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Malaria and Related Haemosporidian Parasites of Wildlife in Southeast Asia: A Risk for Global Health

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Abstract

Malaria and related haemosporidian parasites are widespread diseases that can inflict severe harm on both humans and animals. These parasites are protozoans classified within the order Haemosporidia, which encompasses four families: Garniidae, Haemoproteidae, Leucocytozoidae, and Plasmodiidae. The majority of species belong to three primary genera—Haemoproteus, Leucocytozoon, and Plasmodium—which have the capacity to infect a diverse array of animal species, including birds, reptiles, snakes, and mammals. Diagnostic techniques, such as light microscopy and molecular methods like *polymerase chain reaction* (PCR), have been extensively developed to identify these infections. Despite these advancements, research on the prevalence of malaria in wildlife across Southeast Asia remains sparse. This review article examines the significance of malaria and related haemosporidian parasites in wildlife within Southeast Asia and their potential implications for global human health. A total of 285 articles were reviewed, with 42 qualitative studies being included in this analysis. The majority of these studies were conducted in Malaysia, Indonesia, Thailand, the Philippines, Singapore, Myanmar, Laos, and Cambodia. Among the reviewed studies, 27 out of 42 (64.28%) focused on non-human primates, while 15 out of 42 (35.71%) addressed other wildlife such as birds and bats. *Macaca fascicularis* (long-tailed macaque) was the primary subject in 18 studies (66.66%), followed by *M. nemestrina*, *Pongo pygmaeus*, and various other macaque species and gibbons. In contrast, studies involving other wildlife, including birds and bats, exhibited considerable variability in species and sample sizes, ranging from a minimum of 4 individuals to a maximum of 400 individuals. Molecular diagnostics are predominantly used for non-human primates and other wildlife, as opposed to conventional methods like blood smears. Zoonotic malaria has emerged as a significant concern due to factors such as deforestation, agricultural expansion, and forest fragmentation, which increase human-wildlife interactions and facilitate mosquito breeding, thereby heightening the risk of *Plasmodium knowlesi* malaria. In summary, malaria and related haemosporidian parasites represent a substantial public health threat in Southeast Asia.

Keywords: malaria, non-human primates, related haemosporidian, Southeast Asia, wildlife

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INTRODUCTION

Malaria and related haemosporidian parasites are widely distributed and may cause severe infections in various living organisms, including humans and animals (Muriel *et al*., 2021). These infections are caused by protozoan parasites of the order Haemosporidia, which comprises over 500 species categorized into four families namely Garniidae, Haemoproteidae, Leucocytozoidae, and Plasmodiidae (Ong *et al*., 2015). Most species fall into three primary genera, including *Haemoproteus*, *Leucocytozoon*, and *Plasmodium*, which have the capacity to infect a broad spectrum of animal species, including birds, reptiles, snakes, and mammals (Ishtiaq *et al*., 2007). Avian haemosporidian, including *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*, is prevalent vector-borne parasite (Ong *et al*., 2015; Pornpanom *et al*., 2021; Silva-Iturriza *et al*., 2012). Over 50 species of this parasite have been identified through light microscopy. Meanwhile, human haemosporidian is primarily categorized into four species, namely *Plasmodium falciparum*, *Plasmodium vivax*, *Plasmodium malariae*, and *Plasmodium ovale*. *Plasmodium knowlesi*, which naturally infects monkeys, causes zoonotic malaria across Southeast Asia (Amir *et al*., 2020; Baird, 2009; Li

et al., 2021; Lubis *et al*., 2017; Aryaloka *et al*., 2024).

In 2021, more than 3,575 cases of *P. knowlesi* were reported with an estimated number of 13 deaths. World Health Organization (WHO) reported an additional 435 cases in Southeast Asia Region (SEAR), including Indonesia, the Philippines, and Thailand (Muhammad *et al*., 2022; World Health Organization, 2022). Furthermore, macaque malaria is widespread from east of Bengal Bay, extending from Bangladesh to Taiwan, south to Java, India, and the Philippines, as well as west to southwestern India and Sri Lanka (Fooden, 1994; Subbarao, 2011). In Southeast Asia, there are 13 non-human primate (NHP) malaria parasites, 7 of which infect monkeys (Collins WE, 2012; Fooden, 1994; Dhamayanti *et al*., 2025).

Since the 1930s, three Plasmodium species known to infect wild monkeys have been demonstrated to affect humans, including *P. knowlesi, P. cynomolgi,* and *P. inui* (Gamalo *et al*., 2019; Knowles and Gupta, 1932; Schmidt *et al*., 1961; Zhang *et al*., 2016). The natural hosts of *P. knowlesi* and *P. cynomolgi* are long-tailed macaque (*M. fascicularis*) and pig-tailed macaque (*M. nemestrina*) (Akter *et al*., 2015; Gamalo *et al*., 2019; Zhang *et al*., 2016). Long-tailed macaque is widespread in Southeast Asia and has the third largest geographic distribution among primates, following humans (*Homo sapiens*) and rhesus macaques (*M. mulatta*) (Fooden, 1995; Zhang *et al*., 2016). The distribution extends south and east from southeastern Bangladesh and Myanmar, through the southern Indochinese Peninsula (Thailand, Cambodia, Laos, and Vietnam), and into Malaysian Peninsula, including Singapore, and the islands of Sumatra, Kalimantan, Java, and the Philippines (Eudey, 2008; Zhang *et al*., 2016; Purnama *et al*., 2022).

Aside from *P. knowlesi* and *P. cynomolgi*, long-tailed macaque also serves as natural host for *P. coatneyi, P. fieldi,* and *P. inui* (Jeslyn *et al*., 2011; Singh *et al*., 2004). However, the prevalence and distribution of these parasites in regional long-tailed macaque populations have only been documented in Malaysia and Singapore (Akter *et al*., 2015; Lee *et al*., 2011; Li *et al*., 2021; Zhang *et al*., 2016). Other studies have focused on molecular detection assays for *P. knowlesi* in Thailand, Peninsular Malaysia, and Indonesia, or on sequencing the mitochondrial genome of Plasmodium in Kalimantan, Malaysia (Jongwutiwes *et al*., 2011; Putaporntip *et al*., 2010; Seethamchai *et al*., 2008; Indra Vythilingam *et al*., 2008).

Diagnostic methods, including light microscopy and molecular techniques such as polymerase chain reaction (PCR), have been extensively developed for identifying infections (Muehlenbein *et al*., 2015; Indra Vythilingam *et al*., 2008; Zhang *et al*., 2016). Despite these advancements, comprehensive data on the prevalence of malaria in wildlife remains limited. A thorough investigation of infection with haemosporidian in wildlife is essential to assess the potential as a public health threat. Therefore, this study aimed to explore the significance of malaria and related haemosporidian parasites in Southeast Asian wildlife and the potential implications for global human health.

MATERIALS AND METHODS

Ethical Approval

This is a systematic review and all the data recruited are publicly available. Therefore, ethical approval was not obtained.

Study Period and Location

The review article was conducted at Padjadjaran University, West Java, Indonesia. The research took place over a period of six months, from March to August 2023. This period allowed for an extensive review of existing literature and collection of data pertinent to the prevalence and impact of malaria and related haemosporidian parasites in wildlife across Southeast Asia, assessing their potential risks to global health.

Literature Search Strategy

This study utilized Population, Intervention, Comparison, Outcome (PICO) framework to guide the systematic review. Population was wildlife in Southeast Asia, specifically non-

human primates, birds, reptiles, and mammals. The focus was on studies examining wildlife malaria, particularly infections caused by Plasmodium and related haemosporidian species in countries such as Brunei Darussalam, Indonesia, Cambodia, Laos, Malaysia, Myanmar, the Philippines, Singapore, Thailand, and Vietnam. Furthermore, Intervention refers to the diagnostic methods used to detect malaria and related haemosporidian infections in wildlife populations. Although this study did not specify a direct comparison group, Comparison was addressed by excluding certain types of studies, including those focused on human malaria, Plasmodium in vectors, genomic studies, and anti-malarial treatments. Outcome of interest was the presence and prevalence of Plasmodium and related haemosporidian species infections among the wildlife, with a focus on data related to subjects, sample sizes, study sites, diagnostic methods, and infection rates. For this systematic review, databases such as Google Scholar and PubMed were searched using terms including "Malaria, Plasmodium, Simian Malaria, Primates, Wildlife, Southeast Asia, Avian Malaria, Haemosporidian," and names of specific countries in the region.

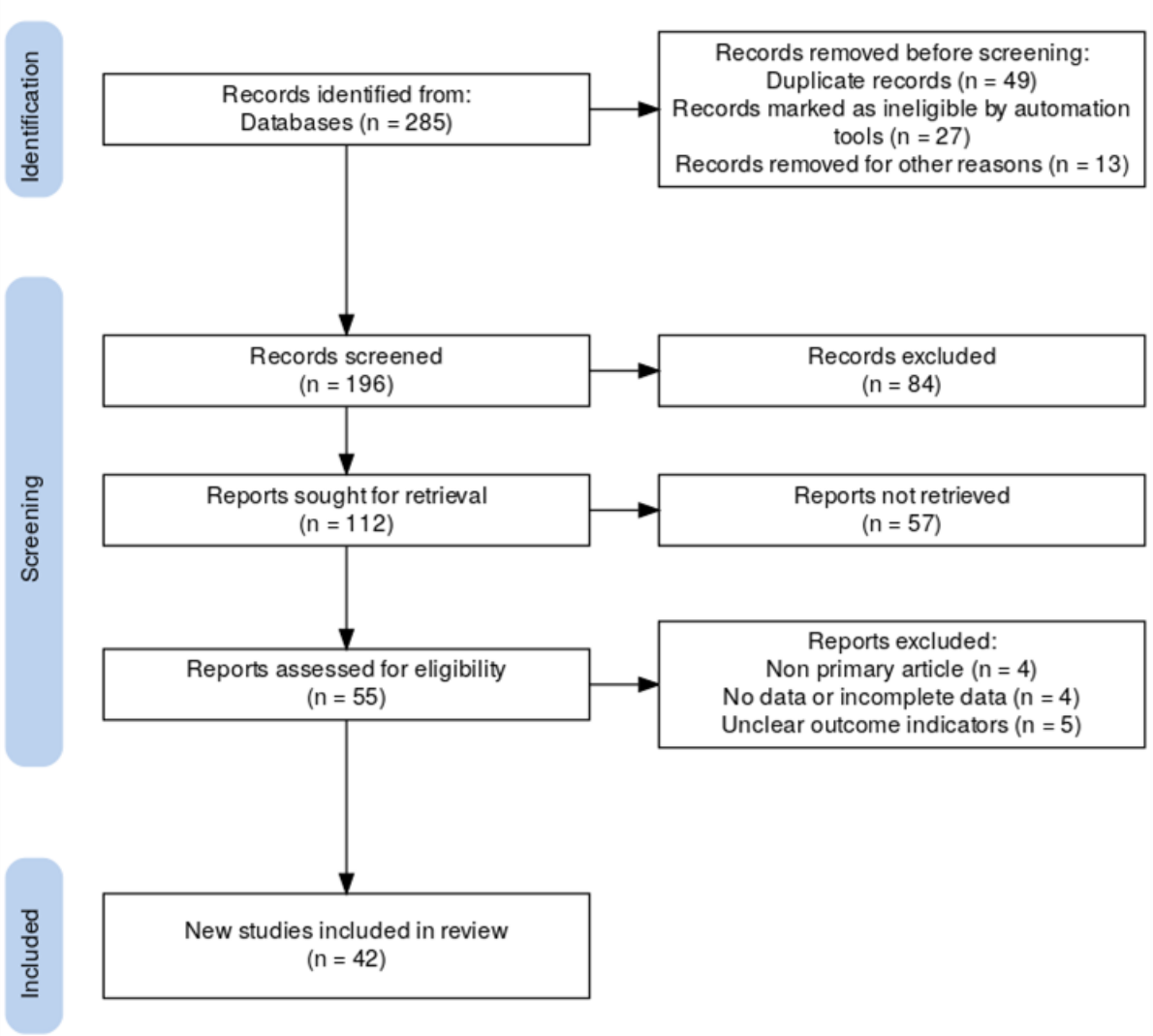

Figure 1. PRISMA flow diagram.

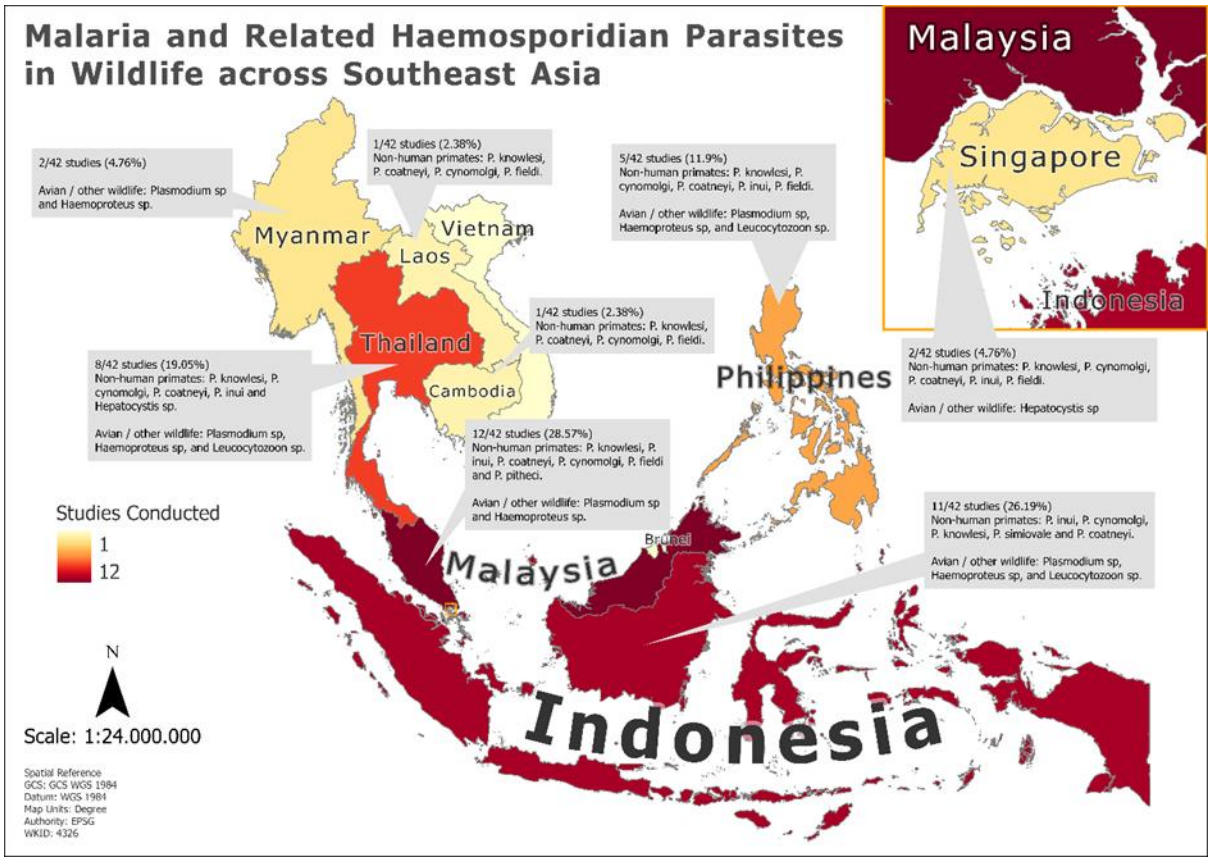

Figure 2. Geographical distribution of malaria and related haemosporidian parasites in Southeast Asia mapped using QGIS.

Eligibility Criteria

Inclusion criteria for the article selection were (a) primary wildlife malaria studies conducted in Southeast Asia, (b) subjects were non-human primates, birds, reptiles, and mammals, (c) studies were published from 1990–2023, (d) full-text in English or Indonesian; (e) studies must also provide a description of subjects, sample size, study site/region/country, (f) studies with detailed diagnosis method, as well as the Plasmodium and related haemosporidian species and the number or percentage of infection.

This study excluded review studies and those that focused on (a) human malaria, (b) simian malaria and related haemosporidian infection in humans, (c) Plasmodium in vector, (d) Plasmodium and related haemosporidian genomic studies, (e) antimalaria, (f) geographical and landscape. This systematic review was guided by Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines. The PRISMA diagram detailing the selection process is shown in Figure 1.

Study Selection and Data Extraction

Two individuals independently reviewed the titles and abstracts for initial screening. This was followed by a comprehensive evaluation of the full texts of the selected studies, including literature screening and data extraction in accordance with the established inclusion and exclusion criteria (https://www.rayyan.ai/). Any disagreements were resolved through consultation with a third individual, who made the final decision. The data extracted include the year of publication, first author, type of non-human primates or other wildlife, diagnostic method, type of Plasmodium, type of haemosporidian, and the number or percentage of infections.

Data Analysis

Due to the heterogeneity among the included studies, a meta-analysis was deemed inappropriate. Data analysis was conducted descriptively using Microsoft Excel 2019. The total number of samples collected from each Southeast Asian country was illustrated on a map.

Table 1. Several studies related to malaria and related haemosporidian in non-human primates in the Southeast Asia region

Subject	Sample (n)	Sample collection period	Method	Plasmodium (%)	*P. knowlesi* (%)	*P. cynomolgi* (%)	*P. coatneyi* (%)	*P. feldi* (%) *P. inui* (%)	*P. simiovale* (%)	*P. pitheci* (%)	*Haemoproteus sp*	*Leucocytozoon sp*	*Hepatocystis sp*	Country	Reference
M. fascicularis	274	NA	PCR SS rRNA gene	13.87	NA	NA	NA	NA	13.87	NA	NA	NA	NA	NA	Indonesia	(Kesumawati *et al*., 2021)
P. pygmeus	24	2003	PCR-mitochondrial cytochrome b	62.50	NA	NA	NA	NA	62.50	NA	NA	NA	NA	NA	Indonesia	(Pacheco *et al*., 2012)
P. pygmeus	86	2003	PCR 18srRNA	16.27	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Indonesia	(Reid *et al*., 2006)
M. nemestrina	24	NA	PCR	50	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Indonesia	(Rosmanah *et al*., 2022)
P. pygmaeus	131	2017–2021	PCR	68	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Indonesia	(K. L. Sanchez *et al*., 2022)
M. brunnecens	26	2020–2021	PCR	50	NA	15.38	NA	NA	76.90	7.69	NA	NA	NA	NA	Indonesia	(Lempang *et al*., 2023)
1. M. fascicularis *2. M. nemestrina* *3. Hylobates sp* *4. Hylobates albibarbis* *5. M. arctoides* *6. M. brunnescens* *7. M. mulatta*	110	August–November 2022	Light microscopy and Nested PCR	50	16.36	18.18	1.80	NA	34.50	NA	NA	NA	NA	NA	Indonesia	(Permana *et al*., 2023)
M. fascicularis	276	NA	Nested PCR	64.10	0.40	53.30	20.40	3.40	12.30	NA	NA	NA	NA	NA	Laos, Singapore, Cambodia, Philippines, Indonesia, Bintan island	(Zhang *et al*., 2016)
1. M. fascicularis; *2. M. nemestrina;* *3. Presbytis melalophos*	145	2017	Nested PCR 18S rRNA	51.72	13.33	NA	NA	NA	NA	NA	NA	NA	NA	NA	Malaysia	(Indra Vythilingam *et al*., 2008)
1. M. fascicularis; *2. M. nemestrina*	108	2004–2008	Nested PCR 18S rRNA	94	83.16	59.40	70.29	3.90	87.12	NA	NA	NA	NA	NA	Malaysia	(Lee *et al*., 2011)

M. fascicularis	70	June 2014	Nested PCR 18S rRNA	50	21 60	51.40	45.70	2.90	65.70	NA	NA	NA	NA	NA	Malaysia	(Akter *et al*., 2015)
1. M. fascicularis *2. M. nemestrina*	41	July 2010–November 2011	Nested PCR CytB gene	100	14.63	9.75	4.80	9.75	41.46	NA	NA	NA	NA	7.60	Malaysia	(Muehlenbein *et al*., 2015)
M. fascicularis	415	NA	Nested PCR 18S rRNA	11.60	11.60	NA	NA	NA	NA	NA	NA	NA	NA	NA	Malaysia	(Saleh Huddin *et al*., 2019)
1. M. fascicularis *2. M. nemestrina*	103	March–August 2016	Nested PCR 18S rRNA	62.10	10.68	40.77	13.59	3.88	40.77	NA	NA	NA	NA	NA	Malaysia	(Amir *et al*., 2020)
1. M. fascicularis *2. M. nemestrina*	212	May–August 2018	Real Time PCR	50.47	36.30	NA	NA	NA	NA	NA	NA	NA	NA	NA	Malaysia	(Ihsan *et al*., 2020)
Wild macaques	50	2019–2021	Nested PCR 18srRNA	100	NA	100	NA	NA	NA	NA	NA	NA	NA	NA	Malaysia	(Latif *et al*., 2022)
1. M. fascicularis *2. M. nemestrina*	73	January 2007–February 2008, June 2008, June 2007–June 2008, September–October 2012, October 2003–August 2012, October 2004	Nested PCR	43.80	5.50	5.50	2.77	NA	19.40	NA	NA	NA	NA	NA	Malaysia	(Nada-Raja *et al*., 2022)
M. fascicularis	419	July 2016–January 2019	Light microscopy and Nested PCR	42	38.60	65.90	38.10	18.80	19.30	NA	NA	NA	NA	NA	Malaysia	(Yusuf *et al*., 2022)
Pongo pygmaeus	84	1996–1998	Light microscopy and Nested PCR	100	NA	NA	NA	NA	NA	NA	100				Malaysia	(Kilbourn *et al*., 2003)
M. fascicularis	95	August–September 2017	PCR	47.40	19	21.20	23.20	41.10	44.20	NA	NA	NA	NA	NA	Philippine	(Gamalo *et al*., 2019)

Wild macaques	379	March 2009–March 2017	Light microscope and PCR	80.50	47.50	71.50	28.50	42	32.50	NA	NA	NA	NA	NA	Singapore	(Li *et al*., 2021)
M. fascicularis	13	November 2007, January 2008, June 2009	Nested PCR	23.07	23.07	NA	NA	NA	NA	NA	NA	NA	NA	NA	Singapore	(Jeslyn *et al*., 2011)
M. fascicularis	655	December 2008–June 2009	Light microscope and PCR	29	2.30	NA	1.20	NA	36.30	NA	NA	NA	NA	NA	Thailand	(Putaporntip *et al*., 2010)
M. fascicularis	649	March–September 2019	Nested PCR 18S rRNA	2.20	NA	NA	NA	NA	2.20	NA	NA	NA	NA	NA	Thailand	(Kaewchot *et al*., 2022)
M. nemestrina	5	2008–2009	PCR	100	100	NA	NA	NA	NA	NA	NA	NA	NA	NA	Thailand	(Jongwutiwes *et al*., 2011)
M. fascicularis	99	May 2006	Light microscope and PCR	6.06	NA	NA	16.67	NA	83.30	NA	NA	NA	NA	16.67	Thailand	(Seethamchai *et al*., 2008)
1. M. fascicularis *2. M. leonine* *3. M. arctoides*	93	2017–July 2019	Nested PCR	29	3.70	14.80	3.70	NA	25.92	NA	NA	NA	NA	NA	Thailand	(Fungfuang *et al*., 2020)

*NA = Not Available.

Table 2. Classification of zoonotic malaria

Species Primary NHP	Host	Vector	Geographical distribution	Morphological similarity	Human infections reported
P. knowlesi	Old world monkey	*An. balabacensis An. latens, An. Dirus*	Malaysia, Thailand, Cambodia, Myanmar, Philippines, Vietnam, Laos, Singapore, Indonesia	*P. falciparum*	Yes
P. inui	Old world monkey	*An. balabacensis, An. dirus, An. maculates, An. Stephensi*	Malaysia	*P. malariae*	Yes
P. cynomolgi	Old world monkey	*An. dirus, An. maculatus*	Cambodia, Malaysia	*P. vivax*	Yes
P. coatneyi	Old world monkey	*An. dirus, An. freeborni*	Malaysia	*P. falciparum, P. knowlesi*	Yes
P. simiovale	Old world monkey	*An. barbadensis, An. stephensi*	Sri Lanka	*P. ovale*	No
P. fieldi	Old world monkey	*An. barbadensis, An. dirus, An. freeborni*	Malaysia	*P. ovale*	No
P. pitheci	Orangutan	*Unknown*	Southeast Asia	*P. vivax*	No
Hepatocystis sp.	Old World primates, bats, hippopotamus, and squirrels	*Culicoides nubeculosus, Culicoides adersi, Culicoides nubeculosus*	Southeast Asia	*P. malariae*	No

Table 3. Several studies related to malaria and related haemosporidian in wildlife in the Southeast Asia region

Subject	Sample size (n)	Sample collection period	Method	*Plasmodium positive* n (%)	*P. knowlesi* n (%)	*P. cynomolgi* n (%)	*P. coatneyi* n (%)	*P. feldi* n (%)	*P. inui* n (%)	*P. simiovale* n (%)	*P. pitheci* n (%)	*Haemoproteus sp*	*Leucocytozoon sp*	*Hepatocystis sp*	Country	Reference
1. Ixobrychus sinensis *2. Turnix suscica tor* *3. Charadrius javanicus* *4. Tringa hypoleucos* *5. Gallinago stenura* *6. Sterna bergii* *7. Streptopelia chinensis* *8. Cacomantis merulinus* *9. Chrysococcyx basalis* *10. Chrysococcyx basalis* *11. Collocalia linchi* *12. Alcedo coerulescens* *13. Halcyon cyanoventris* *14. Pycnonotus goiavier* *15. Orthotomus sutorius* *16. Orthotomus ruficeps* *17. Anthus hodgsoni* *18.Lanius schach* *19. Anthreptes malacensis* *20. Cinnyris jugularis* *21. Passer montanus* *22. Lonchura leucogastroides*	22	2009	Nested PCR	13.63	NA	NA	NA	NA	NA	NA	NA	9.09	9.09	NA	Indonesia	(Yuda, 2019)
Serinus canaria	4	NA	Light microscopy	NA	NA	NA	NA	NA	NA	NA	NA	100	NA	NA	Indonesia	(Bayu *et al*., 2020)
1. Dicrurus leucophaeus *2. Malaconcincla*	24	Februari–Maret 2016	Nested PCR	NA	NA	NA	NA	NA	NA	NA	NA	12.50	NA	NA	Indonesia	(Sainawal *et al*., 2016)

sepiarium *3. Zosterops palpebrosus* *4. Lanius scach* *5. Phylloscopus trivirgatus* *6. Ptilinopus poryphyreus* *7. Halycon cyanoventris* *8. Arachnotera longirostra* *9. Streptopelia chinensis* *10. Myophonus glaucinus* *11. Pcynonotus bimaculatus*																
Tribolonotus gracilis	8	early 2003	Blood smear (light microscopy)	12.50	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	Indonesia	(Telford and Wellehan, 2005)
1. Alcedo euryzona *2. Ceyx erythaca* *3. Collocalia esculenta* *4. Chalcophaps indica* *5. Lacedo pulchella* *6. Chloropsis cochinchinensis* *7. Philentoma pyrhopterum* *8. Megalaima henrii* *9. Motacilla cinerea* *10. Copsychus malabaricus* *11. Culicicapa ceylonensis* *12. Cyornis concretus* *13. Cyornis tickelliae* *14. Enicurus ruficapillus* *15. Arachnothera longirostra* *16. Dicaeum cruentatum* *17. Dicaeum trichonostigma*	79	July–August 2010	Light microscopy and Nested PCR	5.06	NA	NA	NA	NA	NA	NA	NA	24.05	NA	NA	Malaysia	(Ivanova *et al*., 2015)

18. Hypogramma hypogrammicum *19. Prionochilus maculatus* *20. Prionochilus percussus* *21. Blythipicus rubiginosus* *22. Sasia abnormis* *23. Alophoixus bres* *24. Iole olivacea* *25. Pycnonotus atriceps* *26. Pycnonotus brunneu* *27. Pycnonotus cyaniventris* *28. Pycnonotus melanicterus* *29. Tricholestes criniger* *30. Orthotomus sericeus* *31. Alcippe brunneicauda* *32. Malacocincla malaccensis* *33. Pellorneum capistratum* *34. Stachyris nigriceps* *35. Stachyris poliocephala*																
Birds	335	November 1994–March 2001	Light microscope PCR	68	NA	NA	NA	NA	NA	NA	NA	11	NA	NA	Myanmar	(Ishtiaq *et al*., 2007)
Birds	127	March 2019–July 2019	PCR	25	NA	NA	NA	NA	NA	NA	NA	75	NA	NA	Myanmar	(Muriel *et al*., 2021)
Birds	215	March 2004–March 2006	Nested PCR	6	NA	NA	NA	NA	NA	NA	NA	14	8	NA	Philliphine	(Silva-Iturriza *et al*., 2012)
Birds	95	NA	Nested PCR	14.80	NA	NA	NA	NA	NA	NA	NA	33.30	25.90	NA	Philliphine	(Ong *et al*., 2015)

1. Cyornis rufigastra *2. Hypsipetes philippinus* *3. Pycnonotus goiavier* *4. Hypsipetes philippinus* *5. Todirhamphus chloris* *6. Treron vernans* *7. Pycnonotus goiavier* *8. Rhipidura nigritorquis*	192	July 2014	Blood smear (light microscopy)	6.77	NA	NA	NA	NA	NA	NA	NA	5.20	NA	NA	Philliphine	(Sanchez and Paller, 2022)
1. Otus megalotis *2. Bubo philippensis*	8	June 2009–February 2010	Blood smear (light microscopy)	NA	NA	NA	NA	NA	NA	NA	NA	50	NA	NA	Philliphine	(Desamero and Eduardo, 2010)
Cynopterus brachyotis	101	2011–2014	Light microscopy and Nested PCR	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	31.70	Singapore	(Low *et al*., 2021)
Raptors	400	January 2012–December 2019	Nested PCR CytB gene	NA	NA	NA	NA	NA	NA	NA	NA	NA	2		Thailand	(Lertwatcharasarakul *et al*., 2021)
1. *Glaucidium cuculoides* *2. Tyto alba* *3. Otus lettia* *4. Athene brama* *5. Bubo sumatranus* *6. Ketupa ketupu* *7. Ninox scutulata* *8. Strix leptogrammica* *9. Phodilus badius* *10. Otus sunia* *11. Asio flamneus* *12. Bubo nipalensis*	167	September 2012–February 2018	Nested PCR	9	NA	NA	NA	NA	NA	NA	NA	24.60	NA	NA	Thailand	(Pornpanom *et al*., 2019)
Raptors	198	February 2012–September 2019	Nested PCR	2.53	NA	NA	NA	NA	NA	NA	NA	4.04	NA	NA	Thailand	(Pornpanom *et al*., 2021)

*NA = Not Available.

The results of the data analysis were presented in a narrative format.

RESULTS AND DISCUSSION

Selection Studies

A total of 285 studies were initially identified according to the established search strategy. Following the removal of duplicates, 112 studies were retained. Subsequent filtering by title and abstract led to the exclusion of 173. The remaining 55 were further assessed by reviewing the full texts, resulting in the exclusion of an additional 13. Finally, this review included 42 qualitative studies as shown in Tables 1 and 2.

Among the included studies, 8 (19.04%) were published between 2001 and 2010, 20 (47.61%) between 2011 and 2020, and 14 (33.33%) between 2021 and 2023. Furthermore, 12 (28.57%) were conducted in Malaysia, 11 (26.19%) in Indonesia, eight (19.05%) in Thailand, five (11.90%) in the Philippines, two (4.76%) in both Singapore and Myanmar, and one (2.38%) each in Laos and Cambodia. A total of 27 (64.28%) focused on non-human primates, while 15 (35.71%) investigated other wildlife, such as birds and bats (Figure 2).

Long-tailed macaque was the predominant subject in 18 studies (66.66%), followed by pig-tailed macaque, *Pongo pygmaeus*, and other macaque species, as well as gibbons. Sample sizes for non-human primates ranged from a minimum of 5 individuals to a maximum of 655. In contrast, studies on other wildlife, including birds and bats, showed a diverse range of species and sample sizes, from a minimum of 4 to a maximum of 400 individuals. Blood samples were collected in all studies to detect Plasmodium and other related Haemosporidian parasites.

The diagnostic methods used varied widely with 4 studies (9.52%) using light microscopy, 17 (40.47%) PCR, 12 (28.57%) PCR with specific gene targets such as 18S rRNA or Cytochrome B, and 9 (21.42%) combined light microscopy with PCR confirmation. Furthermore, molecular diagnostics were predominantly used for both non-human primates and other wildlife, compared to conventional methods such as blood smears.

Among the studies, 37 demonstrated positive detection of Plasmodium parasites in the subjects, with the percentage of Plasmodium-positive cases ranging from 2.2% to 100%. Additionally, five studies on other wildlife detected Haemosporidian parasites such as *Haemoproteus spp., Leucocytozoon spp*., and *Hepatocystis spp.*

Malaria and Related Haemosporidian Parasites in Non-Human Primates in Southeast Asia Region: A Risk to Global Health

A total of 42 primary studies were identified, of which 27 focused on non-human primates (Table 1). These studies indicate that non-human primates are susceptible to various species of Plasmodium, some of which are zoonotic. The highest infection rates were observed for *P. knowlesi* and *P. inui*, with 17 studies (62.96%) reporting these infections. Other species reported include *P. cynomolgi*, *P. coatneyi*, *P. fieldi*, *P. simiovale*, *P. pitheci*, and *Hepatocystis* spp.

The highest average infection rate for *P. knowlesi* (35.33%) was recorded in Thailand, while the lowest (16%) was found in Indonesia. For *P. inui*, the highest average infection rate (46.94%) occurred in Indonesia, with the lowest (32.50%) in Singapore. The highest average infection rate for *P. cynomolgi* (71.50%) was observed in Singapore, and the lowest (14.8%) was in Thailand. Furthermore, the highest average infection rate for *P. coatneyi* (29.21%) was recorded in Malaysia, with the lowest (1.80%) in Indonesia. For *P. fieldi*, the highest average infection rate (42%) was noted in Singapore and the lowest (7.85%) in Malaysia. Additionally, the average infection rates were 7.69% for *P. simiovale* in Indonesia, 100% for *P. pitheci* in Malaysia, and 16.67% for *Hepatocystis* spp. in Thailand, respectively.

Malaria, caused by protozoa of the genus Plasmodium, remains a significant public health issue despite global control efforts, with 247 million cases and 619,000 deaths reported in 2021 (WHO, 2022). Approximately 250 Plasmodium species are believed to infect various animal species, including birds, reptiles, and mammals. Among these, 27 species have been documented

to infect non-human primates worldwide, including New and Old-World monkeys, macaques, orangutans, and gibbons. Consistent with the data presented in this review, long-tailed macaque is the most frequently infected non-human primates in Southeast Asia, followed by pig-tailed macaque, and *P. pygmaeus*.

The long-tailed macaque has one of the widest geographical distributions among primates, second only to humans (*Homo sapiens*) and rhesus macaques (*M. mulatta*). According to (Fooden, 1995), the range extends across most of mainland Southeast Asia, including southeastern Bangladesh, coastal Myanmar, southern Thailand, all of Cambodia, the southeastern tip of Laos, and southern Vietnam. The population also extends through Thailand, past the Isthmus of Kra, into Sundaland (peninsular Malaysia and the Indonesian archipelago west of the Wallace Line), reaching the Philippines. The distribution further spread to several smaller islands, including those off the northern coast of Sumatra, the Nicobar Islands, and other islands such as Simeulue, Lasia, Maratua, Karimunjawa, Koh Khram Yai, and Con Son. Although long-tailed macaque is predominantly found on the western side of the Wallace Line and considered Asian fauna, populations in Wallacea on the eastern side of the line, such as Lombok, Nusa Tenggara, and East Timor, may be the result of historical human introductions.

P. knowlesi is primarily parasite of long-tailed or crab-eating macaque, pig-tailed macaque, *Trachypithecus obscurus* (dusky leaf monkey or spectacled langur), and *Presbytis melalophus* (banded leaf monkey or brown langur) (Amir *et al*., 2020; Nada-Raja *et al*., 2022; Yusuf *et al*., 2022). In 1927, Italian physician Franchini discovered parasite in the blood of a long-tailed macaque, which was later identified by HGM Campbell in 1931 (Mewara *et al*., 2023). Experimental inoculation into a rhesus monkey led to a severe infection compared to low parasitemia in the native host. Parasite was subsequently maintained by Das Gupta and supervisor Robert Knowles, who described the ability to cause infection in humans and the morphology in macaques (Baird, 2009; Mewara *et al*., 2023; van Rooyen and Pile, 1935). In honor of Knowles' work, parasite was named *P. knowlesi*. Further experimental infections in three human volunteers led to daily fevers and showed a morphology resembling *P. malariae*. Julius Wagner-Jauregg used *P. knowlesi* to induce fever for treating tertiary syphilis before the discovery of penicillin (Baird, 2009; Mewara *et al*., 2023; van Rooyen and Pile, 1935). The first human infection was reported in 1965 in a US Army surveyor who fell ill after returning from Peninsular Malaysia (Chin *et al*., 1965). However, a subsequent study in Malaysia in 1999 found that one-fifth of positive cases previously identified as *P. malariae* were *P. knowlesi* (Lee *et al*., 2009).

Malaria parasite is prevalent in long-tailed and pig-tailed macaques in Singapore and Peninsular Malaysia, making these macaques the third most common primate species infected in SEAR (Cox-Singh *et al*., 2008). *P. knowlesi* has also been isolated from macaques in Palawan Island and the Philippines (Cox-Singh *et al*., 2008; Singh *et al*., 2004). Despite the low prevalence in macaques, it has established infections and caused malaria in humans, underscoring the need for further exploration of other zoonotic malaria parasites that can bypass host barriers (Baird, 2009; Mewara *et al*., 2023; Fikri *et al*., 2024). Cross-species malaria infections are rare due to the host specificity and the different Red Blood Cell (RBC) receptors needed for invasion.

Increased contact between humans and other species has elevated the chances of malaria transmission. *P. knowlesi* infections in humans have increased but are generally mild with low parasitemia compared to *P. falciparum* (Chotivanich *et al*., 2000; Mewara *et al*., 2023; Pasvol *et al*., 1980; Permana *et al*., 2023). However, *P. knowlesi* can cause fatal infections in the natural reservoir hosts. The most common vector is the *Anopheles leucosphyrus* group, consisting of nearly 20 species. The distribution of these mosquitoes overlaps with the natural reservoir hosts, restricting infections to specific regions. *P. knowlesi* is a recognized common cause of severe and fatal human malaria in many

SEAR countries, with the Sabah state of Malaysia contributing to 98% of all globally reported cases (Collins *et al*., 1971; Marchand, 2011; Mewara *et al*., 2023; Tan *et al*., 2008; I. Vythilingam *et al*., 2006).

P. inui is a major non-human primate malaria parasite with a quartan life cycle and is included in the same clade as *P. vivax*. Originally isolated from Javan *M. fascicularis*, it can infect a wide range of monkeys, including the New World Platyrrhine (Coatney *et al*., 1966). Furthermore, *P. inui* has an extended period of development in the vector approximately 15 days, takes longer to develop during the liver stage (9–10 days), and follows a quartan (72-hour) development period in the blood (Collins *et al*., 2009; Dian *et al*., 2022; Fikri *et al*., 2023).

Parasite tends to produce a long-term chronic infection in *M. mulatta*, with blood-stage parasitemia lasting for 14 years or more. Although parasitemia remains low during chronic infections, kidney damage reminiscent of nephrotic syndrome with chronic glomerulonephritis has been documented, similar to that associated with *P. malariae* infection. The OS strain of *P. inui* can cause patent infections in humans, making it a potential zoonotic infection of medical significance (Collins *et al*., 2009; Seethamchai *et al*., 2008; Wyler *et al*., 1977).

The sporozoites have been found naturally occurring in *An. Cracens* mosquitoes, and other species from the *Leucosphyrus* group (Kesumawati *et al*., 2021; Liew *et al*., 2021; Seethamchai *et al*., 2008; Yusuf *et al*., 2022). According to laboratory experiments, parasite can adapt to co-indigenous *Anopheles* mosquito species. *P. inui* also has a wide geographic range in Asia, including southern India, Southeast Asia, and Taiwan. A surveillance study reported that the prevalence among wild macaques in Pahang was 66.7%, with 76.9% being co-infections with other *Plasmodium* species (Amir *et al*., 2020; Collins *et al*., 2007; Liew *et al*., 2021). *Plasmodium inui* could evolve to efficiently infect humans, especially considering patent human infections can be established by just a few parasites. Investigators should employ ultrasensitive methods for epidemiological and entomological studies of simian malaria transmissions in Malaysia and other countries in malaria elimination efforts (Jeyaprakasam *et al*., 2020; Liew *et al*., 2021).

P. cynomolgi, a zoonotic malarial parasite, was first discovered in 1907 by Martin Mayer from *M. cynomolgus* monkeys imported into Germany. Meanwhile, previous studies demonstrated human transmission by mosquitoes (Akter *et al*., 2015; Eyles *et al*., 1960; Mewara *et al*., 2023). An accidental infection was first reported in 1960 when a scientist in Memphis, Tennessee, contracted the infection through simian mosquitoes. Two human volunteers were subsequently bitten by mosquitoes infected with *P. cynomolgi*, confirming parasite role. Parasite has been used as a surrogate for studying *P. vivax* characteristics and in the development of the drug primaquine. The first naturally acquired *P. cynomolgi* infection was reported in 2011 in Peninsular Malaysia from a 39-year-old woman with no previous history of malaria. Subsequently, three additional natural infections have been reported (Chua *et al*., 2019; Ta *et al*., 2014; Tavinia *et al*., 2023).

Long-tailed and pig-tailed macaques are natural hosts for *P. knowlesi* and *P. cynomolgi*, which can also infect other monkey species. Specifically, *P. cynomolgi* is the most widely distributed parasite among macaques in the Philippines, Cambodia, Singapore, and Indonesia (Latif *et al*., 2022; Li *et al*., 2021; Nada-Raja *et al*., 2022; Yusuf *et al*., 2022). This parasite infects monkey RBC indiscriminately but shows high specificity for human RBC invasion, leading to limited proliferation and fewer zoonotic cases. *P. cynomolgi* invades reticulocytes of human RBC expressing the Duffy antigen/chemokine receptor (CD234) and transferrin receptor 1 (Trf1 or CD71) (Kosaisavee *et al*., 2017). It is an oligoxenous parasite, infecting and being transmitted by various co-indigenous and exotic mosquitoes. *Anopheles balabacensis* is the most efficient vector, while *Anopheles roperi* is the least. Although *Mansonia* and *Culex* species have been experimentally infected with *P. cynomolgi*, there is no indication of disease transmission. In Cambodia and Vietnam, *An. dirus* and *An.*

maculatus vectors of human malaria harbor both *P. cynomolgi* and *P. knowlesi* (Klein *et al*., 1991; Maeno *et al*., 2015). A study in Vietnam found six different Plasmodium species in *An. dirus* mosquitoes, including human and primate parasite. Despite *P. vivax* being the most common parasite, 26 out of 79 mosquitoes showed multiple infections (Maeno *et al*., 2015).

Based on the description, *P. cynomolgi* is identified as a common cause of malaria in primates in Southeast Asia, predominantly found in long-tailed macaques. Several studies have been conducted on the wide distribution of this parasite across states, including Malaysia, Singapore, Indonesia, Vietnam, Laos, and the Philippines (Latif *et al*., 2022; Lee *et al*., 2011; Zhang *et al*., 2016). Monkeys serve as an intermediate host, with risk factors including males, close contact with monkeys, agricultural land expansion, and deforestation. However, human-to-human transmission of *P. cynomolgi* has not been reported, making monkeys the intermediate host, with significant risk factors (Baird, 2009; Mawson, 2013; Mewara *et al*., 2023; Scott, 2020).

Zoonotic malaria has become a significant concern in recent years, as shown in Table 2, particularly as several elimination programs aim to achieve their targets. The rise in zoonotic malaria is primarily due to factors such as deforestation, agricultural expansion, and forest fragmentation, which increase human-primate interaction (Brown *et al*., 2020; Fornace *et al*., 2019; Mewara *et al*., 2023). Poor environmental conditions also enhance mosquito breeding, increasing the risk of *P. knowlesi* malaria. A case-control study found the highest transmission of cases at forest edges, affecting those engaged in clearing vegetation. The vulnerable groups were identified as male gender, plantation work, outdoor sleeping, and travel. Factors associated with decreased risk included glucose-6-phosphate dehydrogenase deficiency, insecticide spraying, and the presence of rice and paddy fields around homes (Baird, 2009; Lempang *et al*., 2023; Su and Wu, 2021; Indra Vythilingam *et al*., 2008).

Despite advances in malaria control, there is an increasing number of reports of non-human parasitic (NHP) cases, posing a challenge to achieving elimination targets with current preventive measures (Angelika *et al*., 2021; Purnama *et al*., 2020; Scott, 2020). To address this challenge, molecular diagnostic methods should be used in all resource settings to accurately identify NHP malaria infections. Many countries have observed a parallel rise in zoonotic malaria cases alongside a reduction in human infections due to changes in human behavior, parasite adaptation to different hosts, and variations in vector bionomics (Bordier and Roger, 2013; Jeyaprakasam *et al*., 2020; Li *et al*., 2021; Indra Vythilingam *et al*., 2008).

Control strategies for malaria must be implemented through an integrated method rather than a single intervention. Basic methods of vector control include insecticides such as insecticide-treated nets (ITNs), repellents, and indoor residual spraying (IRS), which have significantly reduced the burden of malaria (Chinsembu, 2015; Fornace *et al*., 2019; Purnama *et al*., 2019; Scott, 2020). However, implementation in forest regions may be impractical and require being customized based on specific regional needs. In this context, zoo prophylaxis, which includes using animals not as reservoir hosts for a particular organism/parasite, has gained attention in controlling disease transmission, as active, passive, combined, or used along with insecticides. Recently, endectocides have been used in livestock to reduce mosquito survival and fecundity (Asale *et al*., 2017; Indra Vythilingam *et al*., 2008).

Emphasizing Malaria and Related Haemosporidian Parasites in Birds and Other Wild Animals in Southeast Asia

Malaria and related haemosporidian parasite in birds and other wild animals, particularly in Southeast Asia, are of significant concern due to their impact on biodiversity, ecosystems, and public health (Ivanova *et al*., 2015; Silva-Iturriza *et al*., 2012; Yuda, 2019). The prevalence of Plasmodium and other haemosporidian infections in wildlife, such as birds and bats, is shown in Table 3. The average percentage of *Plasmodium* infections is 47%, followed by *Haemoproteus* at

43% in Myanmar, the highest average *Hepatocystis* at 31.70% in Singapore, and *Leucocytozoon* at 17% in the Philippines.

Avian malaria and related haemosporidian are widespread, abundant, and diverse apicomplexan parasite infecting most avian clades (Bayu *et al*., 2020; Ishtiaq *et al*., 2007; Ivanova *et al*., 2015; Sainawal *et al*., 2016; Telford and Wellehan, 2005; Yuda, 2019). This parasite has complex life cycles including stages within blood-sucking dipteran vectors, tissues, and circulating blood cells of vertebrate hosts (Muriel *et al*., 2021; Ong *et al*., 2015; Sanchez and Paller, 2022; Silva-Iturriza *et al*., 2012). Additionally, it can cause tissue damage, diminish survival, and reduce reproductive success, potentially leading to population declines or extinctions (Su and Wu, 2021; Purnama *et al*., 2021). Although avian haemosporidian is present in almost all geographical regions, the species has not been extensively explored across biogeographical regions, with some host families receiving less attention (Low *et al*., 2021; Pornpanom *et al*., 2019; Sainawal *et al*., 2016; Silva-Iturriza *et al*., 2012). Myanmar, recognized as a biodiversity hotspot, hosts rich ecosystems and a high concentration of endemic species. However, limited studies have explored the genetic diversity of bird haemosporidian parasite, showing the lack of investigation into Myanmar haemosporidian diversity(Ishtiaq *et al*., 2007; Muriel *et al*., 2021).

The hosts of Avian are infected with several species of malaria parasite, including *Plasmodium, Haemoproteus,* and *Leucocytozoon* (Lertwatcharasarakul *et al*., 2021; Low *et al*., 2021; Muriel *et al*., 2021; Pornpanom *et al*., 2021). Currently, tropical biodiversity is being threatened by multiple human activities, such as deforestation, habitat fragmentation, and land-use change, which potentially affect the prevalence, diversity, and pathogenicity of avian haemosporidian parasite (Permana *et al*., 2023; Su and Wu, 2021). Vector and bird migration by human actions into non-endemic habitats represents a risk for endangered species. Moreover, the high rates of habitat alteration in Southeast Asia have led to host shifts and the occurrence of new pathogens, causing infectious diseases to affect humans and wildlife (Ishtiaq *et al*., 2007; Ivanova *et al*., 2015; Muriel *et al*., 2021; Pornpanom *et al*., 2021).

The identification of parasite in areas that have passed through transformations of natural habitats is urgently needed. Currently, over 4,000 unique avian malaria and related haemosporidian lineages have been characterized by molecular barcoding methods in more than 1,900 bird species worldwide (Su and Wu, 2021). This parasite has been unevenly studied across different biogeographical regions. For example, only 2.39% of known avian haemosporidian lineages have been recorded in Asia despite significant diversity accounting for 20%. The results correlate with this study, showing a scarcity of reports on malaria in birds and wildlife in Southeast Asia (Desamero and Eduardo, 2010; Ong *et al*., 2015; Sanchez and Paller, 2022; Telford and Wellehan, 2005; Yuda, 2019).

Although this parasite does not infect humans, the transmission from wild birds to domestic fowl can cause economic losses in the poultry industry (Pornpanom *et al*., 2021; Su and Wu, 2021). The transmission of many avian malaria species is mediated by *Culicidae* mosquitoes belonging to different genera (*Culex, Coquillettidia, Aedes, Mansonia, Culisetta, Anopheles, Psorophora*), rather than the *Anopheles* species for mammalian malaria parasite (Muriel *et al*., 2021; Yuda, 2019). Species of avian malaria parasite has been identified among wild birds, but there are still limited studies on the disease severity and pathology in wild birds. Traditionally, wild birds infected with this parasite are considered to experience mild disease (Muriel *et al*., 2021; Su and Wu, 2021). Various clinical signs have been observed in birds and wild animals following infection with *Plasmodium, Haemoproteus*, or *Leucocytozoon*, including depression, fever, anorexia, reduced weight gain, poor feed conversion, anemia, green feces, and even death (Su and Wu, 2021). Therefore, the transmission of avian malaria parasite between wild birds and pets can be considered an example of zoonotic transmission of malaria parasite (Silva-Iturriza *et*

al., 2012; Su and Wu, 2021). It is anticipated that the transmission will be considered and studied more deeply, particularly in the Southeast Asia region.

This study has several limitations that should be acknowledged. First, the reliance on published literature may introduce publication bias, as studies with significant results have a high tendency to be published. Second, the inclusion criteria restricting language to English and Indonesian can exclude relevant studies published in other languages, potentially neglecting important data. Third, variations in diagnostic methods across studies influence the comparability of prevalence rates and infection data. Fourth, the focus on non-human primates, birds, reptiles, and mammals excludes other wildlife species that also harbor malaria and related haemosporidian parasite, limiting the comprehensiveness of the results. Fifth, the temporal scope of the study, covering publications from 1990 to 2023, does not capture trends or recent changes in parasite dynamics and host interactions. Despite these limitations, this study provides valuable insights into the distribution as well as impact of malaria and related haemosporidian parasite in Southeast Asian wildlife, showing the importance of continued surveillance and investigation in this region.

CONCLUSION

In conclusion, this study showed the significant presence as well as diversity of malaria and related haemosporidian parasite in wildlife across Southeast Asia. The results showed that non-human primates, birds, reptiles, and mammals in this region were hosts to a variety of Plasmodium and haemosporidian species, indicating a complex and widespread transmission network. The prevalence data and species diversity showed the potential for the wildlife populations to serve as reservoirs for zoonotic transmission, posing a risk to both regional and global health. The study also emphasized the need for standardized diagnostic methods and comprehensive surveillance programs to accurately assess and monitor these infections. Moreover, further studies were recommended to understand the ecological dynamics of parasite and develop effective strategies for mitigating the risk of cross-species transmission, contributing to better public health outcomes and wildlife conservation efforts.

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AUTHORS' CONTRIBUTIONS

All authors made significant contributions to the conception, design, data acquisition, analysis, and interpretation of the data. SK was involved in drafting, reviewing, and editing the manuscript, EYS contributed to the visualization, and IK handled project administration.

COMPETING INTERESTS

The authors declare that there is no conflict of interest regarding the publication of this article.

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