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Biological Sciences

Parasitism in wild penguin populations: a comprehensive global assessment of macro- and microparasites and their implications

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Abstract

Penguins include 18 species of seabirds distributed in the Southern Hemisphere. Climate change is a growing problem that affects penguins, especially those living in Antarctica, making them some of the most currently endangered species. Loss of habitat, commercial fishing and infectious diseases spread by anthropogenic activities in the Southern Ocean are threats facing penguins. In addition, environmental changes affect the distribution of free-living species that act as intermediate hosts for parasites (e.g. krill, fish) and consequently their transmission dynamics and distribution. The present work aims to provide an update on macro- and microparasites recorded in all penguin species in wildlife. Based on published records from penguins, we provide a list of 157 parasite taxa recorded in all penguin species. The list includes 54 helminths, 45 arthropods, 39 bacteria and 19 protozoa reported in 207 scientific publications. Most papers were focused on the genus *Spheniscus*. In the analysis, we identify the distribution of parasites among hosts to better predict the disease risk facing their populations worldwide. Some pathogenic effects of the parasites found are discussed.

Keywords: Conservation; parasites; pathogens; seabirds; Sphenisciformes

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Introduction

Penguins (Aves, Sphenisciformes) are a charismatic group of seabirds including 18 species that are widely distributed in the Southern Hemisphere. Their populations have pelagic habits, feeding at sea and returning to land to breed (Williams & Boersman 1995, Winkler *et al.* 2020). Currently, 12 of the 18 recognized penguin species are in a state of population decline (BirdLife International 2019). The main reasons for this decline are linked to anthropogenic factors such as climate change, habitat destruction, pollution, fisheries and diseases (Ropert-Couder *et al.* 2019).

Human activities are altering the functioning of ecosystems at an increasing rate, a phenomenon widely known as 'global change'. This phenomenon acts as a population modeller, impacting species distribution and predator/prey relationships (Hinke *et al.* 2017, Lee *et al.* 2022), while fisheries directly affect the availability of marine prey for penguins (Pauly & Zeller 2016). Another important consequence of environmental disturbances is the emergence of new diseases, which modify the dynamics and distribution ranges, abundance and/or virulence of parasites and pathogens, as well as their hosts' susceptibility and tolerance to infection (Altizer *et al.* 2013, Koprivnikar & Leung 2015). An example of this is the extremely rapid spread of highly pathogenic avian influenza (HPAI) at South Georgia from the first confirmed case on Bird Island on 23 October 2023 to numerous skuas, gulls, elephant seals and fur seals across the island group within weeks (https://scar.org/library-data/avian-flu). As such, the identification of high-risk pathogens, their reservoir hosts and the other host species that are most vulnerable to a diseased outbreak is of paramount importance.

Parasitism is considered among the most successful forms of life. Parasites comprise almost half of all described species and infect virtually all known taxa (Poulin & Morand 2000, Dobson *et al.* 2008). Infection by both macro- and microparasites provokes different immune responses in infected hosts (Hatcher & Dunn, 2011), and in many cases can alter their morphology (e.g. limb malformation, muscle mass, skeletal characteristics), physiology (e.g. immune response, deficiency in nutrient absorption) and behaviour (e.g. foraging behaviour, predator avoidance, mating; Clayton & Moore 1997, Merino *et al.* 2000, Gómez Díaz et al. 2012, Martin et al. 2016, Montero *et al.* 2016). Such infections can induce changes in the host population structure, dynamic and density (Poulin 2011) and, consequently, alter the dispersal patterns of migratory hosts (Binning *et al.* 2017, Hicks *et al.* 2018). Therefore, parasites are co-responsible for the abundance and diversity of organisms in ecosystems, and also for generating various defence mechanisms and behavioural traits in their hosts. For this reason, parasites play a decisive role in driving the evolutionary processes that take place on the planet (Dougherty *et al.* 2016).

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The study of parasites in wild penguins has been focused on the identification and distribution analysis of endemic parasite species and the possibility of detecting exotic parasites (Clarke & Kerry 2000, Barbosa & Palacios 2009). Monitoring the presence of parasites over time provides an overview of the pressures birds face and the actions that can be undertaken for their conservation and management. This is crucial for understanding whether climate change-related conditions increase the risk of pathogen introduction into pristine ecosystems, exposing penguins to new diseases (Grilo *et al.* 2016).

The last comprehensive review of the presence of parasites recorded or isolated from penguins worldwide was published in 1993 (Clarke & Kerry 1993). Subsequently, some updates on particular species or locations were published (e.g. Clarke & Kerry 2000, Barbosa & Palacios 2009, Brandão *et al.* 2014, Vanstreels *et al.* 2020). The number of parasites associated with penguins worldwide is probably higher than what is currently known, and for many species this information is fragmented across time and space (Diaz *et al.* 2017). Further research is therefore needed to understand their spatial and temporal transmission and comprehend how they affect penguin populations. This type of study will allow us to more accurately identify hosts with higher prevalence and richness of parasites, detect species requiring close monitoring and predict conditions under which increased pathogenicity or disease transmission occur.

The present work aims to provide an update on macro- and microparasites recorded for all penguin species in wildlife, as well their impact on host health, to analyse the disease risk facing penguin populations worldwide and to propose which penguin species and areas will be included in future health studies.

Methods

The species-level taxonomy and nomenclature for penguins used in this study are based on the Handbook of the Birds of the World (HBW) and BirdLife Taxonomic Checklist v4 (http://datazone.birdlife.org/species/taxonomy). Records of bacteria, protozoa, helminths and arthropods for each penguin species and localities were taken from the literature, such as peer-reviewed scientific papers and documents referenced in the Scopus, PubMed and Google Scholar databases up to January 2024. A database was generated associating all penguin species with each parasitic taxa found from the search. From the resulting database, graphs were made to express the number of published articles by penguin species and by parasite groups using *RStudio* version 1.3.959 (R Core Team 2020). Inferences were made regarding the geographical distribution of the parasites recorded in published articles. These data were compared with geographical information systems (GIS) using a cartographic projection: equirectangular (cylindrical equidistant or 'Plate carrée'); standard parallel: equator; sphere: WGS84; and geographical coordinate system (latitude/longitude; units: decimal degrees) for a study area analysis from the QGIS Development Team (2016) and SCAR Antarctic Digital Database (ADD) version 7.0 tools.

Results

This database was generated from 207 published articles. Publications cover all penguin species, although heterogeneously, as many of these publications covered more than one penguin species and more than one parasite species. All records related to macro- and microparasites are shown in Table S1. There is significant disparity in the publication percentages among the different genera, penguin species and parasites. Most contributions include data about parasites of the *Spheniscus* genus, followed by *Pygoscelis* and *Eudyptes*. The genera with the fewest publications on this topic were *Eudyptula*, *Aptenodytes* and *Megadyptes*.

The Magellanic penguin (*Spheniscus magellanicus*) stood out as the most extensively studied penguin. It is closely followed by the little penguin (*Eudyptula minor*) and gentoo penguin (*Pygoscelis papua*). On the other hand, the erect-crested penguin (*Eudyptes sclateri*) and the northern rockhopper penguin (*Eudyptes moseleyi*) are among the least studied species (Fig. 1). Regarding parasite groups, helminths are the most broadly studied, followed by arthropods (Fig. 2).

Parasite groups

Bacteria have been mainly reported in *Pygoscelis* penguins, while in species such as the king penguin (*Aptenodytes patagonicus*), the Magellanic penguin and the macaroni penguin (*Eudyptes chrysolophus*) a few such studies have been performed. *Campylobacter* and *Salmonella* were the most represented genera. In the Fiordland penguin (*Eudyptes pachyrhynchus*), northern rockhopper penguin, royal penguin (*Eudyptes schlegeli*) and Snares penguin (*Eudyptes robustus*) no bacterial studies were found.

Studies on protozoa are well represented among *Megadyptes*, *Eudyptula*, *Pygoscelis* and *Spheniscus*, while studies are scarce or absent regarding the emperor penguin (*Aptenodytes forsteri*) and *Eudyptes* species. *Plasmodium* was the most represented protozoan genus reported in almost all host species, with *Plasmodium relictum* Grassi & Feletti, 1891 being the species most frequently recorded. Coccidia, another well-represented group of protozoa, were documented in seven penguin species.

A total of 54 helminth species were reported on penguins, being 42.6% nematodes, 31.5% trematodes, 13.0% cestodes and 13.0% acanthocephalans. Many of them (23) were recorded in the Magellanic penguin, whereas there is no such information for the erect-crested penguin nor northern rockhopper penguin. The genus *Contracaecum* (Nematoda: Anisakidae) was represented by nine species, recorded in 11 penguin species, being the helminth genus with the greatest host distribution, followed by *Tetrabothrius* (Eucestoda: Tetrabothriidae), represented by five species recorded in 10 penguin species. Trematodes were found only in four penguin species, with *Cardiocephaloides* being the most represented genus. The acanthocephalans were represented mainly by the genus *Corynosoma*, in four species of penguins.

Arthropod is the only parasite group recorded in all penguin species and is the second most reported after helminths, with 45 identified species. Among these, 42% were chewing lice, 23% were ticks, 21% were mites and 14% were fleas. Little penguins and the Macaroni penguins had the highest number of records (14 and 11, respectively), while emperor penguins had the least (2). Lice were observed in all penguin species, with *Austrogonioides* being the most represented genus. Ticks were the second most prevalent ectoparasite group, present in all penguin species except the emperor penguin. The tick *Ixodes uriae* White 1852, being found in 13 penguin species, is the tick species with the widest distribution (Capasso *et al.* 2024).

Concerning the geographical distribution of macro- and microparasites, helminths exhibit a predominant number of reports in Patagonia and the Antarctic Peninsula (Fig. 3a), while arthropod reports are more prevalent in New Zealand (Fig. 3b). Trematodes is the only helminth group not recorded in penguins

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Figure 1. Numbers of publications reporting parasites in each penguin species. Colores represent each penguin genus.

from the Antarctic region. Bacteria records are most abundant in the Antarctic Peninsula, partially in Patagonia, and also in the New Zealand region (Fig. 3c). Protozoa display the broadest geographical range of records, with the highest incidence observed in the Galápagos Islands and Southern Africa (Fig. 3d).

Discussion

We found information on both macro- and microparasites in wild populations of all penguin species, although the number of publications varied significantly across the 18 species. This variability may be attributed to several factors, including penguin distribution, accessibility of colonies, colony size, regional research priorities, disciplines of researchers in each region and/or species-specific interests. In addition, variation in the research efforts can be directly related to each parasite group, including challenges regarding sampling, detection or identification. Based on the information obtained and considering the known effects that each parasite group has on these or other birds, we discuss the health risks faced by different penguin species. Subsequently, by analysing the geographical distribution of these records, we identify priority sampling areas and key penguin species to advance our understanding of host-parasite interactions and contribute to the conservation efforts of these birds.

Pathogenic effects

The scientific literature has documented various instances of massive mortality in birds caused by pathogens; however, the scenario is less clear for penguins (Kleyheeg *et al.* 2017, Walter *et al.* 2018), for which mass mortality events were not always attributed to a specific parasite or pathogen (Ropert-Coudert *et al.* 2019). All records concerning penguin mortality and pathogenesis are presented in Table I.

Bacteria can cause diverse pathological effects in penguins. Sporadic mass mortality events, such as those observed in the yellow-eyed penguin (*Megadyptes antipodes*) due to diphtheritic stomatitis caused by *Corynobacterium amycolatum*, have resulted in significant losses, and the population has taken several years to recover (Alley *et al.* 2017). Mortality events resulting from outbreaks of avian cholera (*Pasteurella multocida*) have been documented in the Adélie penguin (*Pygoscelis adeliae*) and the southern rockhopper penguin (*Eudyptes chrysocome*; Stidworthy 2018). Additionally, outbreaks of enterotoxaemia caused by *Clostridium* species have been associated with acute infections in penguins (Greenwood 2000). Although *Salmonella* was not associated with any mortality event in wild penguins, it is usually a cause of enteric disease, mainly under conditions of stress (Tizard 2004). Even though its pathogenic effects were not reported in penguins, it is known that *Rickettsia* generates different types of fevers, inflammation in the lymph nodes and muscle pain (Fournier & Raoult 2020), and *Borrelia* is the cause of Lyme disease in various vertebrates (Sürth *et al.* 2021), but their effects on penguins are still unclear.

Regarding blood protozoans, *Plasmodium* species are commonly found in free-living penguins, causing avian malaria, but without records of massive mortality events in the wild (Clarke & Kerry 1993, Atkinson 2008). Another concerning blood protozoan is *Babesia* species, which attack the cytoplasm of penguin erythrocytes (Schnittger *et al.* 2012) and have been

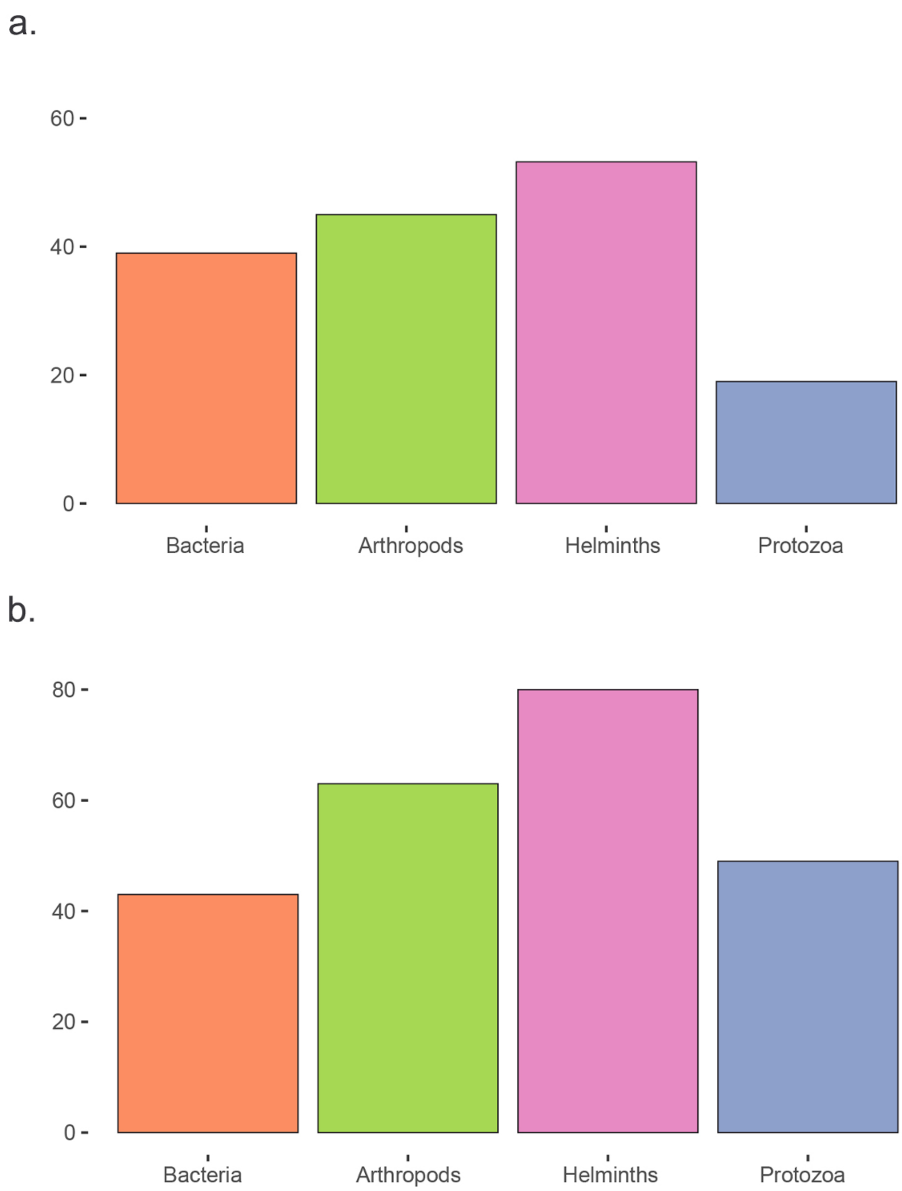

Figure 2. a. Numbers of parasite or pathogen species reported in all penguin species. **b.** Numbers of publications reporting each parasite or pathogen group in all penguin species.

recorded in the little penguin (Vanstreels *et al.* 2015) and chinstrap penguin (*Pygoscelis antarcticus*; Montero *et al.* 2016).

Helminths mainly infect the viscera of their hosts, and their degree of pathogenicity can be related to the type and abundance of parasites and the host immune system (Hoberg 2005). Anisakiasis, caused by a high number of anisakid nematodes in the stomachs of piscivorous birds, manifests in various clinical forms. In Humboldt penguins (*Spheniscus humboldti*), ulcerative gastric lesions have been associated with the presence of *Contracaecum pelagicum* (Oyarzún *et al.* 2012). Additionally, helminths such as *Parorchites zederi* and *Cardiocephaloides physalis* cause lacerations in the intestinal mucosa, affecting the absorption of nutrients (Horne *et al.* 2011, Martín *et al.* 2016). *Mawsonotrema eudyptulae* parasitizes the liver, causing necrosis and inflammation with subsequent loss of hepatic fluid and haemorrhage (Harrigan 1991). Members of *Renicola*, living in cyst-like structures within the kidney tubules, cause various renal lesions (Jerdy *et al.* 2016).

The effects of arthropod parasites on penguins have been less studied. The tick *I. uriae* is particularly important, impacting both the survival and reproductive capacity of penguin (McCoy *et al.* 2012). Ticks are also relevant for penguins as vectors of *Borrelia*, *Rickettsia* and *Babesia*, among other pathogens (Dietrich *et al.* 2011, Vanstreels *et al.* 2015, Duron *et al.* 2016, Montero *et al.* 2016). Certain lice species can transmit filariae nematodes, whose adult stage affects the heart and other tissues of the birds, causing filariasis (Clayton *et al.* 2008, Vanstreels *et al.* 2018a). Although no pathologies associated with *Rhinonysus* species have been reported in penguins to date, it is known that high concentrations can affect the trachea, lungs and body cavity in birds (Vanstreels *et al.* 2018b).

Potential risks and healthcare proposals

At present, five out of the 18 penguin species are globally classified as 'endangered' while 12 are experiencing declining numbers according to the IUCN Red List (https://www.iucnredlist.org/). It is crucial to prioritize health studies on species with small breeding distributions and low population sizes. By doing so, we will

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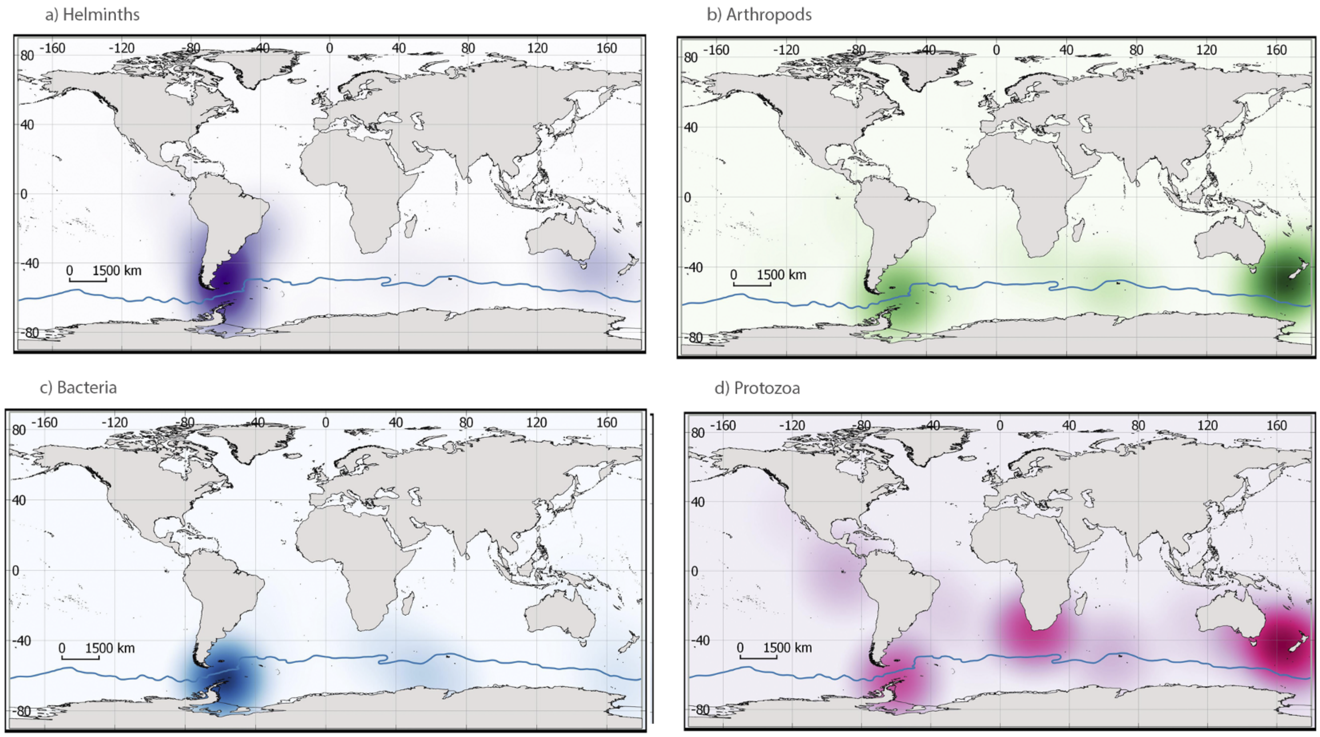

Figure 3. Equirectangular geographical distribution heatmaps of the parasites and pathogens recorded in our database: **a.** helminths; **b.** arthropods; **c.** bacteria; **d.** protozoa. Blue lines depict the Antarctic convergence.

be able to gather enough information to mitigate risks that might compromise their future survival.

Northern rockhopper penguins, erect-crested penguins and Galápagos penguins (*Spheniscus mendiculus*), with 413 000, 150 000 and 1200 breeding pairs, respectively (BirdLife International 2019), are among the species that have received less attention in terms of parasite, pathogen and disease studies. Consequently, they should be given the greatest study priority. Researching the many threats facing these species, including the invasion of their breeding areas by non-native species and the emergence of diseases of unknown origin (likely influenced by human disturbances), should be imperative (Ellenberg *et al.* 2007, 2013, Argilla *et al.* 2013, BirdLife International 2019). Although the African penguin (*Spheniscus demersus*) is currently one of the most researched penguin species, it has suffered a drastic population decline in recent years, from 1.5 million breeding pairs at the beginning of the twentieth century to 21 000 breeding pairs today (Boersma *et al.* 2020). This puts it in a situation of extreme vulnerability. The Galápagos penguin, along with the African penguin, faces impacts from exotic animals in their colonies. Additionally, invasive species could act as reservoirs of pathogens in their habitats (Ropert-Coudert *et al.* 2019). For instance, feral cats act as vectors of *Toxoplasma gondii* (Deem *et al.* 2010) and blood parasites transmitted by mosquitoes, posing a potential threat to the Galápagos penguin. This threat can be exacerbated by the growing human population and increased tourism in the Galápagos Islands. Although knowledge about the health status of these species has increased in recent years, a model for their protection has not been developed. Therefore, the impact of disease on these species requires investigation, and we also need to implement programmes to preclude the introduction of exotic animals and reduce the frequency of tourism to areas containing any colonies of these species (Bestley *et al.* 2020). In the case of the African penguin, recurring infections of avian malaria (*Plasmodium* spp.) are common causes of death, potentially leading to increased transmission of vector-borne pathogens (Ropert-Coudert *et al.* 2019).

We believe it is essential to direct greater attention to the emperor penguin, royal penguin and Snares penguin due to there being limited or no information available regarding their pathogens and parasites. The presence of introduced terrestrial predators poses a significant threat to these penguin species, which are also occasionally disturbed by humans at nest sites (Ellenberg *et al.* 2015). This problem is exacerbated as human activities can also facilitate the spread of disease between colonies (Jones & Shellam 1999, Bestley *et al.* 2020).

We have also noted a concentration of research efforts in two geographical areas: the Antarctic Peninsula and Patagonia, and the region encompassing New Zealand and southern Australia. Consequently, we emphasize the importance of intensifying sampling efforts in currently underrepresented areas, such as the Galápagos Islands, the Pacific coast of South America, various islands in the southern reaches of the Atlantic and Indian oceans and the southern coast of Africa. Despite the Antarctic Peninsula being one of the regions of greatest research effort, investigations should continue here. This area is significantly affected by global change, and as can observed by the dispersion of viruses such as coronaviruses and avian influenza viruses, substantial changes in the distribution, abundance and pathogenicity of parasites are expected (Barbosa & Palacios 2009, Barbosa *et al.* 2021, Dewar *et al.* 2023, Banyard *et al.* 2024).

Boersma *et al.* (2020) conducted a comprehensive analysis to determine critical research and conservation needs for all penguin species, emphasizing that disease monitoring is a priority.

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Table I. Records of pathogenic effects and mortality caused by microparasites and macroparasites in penguins.

Microparasite/macroparasite	Pathogenic effects	Penguin species	Reference(s)
Pasteurella multocida	Mortality events	*Pygoscelis adeliae* *Eudyptes chrysocome*	Stidworthy & Denk (2018)
Clostridium sp.	Acute infections	*Spheniscus humboldti*	Greenwood (2000)
Corynebacterium amycolatum	Diphtheritic stomatitis	*Megadyptes antipodes*	Alley *et al.* (2017)
Plasmodium sp.	Avian malaria	*Megadyptes antipodes* *Eudyptula minor* *Aptenodytes patagonicus* *Spheniscus demersus* *Spheniscus mendiculus* *Spheniscus magellanicus* *Eudyptes sclateri* *Eudyptes pachyrhynchus* *Eudyptes moseleyi* *Eudyptes robustus* *Eudyptes chrysocome*	Clarke and Knowles (1993), Grilo *et al.* (2016), Vanstreels *et al.* (2016), Stidworthy & Denk (2018)
Babesia sp.	Attacks the cytoplasm of erythrocytes	*Eudyptula minor* *Pygoscelis antarcticus*	Schnittger *et al.* (2012)
Parorchites zederi	Lacerations in the intestinal mucosa, affecting the absorption of nutrients	*Pygoscelis antarcticus* *Pygoscelis papua* *Pygoscelis adeliae*	Martin et al. (2016)
Cardiocephaloides physalis	Lacerations in the intestinal mucosa, affecting the absorption of nutrients	*Spheniscus magellanicus* *Spheniscus demersus*	Horne *et al.* (2011)
Mawsonotrema eudyptulae	Causes necrosis and inflammation with subsequent loss of hepatic fluid and haemorrhages	*Eudyptula minor*	Harrigan (1991)
Renicola sp.	Peritubular renal fibrosis, chronic medullary nephritis and epithelium with corneal metaplasia and dysplasia	*Spheniscus magellanicus*	Jerdy *et al.* (2016)
Ixodes uriae	Lower breeding performance, nest abandonment, vector of *Babesia* sp., in some cases death	*Aptenodytes patagonicus* *Pygoscelis papua* *Pygoscelis adeliae*	Gauthier-Clerc *et al.* (1998), Mangin *et al.* (2003), Lynch *et al.* (2010), Montero *et al.* (2016)
Rhinonysus spp.	Pathologies in trachea, lungs and body cavity	*Spheniscus demersus*	Vanstreels *et al.* (2018b)

Our work, through the collection of data on parasites and potential diseases, identifies penguin species of concern and highlights information gaps that should be the focus of future research efforts. In this regard, we consider the results obtained to be valuable for both scientists and decision-makers.

Conclusions

This review highlights penguin species and geographical areas on which future studies of parasites and diseases should focus. The Galápagos Islands, the South American Pacific coast, small Atlantic and Indian islands and the Southern African coast merit further explorations. Considering the impacts of climate change, continuous monitoring of parasite and pathogen distributions, particularly in Antarctic and sub-Antarctic areas, is crucial. Species at the highest risk, such as the yellow-eyed penguin, erect-crested penguin, northern rockhopper penguin, African penguin and Galápagos penguin, require a greater research focus on their parasites, pathogens and diseases and their potential impacts on these populations. Enhanced efforts to obtain high-quality health and parasitological data for the most threatened species and in less studied geographical areas, coupled with long-term studies, will facilitate the establishment of robust sanitary monitoring systems for penguins. Although various macro- and microparasites can be associated with the emergence of diseases or pathologies, it is of vital importance to increase studies related to bacteria and protozoa due to their role in mass mortality events. Similarly, monitoring the distribution of arthropod vectors is fundamental to anticipating the possible transmission of pathogenic microorganisms to penguins. On the other hand, recognizing changes in the diversity of helminth parasites over time could allow us to understand changes in the trophic dynamics of birds in the environments in which they develop. Such initiatives are fundamental for informing and implementing conservation policies on a global scale.

Supplementary material. To view supplementary material for this article, please visit http://doi.org/10.1017/S0954102024000440.

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Competing interests. The authors declare none.

Author contributions. BF, SC and JID conceived of and designed the research. BF, SC, AZ and JID analysed the data and wrote the manuscript. AB, MA and JID supervised the sampling and provided financial support. All authors read and approved an earlier version of the manuscript.

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