Laird. 1986. "The Epizootiology and Ecological Significance of Malaria in Hawaiian Land Birds." *Ecological Monographs* 56: 327–344.

Viana, D. S., L. Santamaría, and J. Figuerola. 2016. "Migratory Birds as Global Dispersal Vectors." *Trends in Ecology & Evolution* 31: 763–775.

Villar Couto, C. M., G. S. Cumming, G. A. Lacorte, et al. 2019. "Avian Haemosporidians in the Cattle Egret (*Bubulcus ibis*) from Central-Western and Southern Africa: High Diversity and Prevalence." *PLoS ONE* 14: e0212425.

Wilkinson, L. 2011. "ggplot2: Elegant Graphics for Data Analysis by WICKHAM, H." *Biometrics* 67: 678–679.

Wiegmann, A., A. Springer, T. Rinaud, et al. 2021. "The Prevalence of *Leucocytozoon* spp. in Nestlings of Three Wild Raptor Species Including Implications on Haematological and Blood Chemistry Values." *International Journal for Parasitology: Parasites and Wildlife* 16: 236–243.

Yabsley, M. J., R. E. T. Vanstreels, E. S. Martinsen, et al. 2018. "Parasitaemia Data and Molecular Characterization of *Haemoproteus catharti* from New World Vultures (Cathartidae) Reveals a Novel Clade of *Haemosporida*." *Malaria Journal* 17: 12.

Yu, G., D. K. K. Smith, H. Zhu, Y. Guan, and T. Lam. 2017. "ggtree: An R Package for Visualization and Annotation of Phylogenetic Trees with Their Covariates and Other Associated Data." *Methods in Ecology and Evolution* 8: 28–36.

Zerek, A., I. Erdem, H. Alakuş, M. Yaman, and M. E. Altuğ. 2023. "Prevalence of *Haemoproteus* and *Leucocytozoon* spp. in Wild Birds in Hatay, Turkey." *Journal of the Hellenic Veterinary Medical Society* 74: 5651–5656.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.

TABLE S1 Diversity of the three haemosporidian parasite genera (*Haemoproteus*, *Leucocytozoon* and *Plasmodium*) that have been globally reported as causative agents of avian malaria in the world's 23 vulture species inhabiting both the Old and New (colored in gray) World to date. **TABLE S2** Sampled individuals ($n = 383$) by species, age and sex. **TABLE S3** Prevalence values (in percentage) of haemosporidian parasites including the three genera tested according to the age classes (i.e., nestling, juvenile, subadult and adult) found in the blood of free-living obligate (griffon, cinereous, bearded and Egyptian vultures) and facultative (red and black kite) avian scavengers sampled in NE (Pyrenees, Pre-Pyrenees) and central (Toledo) Spain during the period 2017–2022.