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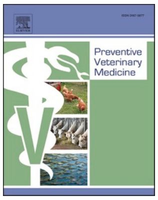

Global prevalence and risk factors associated with *Toxoplasma gondii* infection in wild birds: A systematic review and meta-analysis

Chao Chen [a,b,1], Si-Yuan Qin [c,1], Xing Yang [d,1], Xiao-Man Li [e], Yanan Cai [a], Cong-Cong Lei [c], Quan Zhao [a,*], Hany M. Elsheikha [f,*], Hongwei Cao [b,*]

[a] *College of Animal Science and Technology, Jilin Agricultural University, Changchun, Jilin 130118, PR China*
[b] *School of Pharmacy, Yancheng Teachers University, Yancheng, Jiangsu 224002, PR China*
[c] *Center of Prevention and Control Biological Disaster, State Forestry and Grassland Administration, Shenyang, Liaoning 110034, PR China*
[d] *Department of Medical Microbiology and Immunology, School of Basic Medicine, Dali University, Dali, Yunnan 671000, PR China*
[e] *College of Veterinary Medicine, Qingdao Agricultural University, Qingdao, Shandong 266109, PR China*
[f] *Faculty of Medicine and Health Sciences, School of Veterinary Medicine and Science, University of Nottingham, Sutton Bonington Campus, Loughborough, United Kingdom*

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ABSTRACT

A systematic review and meta-analysis were performed to identify the global prevalence and factors associated with *Toxoplasma gondii* infection in wild birds. Six bibliographic databases (Chinese National Knowledge Infrastructure, VIP Chinese Journal Database, Wanfang Data, PubMed, Web of science and ScienceDirect) were searched from inception to February 2023. The search yielded 1220 records of which 659 articles underwent full-text evaluation, which identified 49 eligible articles and 16,030 wild bird samples that were included in the meta-analysis. The estimated pooled global prevalence of *T. gondii* infection in wild birds was 16.6%. Out of the variables tested, publication year after 2020 and climate type were significantly associated with *T. gondii* infection ($P<0.01$). Our data indicate that the prevalence of *T. gondii* in wild birds can be influenced by epidemiological variables. Further research is needed to identify the biological, environmental, anthropogenic, and geographical risk factors which impact the ecology and prevalence of *T. gondii* in wild birds.

1. Introduction

Toxoplasmosis is a zoonotic disease caused by the opportunistic protozoan *Toxoplasma gondii*, which has a worldwide distribution (Crozier and Schulte-Hostedde, 2014; Jenkins et al., 2015). Approximately one-third of the world's human population are chronically infected by *T. gondii*, which can remain dormant in the host for many years (Zhang et al., 2016). Although *T. gondii* infection is generally asymptomatic in immunocompetent individuals, the parasite can have an adverse impact on the health of the fetus due to congenital transmission during pregnancy and the immunodeficient individuals (Cortes et al., 2019; Dubey, 2010; Elsheikha, 2008; Elsheikha et al., 2020). Many bird species can be infected by *T. gondii*, however canaries and pigeons can experience severe disease (Dubey, 2002).

T. gondii is considered a generalist parasite, with a heteroxenous life cycle involving a broad range of mammalian and avian intermediate hosts and a feline definitive host (Aguirre et al., 2019). *T. gondii* may have originated from South American cats and spread around the world through migratory birds (Lehmann et al., 2006). The migratory behavior of wild birds and ability to travel long distances make them an efficient source and vector for cross-species dispersal of zoonotic pathogens (Rahman et al., 2021).

Birds play an important role in the epidemiology and transmission of *T. gondii* to other hosts (Dubey and Jones, 2008). Birds acquire infection by consuming cysts in the muscle and brain of *T. gondii*-infected animals through hunting or scavenging. They can also consume food or water contaminated with oocysts. When infected birds are preyed on by cats (Abdoli et al., 2018), the parasite undergoes sexual reproduction in the feline intestine, culminating in formation and excretion of many oocysts in the cat feces (Dubey et al., 2020). Infected cats shed oocysts for a short duration and adult cats contribute far less to the environmental contamination with oocysts compared to young cats (Dubey, 1976).

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* Corresponding authors.
E-mail addresses: zhaoquan0825@163.com (Q. Zhao), Hany.Elsheikha@nottingham.ac.uk (H.M. Elsheikha), caohw@yctu.edu.cn (H. Cao).
[1] These authors contributed equally to this work.

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Table 1
Normal distribution test for the normal rate and the different conversions of the normal rate.

Conversion form	W	P
PRAW	0.89191	P<0.001
PLN	0.95676	0.069
PLOGIT	0.98979	0.944
PAS	0.96173	0.111
PFT	0.95874	0.084

“PRAW”: original rate; “PLN”: logarithmic transformation; “PLOGIT”: logit transformation; “PAS”: arcsine transformation; “PFT”: double−arcsine transformation.

The use of wild birds as sentinels for multiple zoonotic pathogens (Hamer et al., 2012) has elicited a growing interest in investigating the prevalence of *T. gondii* infection in wild and domestic birds. However, disparities exist in *T. gondii* prevalence between countries (Costa et al., 2022; Dubey et al., 2020; Wang et al., 2021) and the global prevalence in wild birds remains unknown. To comprehensively examine this topic, we conducted a systematic literature review and meta-analysis to estimate the global prevalence of *T. gondii* in wild birds and identify potential factors associated with *T. gondii* infection in wild birds. The study results highlight the need for more surveillance of *T. gondii* infection in wild birds to improve understanding of the ecology and transmission pathways of *T. gondii* genotypes in wild birds and their relationships to animal and human disease.

2. Materials and methods

2.1. Literature search strategy

The present systematic review and meta-analysis followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses Protocols (PRISMA). To estimate the global prevalence of *T. gondii* infection in wild birds, a comprehensive review of the English and Chinese literature was performed. We searched six online bibliographic databases for articles related to *T. gondii* infection in wild birds, including the China National Knowledge Infrastructure (CNKI), VIP Chinese Journal Database, Wanfang Data, PubMed, ScienceDirect, and Web of Science from inception to February 2023. The advanced search was carried out using “Wild birds (in Chinese)” and “*Toxoplasma gondii* (in Chinese)” as keywords in the three Chinese databases. We used a combination of Medical Subject Headings (MeSH) terms and keywords (“*Toxoplasma gondii*”, “Wild birds”) in the search strategy. We used Boolean operators “AND” to link MeSH terms and “OR” to link the entry terms. Finally, the search formula was (“Birds”[Mesh]) OR (Bird[Title/Abstract]) OR (Aves[Title/Abstract]) OR (Wild bird[Title/Abstract]) OR (Waterfowl[Title/Abstract]) OR (Migratory bird[Title/Abstract])) AND (“*Toxoplasma*”[Mesh]) OR (*Toxoplasmas*[Title/Abstract]) OR (*Toxoplasma gondii*[Title/Abstract]). In ScienceDirect, the keywords "Wild birds", "*Toxoplasma gondii*" and "Prevalence OR Seroprevalence" were used in the search. In Web of Science, the search formula was (AB=(Birds) OR AB=(Bird) OR AB=(Aves) OR AB=(Wild bird) OR AB=(Waterfowl) OR AB=(Migratory bird)) AND (AB=(*Toxoplasma*) OR AB=(*Toxoplasmas*) OR AB=(*Toxoplasma gondii*)). Bibliographies of the included articles and relevant reviews were scrutinized for more references. The search was not restricted by the publication year and geographic origin of the published articles. However, the literature search was limited to articles published in Chinese or English language.

2.2. Study selection and quality assessment

This study focused on wild birds and *T. gondii* for literature search to identify all qualified articles. The quality of studies was graded using the Grading of Recommendations, Assessment, Development and Evaluations (GRADE) framework (Guyatt et al., 2008). The eligible articles were assessed for quality of design and methodology based on five criteria: random sampling, number of samples analyzed (≥100), clear sampling location(s), reporting ≥ 6 epidemiological variables and clear description of the detection method. The studies that fulfilled all 5 criteria received a score of 5. Studies were rated as low (1–2 points), medium (3 points), or high quality (4–5 points). Articles that did not meet these criteria were excluded. Review papers, case reports, reprints, and unpublished reports were also excluded.

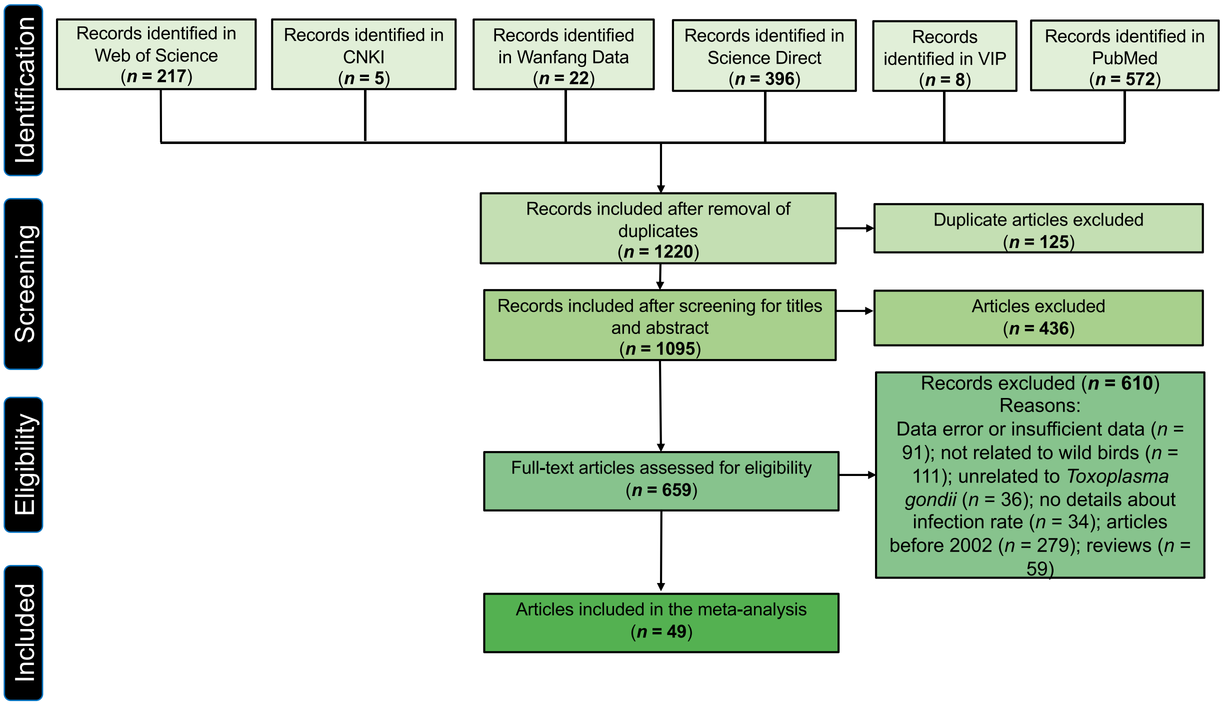


Fig. 1. PRISMA flow chart shows the steps used for article screening and selection.

Table 2
Summary of studies included in the meta-analysis of *T. gondii* prevalence in wild birds.

Study reference	Sampling time	Country	Method	No. positive/ No. tested	Quality score
Tsai et al. (2006)	2004–2004	China	LAT	31/665	High
Murao et al. (2008)	2003–2005	Russia and Japan	ELISA	81/418	High
Dubey et al. (2010)	2008–2010	USA	MAT	38/382	High
Gondim et al. (2010)	2007–2008	Brazil	MAT	3/293	High
Alvarado-Esquivel et al. (2011)	2009–2010	USA	MAT	17/653	High
Cabezon et al. (2011)	1996–2010	Spain	MAT	282/1079	Medium
Darwich et al. (2012)	N/D	Spain	PCR	12/201	High
Huang et al. (2012)	N/D	China	PCR	4/178	Medium
Molina-Lopez et al. (2012)	2006–2010	Spain	MAT	91/113	High
Tian et al. (2012)	2011–2012	China	MAT	35/277	High
Cong et al. (2013)	2011–2011	China	MAT	39/313	High
Khademvatan et al. (2013)	2011	Iran	PCR	25/146	High
Mancianti et al. (2013)	2011–2012	Italy	MAT	9/103	High
Salant et al. (2013)	2010–2011	Israel	MAT	92/223	Medium
Sandstrom et al. (2013)	2006–2010	Russia, Netherlands, Denmark	MAT	247/2675	High
Hu et al. (2014)	2010–2013	China	MAT	36/131	High
Barros et al. (2014)	2010–2011	Brazil	MAT	46/206	High
Gennari et al. (2014)	2010–2011	Brazil	MAT	73/202	High
Miao et al. (2014)	2012–2013	China	MAT	131/659	High
Muz et al., (2015)	2007–2014	Turkey	PCR	7/103	High
Chen et al. (2015)	2013–2014	China	MAT	92/394	High
Zhang et al. (2015)	2013	China	PCR	18/249	High
Andrade et al. (2016)	2011–2013	Brazil	MAT	3/222	High
Cabezón et al. (2016)	2009–2011	Spain	MAT	110/525	High
Gennari et al., (2016a)	N/D	Brazil	MAT	28/100	Medium
Gennari et al. (2016b)	2013	Brazil	MAT	24/69	High
Love et al. (2016)	2012–2014	United States	MAT	97/281	High
Wu et al. (2017)	2016–2016	China	MAT	20/179	High
Tidy et al. (2017)	2014–2015	Portugal	MAT	17/77	High
Luo et al. (2017)	2010–2016	China	IHT	72/751	High
Mirza et al. (2017)	1990–2014	Netherlands	PCR	9/117	High
Amouei et al., (2018)	2014–2015	Iran	MAT	26/50	High
Abdoli et al. (2018)	N/D	Iran	PCR	9/55	Medium
Lukasova et al. (2018)	2014–2015	South Africa	PCR	3/110	High
Nazir et al. (2018)	N/D	Pakistan	PCR	19/54	Medium
Acosta et al. (2019)	2011–2015	Chile	MAT	57/132	High
Huang et al. (2019)	2014–2015	China	MAT	120/350	High
Liu et al. (2019)	2017	China	PCR	13/239	High
Naveed et al. (2019)	2016–2017	Pakistan	LAT	25/200	High
Lohr et al. (2020)	2012–2013	Italy	PCR	45/771	High
Iemmi et al. (2020)	2016–2017	Italy	MAT	91/147	High
Ammar et al. (2021)	2016–2018	USA	MAT	32/155	High
Bata et al. (2021)	2018–2019	Nigeria	ELISA	13/92	High
Gazzonis et al. (2021)	2018–2019	Italy	PCR	35/56	High
Lopes et al. (2021)	N/D	Portugal	MAT	96/263	Medium
Poulle et al., (2021)	2011–2015	Western Indian Ocean	MAT	170/1014	High
Sato et al. (2021)	2014–2015	Brazil	IFAT	6/72	Low
Tayyub et al. (2022)	2018–2018	Pakistan	PCR	46/120	High
Karadjian et al. (2022)	2017–2018	France	MAT	65/166	High

Abbreviation: N/D; data not available; LAT: Latex agglutination test; ELISA: Enzyme linked immunosorbent assay; MAT: Modified agglutination test; PCR: Polymerase chain reaction; IHT: Indirect hemagglutination test; IFAT: Indirect immunofluorescent antibody test.

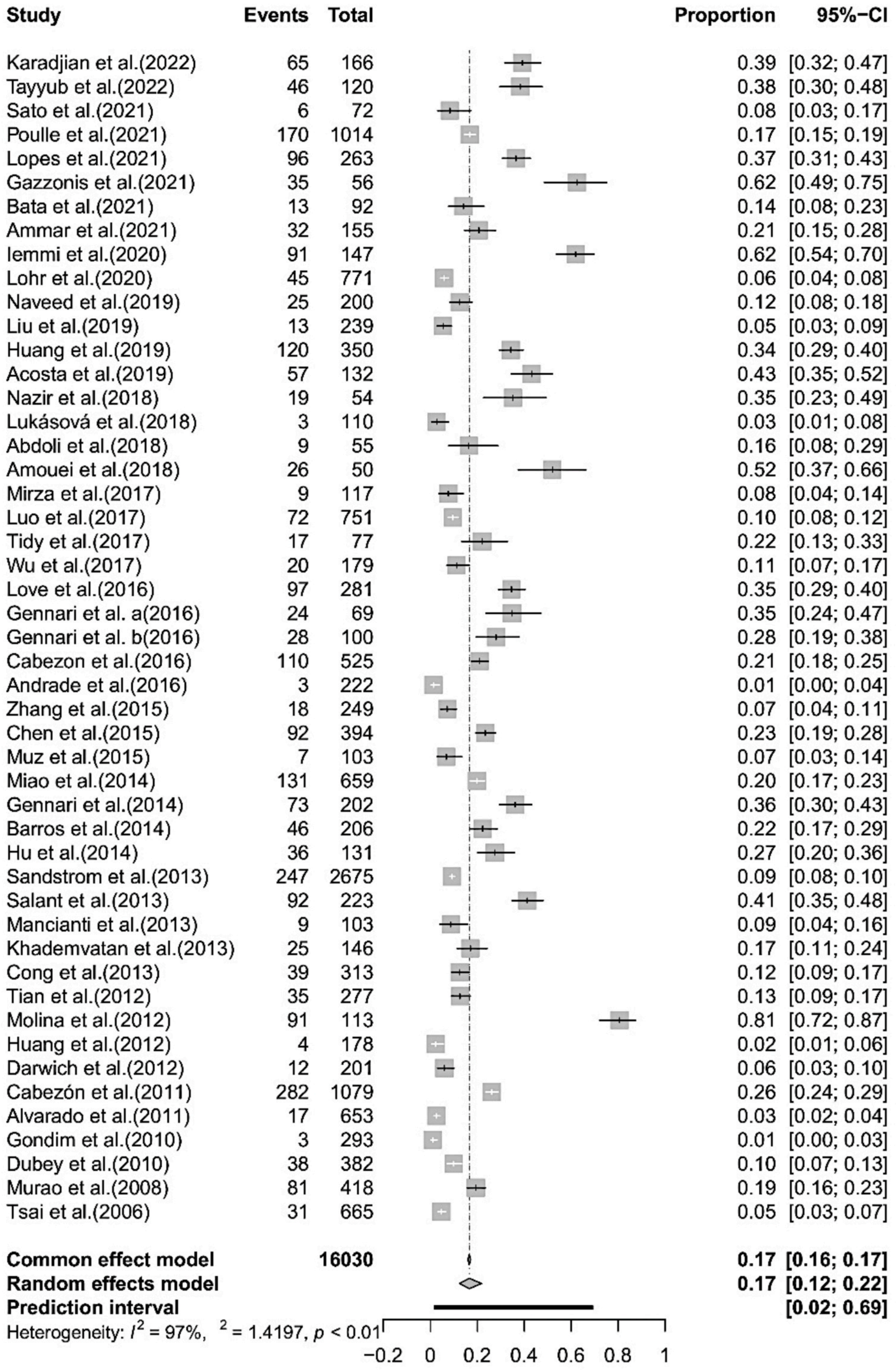
2.3. Data extraction

Two independent reviewers reviewed the abstracts of the selected references to determine whether the studies met the inclusion criteria, in which case a full review of the article was conducted. The information extracted for this study included the detection method, year of publication of the study, continent, sample type, country, order of the wild birds, hemisphere, and climate. The meteorological data were obtained from the National Centers for Environmental Information (https://www.ncei.noaa.gov/maps/monthly/). The data about the geographic location (latitude and longitude) and altitude were obtained by searching for information about the sampling site or neighboring sites at the respective location. The climate of the areas in the included studies was categorized by using the Köppen-Geiger classification (KGC) (Peel et al., 2007). Because of the many different wild bird species worldwide, we presented all bird species at the order level to facilitate data analysis. All wild bird species were classified by https://avibase.bsc-eoc.org/. Data from each of eligible study were extracted and recorded independently.

2.4. Statistical analyses

The quantitative meta-analysis was performed with the R software (4.3.2 version) using the meta package 7.0.0 version (https://cran.r-project.org/web/packages/meta/index.html). We used the random-effects model to determine the pooled prevalence of *T. gondii* and subgroup analysis at 95% confidence interval (CI). To fit the data to Gaussian distribution, five transformation methods were implemented (Table 1). These included logit transformation (PLOGIT), arcsine transformation (PAS), double-arcsine transformation (PFT), logarithmic transformation (PLN), and original rate (PRAW). The normality of the data was checked by Shapiro-Wilk test. The closer the 'W'was to the value 1 (maximum value of this statistic) with a P value ≥ 0.05, the closer the fit to Gaussian normal distribution. The PLOGIT with the largest *p*-value was chosen to analyze the data.

Publication bias was assessed by visual inspection of the inverted funnel plot asymmetry and by using Egger test to assess the small-study effects. To further examine and adjust for publication bias, we imputed



Study	Events	Total	Proportion	95%−CI
Karadjian et al.(2022)	65	166	0.39	[0.32; 0.47]
Tayyub et al.(2022)	46	120	0.38	[0.30; 0.48]
Sato et al.(2021)	6	72	0.08	[0.03; 0.17]
Poulle et al.(2021)	170	1014	0.17	[0.15; 0.19]
Lopes et al.(2021)	96	263	0.37	[0.31; 0.43]
Gazzonis et al.(2021)	35	56	0.62	[0.49; 0.75]
Bata et al.(2021)	13	92	0.14	[0.08; 0.23]
Ammar et al.(2021)	32	155	0.21	[0.15; 0.28]
Iemmi et al.(2020)	91	147	0.62	[0.54; 0.70]
Lohr et al.(2020)	45	771	0.06	[0.04; 0.08]
Naveed et al.(2019)	25	200	0.12	[0.08; 0.18]
Liu et al.(2019)	13	239	0.05	[0.03; 0.09]
Huang et al.(2019)	120	350	0.34	[0.29; 0.40]
Acosta et al.(2019)	57	132	0.43	[0.35; 0.52]
Nazir et al.(2018)	19	54	0.35	[0.23; 0.49]
Lukásová et al.(2018)	3	110	0.03	[0.01; 0.08]
Abdoli et al.(2018)	9	55	0.16	[0.08; 0.29]
Amouei et al.(2018)	26	50	0.52	[0.37; 0.66]
Mirza et al.(2017)	9	117	0.08	[0.04; 0.14]
Luo et al.(2017)	72	751	0.10	[0.08; 0.12]
Tidy et al.(2017)	17	77	0.22	[0.13; 0.33]
Wu et al.(2017)	20	179	0.11	[0.07; 0.17]
Love et al.(2016)	97	281	0.35	[0.29; 0.40]
Gennari et al. a(2016)	24	69	0.35	[0.24; 0.47]
Gennari et al. b(2016)	28	100	0.28	[0.19; 0.38]
Cabezon et al.(2016)	110	525	0.21	[0.18; 0.25]
Andrade et al.(2016)	3	222	0.01	[0.00; 0.04]
Zhang et al.(2015)	18	249	0.07	[0.04; 0.11]
Chen et al.(2015)	92	394	0.23	[0.19; 0.28]
Muz et al.(2015)	7	103	0.07	[0.03; 0.14]
Miao et al.(2014)	131	659	0.20	[0.17; 0.23]
Gennari et al.(2014)	73	202	0.36	[0.30; 0.43]
Barros et al.(2014)	46	206	0.22	[0.17; 0.29]
Hu et al.(2014)	36	131	0.27	[0.20; 0.36]
Sandstrom et al.(2013)	247	2675	0.09	[0.08; 0.10]
Salant et al.(2013)	92	223	0.41	[0.35; 0.48]
Mancianti et al.(2013)	9	103	0.09	[0.04; 0.16]
Khademvatan et al.(2013)	25	146	0.17	[0.11; 0.24]
Cong et al.(2013)	39	313	0.12	[0.09; 0.17]
Tian et al.(2012)	35	277	0.13	[0.09; 0.17]
Molina et al.(2012)	91	113	0.81	[0.72; 0.87]
Huang et al.(2012)	4	178	0.02	[0.01; 0.06]
Darwich et al.(2012)	12	201	0.06	[0.03; 0.10]
Cabezón et al.(2011)	282	1079	0.26	[0.24; 0.29]
Alvarado et al.(2011)	17	653	0.03	[0.02; 0.04]
Gondim et al.(2010)	3	293	0.01	[0.00; 0.03]
Dubey et al.(2010)	38	382	0.10	[0.07; 0.13]
Murao et al.(2008)	81	418	0.19	[0.16; 0.23]
Tsai et al.(2006)	31	665	0.05	[0.03; 0.07]
Common effect model		**16030**	**0.17**	**[0.16; 0.17]**
Random effects model			**0.17**	**[0.12; 0.22]**
Prediction interval				**[0.02; 0.69]**

Heterogeneity: $I^2 = 97\%$, $^2 = 1.4197$, $p < 0.01$

Fig. 2. Forest plot of the global prevalence of *T. gondii* infection in wild birds. Gray squares and their corresponding lines are the point estimates and 95% CI. The diamond represents the pooled estimate (width denotes 95% CI). Heterogeneity was considered high ($I^2 = 97\%$).

potentially missing studies using the trim-and-fill method (Duval and Tweedie, 2000). To evaluate the heterogeneity between studies, Cochran Q test, I^2 statistics and χ^2 test were used (Chen and Benedetti, 2017; Higgins and Thompson, 2002). Subgroup analysis was performed to investigate the differences in the prevalence and potential sources of heterogeneities due to categorical variables, including detection method, sample type, continent, hemisphere, economic status, latitude, altitude, climate type, publication year, and level of study quality.

3. Results

3.1. Study selection and characteristics

The search of the databases yielded 1220 records. After removal of 125 duplicates, 1095 were screened at the title and abstract level, and 659 studies underwent full-text evaluation. Of those, 610 articles were excluded for various reasons listed in the PRISMA flowchart for study selection. Finally, 49 studies met the inclusion criteria and were

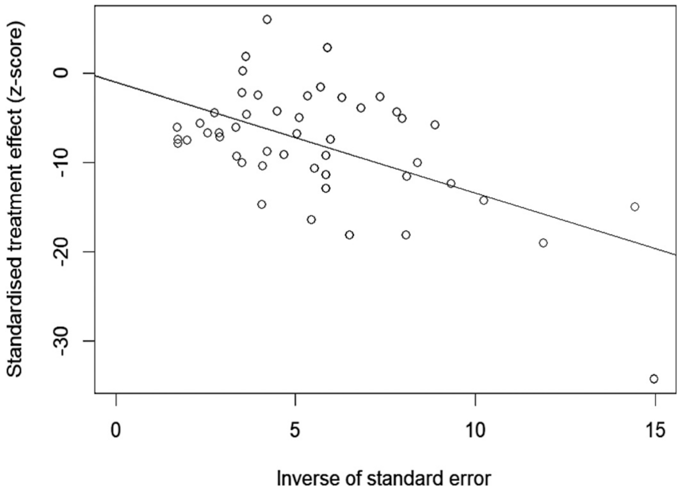


Fig. 3. Egger's test for the assessment of publication bias.

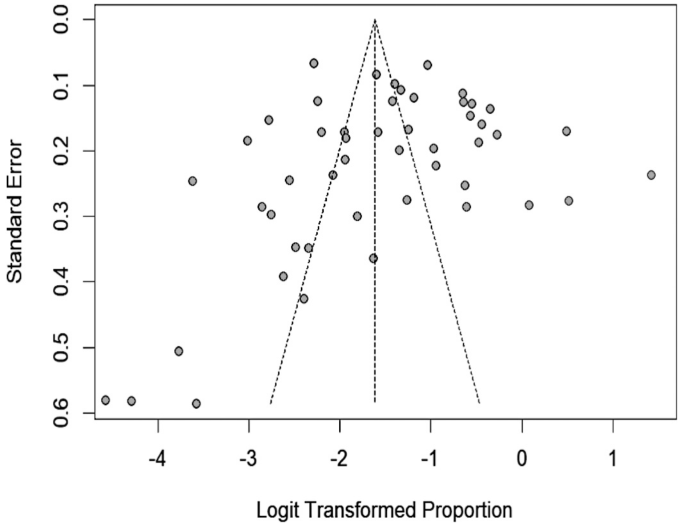


Fig. 4. Funnel plot with pseudo 95% CI for examination of the publication bias. Each dot represents one study.

included in the meta-analysis (Fig. 1). Table 2 summarizes the main characteristics of the 49 articles included in this meta-analysis. Of the 49 eligible studies, 41 (83.67%), seven (14.28%), and one (2.04%) were considered of high, medium, and low quality, respectively.

3.2. Publication heterogeneity, bias and sensitivity analysis

The heterogeneity test showed $I^2 = 97\%$ ($\chi^2 = 1.41$, P < 0.01), suggesting high heterogeneity in *T. gondii* infection prevalence in wild birds (Fig. 2). The publication bias was statistically significant (P<0.0001) as revealed by the Egger's regression test (Fig. 3). Visual inspection of the funnel plot revealed asymmetry, suggesting that the results may have been influenced by publication bias or small sample bias (Fig. 4). The trim and fill analysis identified six studies with negative results (shown as white circles in Fig. 5), indicating potential publication bias. Sensitivity analysis revealed that the reorganized data had no impact on the outcome of the analysis (Fig. 6).

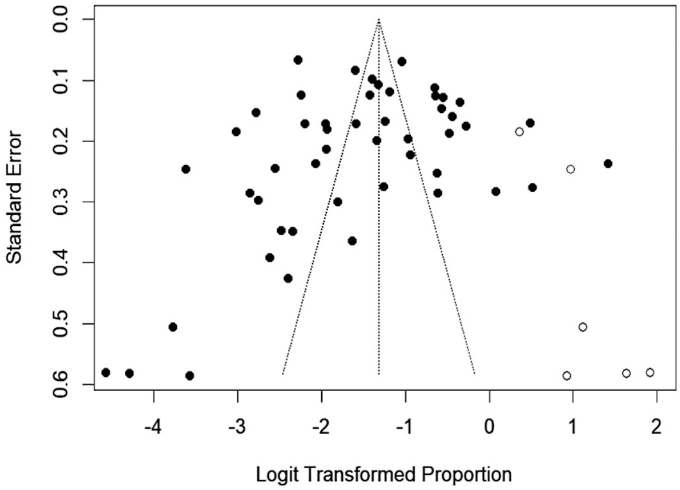


Fig. 5. Funnel plot shows evidence of publication bias in the meta-analysis of *T. gondii* prevalence in wild birds, with missing studies imputed via the trim and fill method. Shaded circles represent the original study estimates, and the unshaded circles represent the missing estimates.

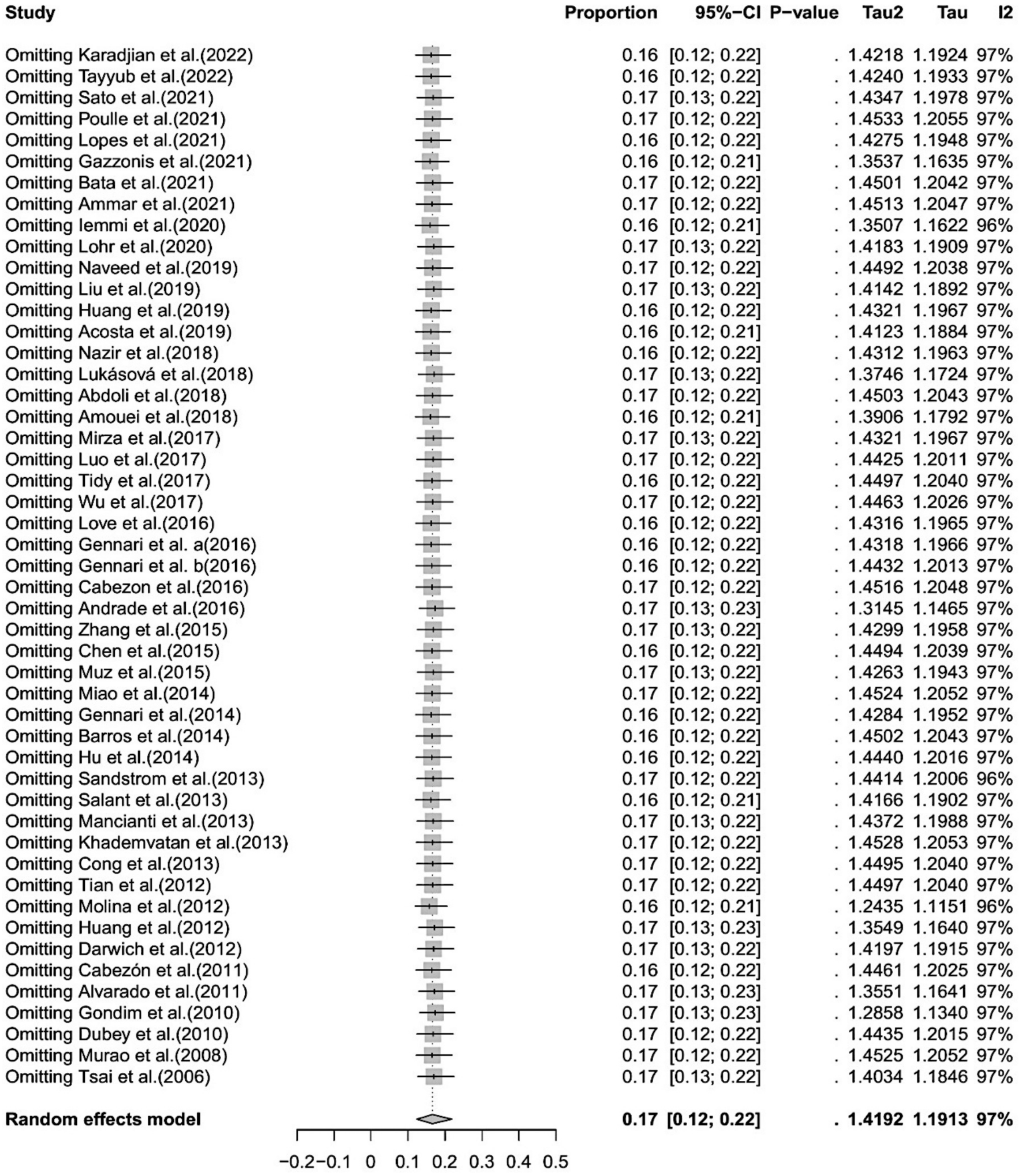
3.3. Global prevalence and study-level covariates of *T. gondii* prevalence in wild birds

The univariate analysis was conducted on 49 eligible studies with 16,030 samples, of which 2660 samples were positive for *T. gondii*. The highest prevalence was detected in Europe (Fig. 7). The estimated pooled global prevalence of *T. gondii* infection in wild birds was 16.6% (95% CI: 12.40–21.87). Strigiformes (33.5%, 95% CI: 21.46–48.16) had the highest prevalence followed by Falconiformes, which had a prevalence close to 30%. Charadriiformes also had a high prevalence (Table 3). However, the order of birds did not have any significant effect on *T. gondii* prevalence (P=0.08).

The results of sub-group and meta-regression analysis considered the following variables: detection method, sample type, continent, hemisphere, economic status, latitude, altitude, climate type, publication year, and level of study quality (Table 4). *T. gondii* detection methods reported in the meta-analysis included enzyme-linked immunosorbent test (ELISA), indirect hemagglutination test (IHT), indirect immunofluorescent antibody test (IFAT), latex agglutination test (LAT), modified agglutination test (MAT), and polymerase chain reaction (PCR). Regarding the detection method subgroup, the highest prevalence 21.3% (95% CI: 14.95–29.44) correlated with the use of MAT. However, there were no significant differences in *T. gondii* prevalence between the detection methods (P=0.44). In the sampling type subgroup (P=0.46), the highest prevalence was associated with blood samples 18.1% (95% CI: 13.05–24.45).

While no significant effect was detected in the continent subgroup (*P*=0.15), Europe had the highest pooled prevalence 14.2% (95% CI: 13.45–15.05). This was followed by Asia 14.1% (95% CI: 13.21–15.10), South America 11.8% (95% CI: 9.98–13.68), North America 10.2% (95% CI: 8.70–11.79), and Africa 6.9% (95% CI: 3.83–10.80). Only one study was reported in Oceania with a prevalence of 7.7% (95% CI: 3.58–13.19). Analysis of the hemisphere (P=0.30) showed that the highest prevalence was detected in northern hemisphere (16.8%; 95% CI: 12.49–22.26) and eastern hemisphere (16.8%; 95% CI: 12.28–22.57). Regarding the economic status (P=0.13), the prevalence was higher in countries with developing economy (14.7%, 95% CI: 12.22–13.81) than in countries with developed economy.

Analysis of the latitude (P=0.13) and altitude (P=0.53) showed that the highest prevalence was detected in the latitude category 30°–60° (19.5%; 95% CI: 13.78–26.90) and altitude category 100–1000 m (16.6%; 95% CI: 9.33–27.89). Of all climate types (P<0.01), tropical monsoon climate had the highest prevalence of *T. gondii* infection (34.8%; 95% CI:24.53–46.67), followed by dry winter subtropical climate (26.3%;95% CI:13.54–44.96) and dry summer, Mediterranean, climate (24.2%;95% CI:9.34–49.67).



Study	Proportion	95%-CI	P-value	Tau2	Tau	I2
Omitting Karadjian et al.(2022)	0.16	[0.12; 0.22]	.	1.4218	1.1924	97%
Omitting Tayyub et al.(2022)	0.16	[0.12; 0.22]	.	1.4240	1.1933	97%
Omitting Sato et al.(2021)	0.17	[0.13; 0.22]	.	1.4347	1.1978	97%
Omitting Poulle et al.(2021)	0.17	[0.12; 0.22]	.	1.4533	1.2055	97%
Omitting Lopes et al.(2021)	0.16	[0.12; 0.22]	.	1.4275	1.1948	97%
Omitting Gazzonis et al.(2021)	0.16	[0.12; 0.21]	.	1.3537	1.1635	97%
Omitting Bata et al.(2021)	0.17	[0.12; 0.22]	.	1.4501	1.2042	97%
Omitting Ammar et al.(2021)	0.17	[0.12; 0.22]	.	1.4513	1.2047	97%
Omitting Iemmi et al.(2020)	0.16	[0.12; 0.21]	.	1.3507	1.1622	96%
Omitting Lohr et al.(2020)	0.17	[0.13; 0.22]	.	1.4183	1.1909	97%
Omitting Naveed et al.(2019)	0.17	[0.12; 0.22]	.	1.4492	1.2038	97%
Omitting Liu et al.(2019)	0.17	[0.13; 0.22]	.	1.4142	1.1892	97%
Omitting Huang et al.(2019)	0.16	[0.12; 0.22]	.	1.4321	1.1967	97%
Omitting Acosta et al.(2019)	0.16	[0.12; 0.21]	.	1.4123	1.1884	97%
Omitting Nazir et al.(2018)	0.16	[0.12; 0.22]	.	1.4312	1.1963	97%
Omitting Lukásová et al.(2018)	0.17	[0.13; 0.22]	.	1.3746	1.1724	97%
Omitting Abdoli et al.(2018)	0.17	[0.12; 0.22]	.	1.4503	1.2043	97%
Omitting Amouei et al.(2018)	0.16	[0.12; 0.21]	.	1.3906	1.1792	97%
Omitting Mirza et al.(2017)	0.17	[0.13; 0.22]	.	1.4321	1.1967	97%
Omitting Luo et al.(2017)	0.17	[0.12; 0.22]	.	1.4425	1.2011	97%
Omitting Tidy et al.(2017)	0.16	[0.12; 0.22]	.	1.4497	1.2040	97%
Omitting Wu et al.(2017)	0.17	[0.12; 0.22]	.	1.4463	1.2026	97%
Omitting Love et al.(2016)	0.16	[0.12; 0.22]	.	1.4316	1.1965	97%
Omitting Gennari et al. a(2016)	0.16	[0.12; 0.22]	.	1.4318	1.1966	97%
Omitting Gennari et al. b(2016)	0.16	[0.12; 0.22]	.	1.4432	1.2013	97%
Omitting Cabezon et al.(2016)	0.17	[0.12; 0.22]	.	1.4516	1.2048	97%
Omitting Andrade et al.(2016)	0.17	[0.13; 0.23]	.	1.3145	1.1465	97%
Omitting Zhang et al.(2015)	0.17	[0.13; 0.22]	.	1.4299	1.1958	97%
Omitting Chen et al.(2015)	0.16	[0.12; 0.22]	.	1.4494	1.2039	97%
Omitting Muz et al.(2015)	0.17	[0.13; 0.22]	.	1.4263	1.1943	97%
Omitting Miao et al.(2014)	0.17	[0.12; 0.22]	.	1.4524	1.2052	97%
Omitting Gennari et al.(2014)	0.16	[0.12; 0.22]	.	1.4284	1.1952	97%
Omitting Barros et al.(2014)	0.16	[0.12; 0.22]	.	1.4502	1.2043	97%
Omitting Hu et al.(2014)	0.16	[0.12; 0.22]	.	1.4440	1.2016	97%
Omitting Sandstrom et al.(2013)	0.17	[0.12; 0.22]	.	1.4414	1.2006	96%
Omitting Salant et al.(2013)	0.16	[0.12; 0.21]	.	1.4166	1.1902	97%
Omitting Mancianti et al.(2013)	0.17	[0.13; 0.22]	.	1.4372	1.1988	97%
Omitting Khademvatan et al.(2013)	0.17	[0.12; 0.22]	.	1.4528	1.2053	97%
Omitting Cong et al.(2013)	0.17	[0.12; 0.22]	.	1.4495	1.2040	97%
Omitting Tian et al.(2012)	0.17	[0.12; 0.22]	.	1.4497	1.2040	97%
Omitting Molina et al.(2012)	0.16	[0.12; 0.21]	.	1.2435	1.1151	96%
Omitting Huang et al.(2012)	0.17	[0.13; 0.23]	.	1.3549	1.1640	97%
Omitting Darwich et al.(2012)	0.17	[0.13; 0.22]	.	1.4197	1.1915	97%
Omitting Cabezón et al.(2011)	0.16	[0.12; 0.22]	.	1.4461	1.2025	97%
Omitting Alvarado et al.(2011)	0.17	[0.13; 0.23]	.	1.3551	1.1641	97%
Omitting Gondim et al.(2010)	0.17	[0.13; 0.23]	.	1.2858	1.1340	97%
Omitting Dubey et al.(2010)	0.17	[0.12; 0.22]	.	1.4435	1.2015	97%
Omitting Murao et al.(2008)	0.17	[0.12; 0.22]	.	1.4525	1.2052	97%
Omitting Tsai et al.(2006)	0.17	[0.13; 0.22]	.	1.4034	1.1846	97%
Random effects model	**0.17**	**[0.12; 0.22]**	**.**	**1.4192**	**1.1913**	**97%**

Fig. 6. Sensitivity analysis of *T. gondii* prevalence in wild birds.

Regarding the year of publication subgroup, the prevalence reported in articles published after 2020 was 26.9% (95% CI: 16.96–39.81; $P<0.01$), the highest prevalence among all articles combined. The highest *T. gondii* prevalence in wild birds correlated with medium quality studies 22.6% (95% CI: 12.03–38.37). However, *T. gondii* prevalence was not influenced by the quality of studies ($P = 0.32$).

4. Discussion

We conducted the first comprehensive evaluation of the global prevalence of *T. gondii* in wild birds. This systematic review and meta-analysis estimated a pooled global prevalence of *T. gondii* in wild birds of 16.6%, suggesting the widespread distribution of *T. gondii* in wild birds. Our results along with others (Dubey, 2002), corroborate the variation in the susceptibility to *T. gondii* among different bird species. In our study, Strigiformes had the highest prevalence followed by Falconiformes. Most species in the Strigiformes and Falconiformes are nocturnal predators that feed primarily on small rodents (Andrle, 2011; Bertolino et al., 2001), the natural intermediate host of *T. gondii* (Krijger et al., 2020), making Strigiformes and Falconiformes more likely to acquire *T. gondii* infection.

By comparing methods used for detection of *T. gondii* infection in wild birds, MAT was found associated with the highest prevalence, followed by ELISA. This result is consistent with a previous study showing MAT as the most appropriate serological test for detection of *T. gondii* in birds (Dubey, 2002). MAT is the gold standard assay for detection of *T. gondii* (Fernandes et al., 2019) and has good sensitivity for measurement of anti-*T. gondii* antibodies (Dubey et al., 2016; Langoni, et al., 2007; Macrì et al., 2009). MAT is also simple to use, requires no special equipment or species-specific reagents, antigens are stable for

Fig. 7. Worldwide map showing the continent-wise prevalence of *T. gondii* infection in wild birds.

Table 3
Pooled prevalence of *T. gondii* in various wild birds.

Order	No. studies	No. examined	No. positive	% (95% CI)	Heterogeneity			Univariate meta−regression	
					$\chi 2$	P−value	I^2 (%)	P−value	Coefficient (95% CI)
Accipitriformes	11	789	180	16.27 (7.49–31.81)	61.2	< 0.01	83.7	0.08	0.9094 (−0.1230 to 1.9418)
Anseriformes	11	3507	395	20.09 (11.49–32.75)	116.9	< 0.01	91.4		
Charadriiformes	7	1938	415	26.43 (18.48–36.29)	28.9	< 0.01	79.3		
Columbiformes	12	1833	130	8.97 (4.76–16.26)	123.9	< 0.01	91.1		
Falconiformes	10	916	278	29.67 (17.54–45.56)	96.1	< 0.01	90.6		
Gruiformes	7	93	10	9.02 (3.04–23.85)	11.0	0.09	45.8		
Passeriformes	21	3120	588	16.28 (9.96–25.48)	411.9	< 0.01	95.1		
Pelecaniformes	6	224	48	21.79 (4.53–62.08)	15.7	< 0.01	68.3		
Strigiformes	12	698	254	33.50 (21.46–48.16)	49.2	< 0.01	77.7		
Others	41	1711	239	9.71 (5.73–15.98)	137.4	< 0.01	70.9		

Abbreviations: CI: Confidence interval; P-value: $P \leq 0.05$ is statistically significant.

months, and reagents are commercially available (Fernandes et al., 2019). The prevalence detected by ELISA, although was lower than that obtained by MAT, it was much higher than the prevalence obtained by the other diagnostic methods. Although ELISA is one of the most reliable methods for detecting anti-*T. gondii* specific antibodies, only two of the articles included in this review used ELISA, presumably because it is time-consuming, laborious, and relatively expensive (Dard et al., 2016). The prevalence was higher in blood samples compared with the brain tissue and muscle samples collected from wild birds. This result may be attributed to the increased number of studies utilizing serological analysis because blood analysis can provide valuable information without the need for constraining or euthanasia of the bird (Angelier et al., 2011).

Subgroup analysis by continent showed that the highest and lowest prevalence was detected in Europe and Africa, respectively. The intercontinental differences may have a plausible explanation. Migrant birds can contribute to the spread and diversity of parasites by hosting more parasites than resident birds and by facilitating long-distance parasite dispersal (Bauer and Hoye, 2014; Jourdain et al., 2007). In Europe, most of the bird habitats are wetlands and marshes, and with the predicted changes in climate, wetter areas can become more humid (Soultan et al., 2022), favoring more spread of *T. gondii*. Warm and humid environments are conducive to the survival *T. gondii* oocysts (Robert-Gangneux and Dardé, 2012). The lowest prevalence detected in Africa may be attributed to the dry and hot climatic conditions, which do not support the survival of *T. gondii* oocysts, and thus may not favor the transmission of *T. gondii*. The modest number of studies reported from Africa is perhaps related to the limited resources which may impede investment in research.

The prevalence was higher in the eastern hemisphere compared with the western hemisphere and higher in the northern hemisphere than the southern hemisphere. Most of the continents are in the northern hemisphere and most of the bird migration occurs in the northern hemisphere. The life cycle of *T. gondii* is closely affected by climatic conditions such as temperature and humidity, which are common features of the northeastern hemisphere's climate. These results are consistent with the results of the continent subgroup analysis which detected the highest prevalence in Europe and Asia.

Table 4
Sub−group analysis of the prevalence of *T. gondii* in wild birds.

Variable	Category	No. studies	No. examined	No. positive	% (95% CI)	Heterogeneity			Univariate meta−regression	
						$\chi 2$	P−value	I^2 (%)	P−value	Coefficient (95% CI)
Detection method	ELISA	2	510	94	18.4 (15.30–22.04)	1.3	0.24	26.9	0.44	0.8740 (−3.0919 to 1.3440)
	IHT	1	751	72	9.6 (7.68–11.91)	0.0	NA	NA		
	IFAT	1	72	6	8.3 (3.79–17.33)	0.0	NA	NA		
	LAT	2	865	56	7.5 (3.72–14.60)	14.4	< 0.01	93.1		
	MAT	30	11,433	2187	21.3 (14.95–29.44)	973.6	< 0.01	97.0		
	PCR	13	2399	245	11.0 (5.93–19.41)	244.4	< 0.01	95.1		
Sample type	Blood	36	14,236	2395	18.1 (13.05–24.45)	1191.4	< 0.01	97.1	0.46	−0.3547 (−1.3006 to 0.5913)
	Brain	8	1030	150	13.3 (5.90–27.41)	143.5	< 0.01	95.1		
	Muscles	3	398	88	17.0 (3.47–53.70)	39.6	< 0.01	95.0		
Continent	Africa	2	202	16	6.9 (3.83–10.80)	9.6	< 0.01	89.6	0.15	0.2368 (−0.0851 to 0.5586)
	Asia	22	5197	811	14.1 (13.21–15.10)	462.2	< 0.01	95.5		
	Europe	17	7332	1161	14.2 (13.45–15.05)	896.0	< 0.01	98.2		
	North America	4	471	184	10.2 (8.70–11.79)	185.9	< 0.01	98.4		
	Oceania	1	117	9	7.7 (3.58–13.19)	0.0	NA	NA		
	South America	7	1164	183	11.8 (9.98–13.68)	247.7	< 0.01	97.6		
Hemisphere	West	11	2764	373	11.40 (5.52–23.00)	261.3	< 0.01	96.2	0.30	−0.4302 (−1.2380 to 0.3776)
	East	36	10,827	1494	16.80 (12.28–22.57)	953.4	< 0.01	96.3		
	South	8	1319	189	9.36 (3.32–23.73)	117.0	< 0.01	94.0		
	North	39	12,272	1678	16.82 (12.49–22.26)	1093.0	< 0.01	96.5		
Economic status	Developed	22	8688	1365	13.8 (13.08–14.53)	1186.8	< 0.01	98.2	0.13	−0.0900 (−0.2067 to 0.0267)
	Developing	31	6795	999	14.70 (12.22–13.81)	650.5	< 0.01	95.4		
Latitude	−60°−−30°	1	117	9	7.96 (4.05–14.13)	0.0	NA	NA	0.13	0.7514 (−0.2111 to 1.7140)
	−30°−0°	7	1202	180	9.59 (2.92–27.26)	101.5	< 0.01	94.1		
	0°−30°	7	2979	332	9.44 (5.23–16.45)	156.7	< 0.01	96.2		
	30°−60°	29	6394	1062	19.52 (13.78–26.90)	794.8	< 0.01	96.5		
	60°−90°	3	2899	284	13.15 (8.38–20.03)	13.8	< 0.01	85.6		
Altitude	<100 m	20	8704	1054	15.46 (11.51–20.44)	403.1	< 0.01	95.3	0.53	0.3037 (−0.6451 to 1.2525)
	100–1000 m	17	2939	566	16.63 (9.33–27.89)	367.7	< 0.01	95.6		
	>1000 m	10	1948	247	12.69 (5.15–28.00)	304.8	< 0.01	97.0		
Climate type	Am	1	69	24	34.78 (24.53–46.67)	0.0	NA	NA	0.01	−2.9073 (−5.2372 to −0.5775)
	Aw	3	715	31	2.68 (0.63–10.68)	28.9	< 0.01	93.1		
	Bs	4	1458	97	5.80 (2.77–11.74)	36.9	< 0.01	91.9		
	Bw	1	146	25	17.12 (11.84–24.12)	0.0	NA	NA		
	Cf	16	5245	771	17.08 (11.08–25.40)	393.1	< 0.01	96.2		
	Cs	6	1208	207	24.18 (9.34–49.67)	244.2	< 0.01	98.0		
	Cw	6	796	236	26.34 (13.54–44.96)	111.7	< 0.01	95.5		
	Df	2	298	51	8.75 (1.68–34.98)	10.4	< 0.01	90.4		
	Dw	4	722	136	17.96 (8.79–33.21)	64.7	< 0.01	95.4		
	ET	4	2934	289	13.10 (8.84–18.98)	14.6	< 0.01	79.5		
Publication year	2000−2010	4	1758	153	6.0 (2.07–16.19)	72.8	< 0.01	95.9	0.01	−1.7430 (−3.1244 to −0.3616)
	2011−2020	37	12,334	2044	16.5 (11.82–22.57)	1138.2	< 0.01	96.8		

(*continued on next page*)

Table 4 (*continued*)

Variable	Category	No. studies	No. examined	No. positive	% (95% CI)	Heterogeneity			Univariate meta−regression	
						$\chi 2$	P−value	I^2 (%)	P−value	Coefficient (95% CI)
	After 2020	8	1938	463	26.9 (16.96–39.81)	132.4	< 0.01	94.7		
Quality level	5	29	11,105	1640	14.8 (10.04–21.20)	982.1	< 0.01	97.1	0.32	−0.3432 (−1.0304 to 0.3441)
	4	12	2901	484	19.4 (10.38–33.28)	259.3	< 0.01	95.8		
	3	7	1952	530	22.6 (12.03–38.37)	64.6	< 0.01	90.7		
	2	1	72	6	8.3 (3.79–17.33)	0.0	NA	NA		
Total		49	16,030	2660	16.6 (12.40–21.87)					

Abbreviations: CI: Confidence interval; NA: not applicable; P−value: $P \leq 0.05$ was set at the statistical significance threshold; LAT: Latex agglutination test; ELISA: Enzyme linked immunosorbent assay; MAT: Modified agglutination test; PCR: Polymerase chain reaction; IHT: Indirect hemagglutination test; IFAT: Indirect immunofluorescent antibody test; Am: Tropical monsoon climate; Aw: Tropical savannah climate; Bs: Arid steppe climate; Bw: Arid desert climate; Cf: Temperate without dry season climate; Cs: Temperate dry summer climate; Cw: Temperate dry winter climate; Df: Cold without dry season climate; Dw: Cold dry winter climate; ET: Polar tund.

In the latitude subgroup analysis, we found that mid-latitude had the highest prevalence, followed by high latitude, whereas low latitudes had the lowest prevalence. Climatic conditions in mid-latitudes are often more humid and warm, which favor the survival of *T. gondii* oocysts (Rostami et al., 2017) and maintain their infectivity (Pereira et al., 2020). In the subgroup analysis of altitude, the highest prevalence was found in the range of 100–1000 m. The prevalence of low altitude (<100 m) was very close to that of 100–1000 m. The low prevalence at the high altitude (>1000 m) is perhaps related to the low air pressure, oxygen deprivation, low temperature, high solar radiation and unpredictable climate (Zhang and Li, 2015), which are not supportive to the survival and transmission of *T. gondii.*

In terms of climate type ($P<0.05$), the present study showed that tropical monsoon climate had the highest prevalence, however this result was based on a single article and cannot reflect the actual effect of climate on *T. gondii* prevalence. The second highest prevalence was correlated with dry-summer, Mediterranean, climate and dry-winter subtropical climate. Temperature, rainfall, and geographic location can influence the occurrence of *T. gondii* infection (Oliveira et al., 2019). *T. gondii* is more prevalent in regions with high humidity and warm climates (Webster, 2010). Tropical monsoon climate is characterized by high temperature and humidity, which favor the maturation and survival oof *T. gondii* oocysts (Hung et al., 2007). Tropical climates are also richer in biodiversity and forests (Sloan et al., 2019), providing a suitable habitat for *T. gondii* transmission. These results highlight the need for more surveillance of *T. gondii* infection in wild birds in humid and warm regions.

Subgroup analysis by publication year ($P<0.01$) revealed an increase in the prevalence from 6.0% in 2000–2010 to 16.5% in 2011–2020 and 26.9% after 2020. This temporal progressive increase in the prevalence of *T. gondii* infection in wild birds may be attributed to increased anthropological activities (Loiselle et al., 2010; Szabo et al., 2012), changes in the agricultural landscapes (Green et al., 2005) or advances in the development of methods that enable better detection and monitoring of pathogens (Suminda et al., 2022). A high attention given to health and environmental issues in recent years may also play a role in increasing the awareness of and reporting *T. gondii* infection in wild birds.

4.1. Limitations and perspectives

Some aspects need to be considered when interpreting the findings of our study. First, our meta-analysis showed high heterogeneity, which is common in meta-analyses of prevalence estimates owing to the methodological variability between studies and residual confounding that are difficult to control. Second, some of the tested variables lack sufficient epidemiological data due to the low number of included studies, with analysis of some categories based on only one article. Therefore, the results should be interpreted with some caution because of the marked differences in the number of studies between the analyzed categories. Future systematic reviews should consider studies published in other languages to increase the number of studies included in the analysis. Future investigations should also consider more surveillance of wild bird migration routes because migratory birds can spread *T. gondii* to a wide range of warm-blooded animals, particularly outdoor reared mammals. The detection and genotyping of *T. gondii* isolates from wild birds can help identify the likely source of infection and trace potential transmission routes. Future research should also assess additional risk factors such as age and gender of the birds.

5. Conclusions

Results from the systematic review and meta-analysis of 49 studies revealed 16.6% pooled global prevalence of *T. gondii* infection in wild birds. Meta-regression analysis showed that two variables, publication year and climate type, can have a significant influence on *T. gondii* prevalence. The inclusion of more studies reporting on the prevalence of *T. gondii* in wild birds may assist in distinguishing actual differences among other variables such as the geographical location, and method of detection. More investigations can improve understanding of *T. gondii* infection epidemiology in wild birds and contribute to the development of measures to prevent the transmission of infection to mammalian hosts and humans.

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CRediT authorship contribution statement

Cong-Cong Lei: Software, Investigation, Formal analysis. **Quan Zhao:** Writing – review & editing, Supervision, Project administration, Conceptualization. **Hany Elsheikha:** Writing – review & editing, Visualization, Validation, Resources, Conceptualization. **Hongwei Cao:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Si-Yuan Qin:** Resources, Investigation, Formal analysis. **Xing Yang:** Writing – original draft, Visualization, Validation, Data curation. **Xiao-Man Li:** Visualization, Software, Resources, Methodology, Data curation. **Yanan Cai:** Methodology,

Investigation, Formal analysis, Data curation. **Chao Chen:** Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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