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Epidemiologic significance of *Toxoplasma gondii* infections in turkeys, ducks, ratites and other wild birds: 2009–2020

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Review

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Abstract

Toxoplasma gondii infections are common in humans and animals worldwide. Wild and domestic avian species are important in the epidemiology of *T. gondii* infections because felids prey on them and excrete millions of oocysts in the environment, disseminating the infection. Herbivorous birds are also excellent sentinels of environmental contamination with *T. gondii* oocysts because they feed on the ground. *Toxoplasma gondii* infections in birds of prey reflect infections in intermediate hosts. Humans can become infected by consuming undercooked avian tissues. Here, the authors reviewed prevalence, persistence of infection, clinical disease, epidemiology and genetic diversity of *T. gondii* strains isolated from turkeys, geese, ducks, ratites and avian species (excluding chickens) worldwide 2009–2020. Genetic diversity of 102 *T. gondii* DNA samples isolated worldwide is discussed. The role of migratory birds in dissemination of *T. gondii* infection is discussed.

Introduction

Toxoplasma gondii infections are prevalent in humans and animals worldwide. The ingestion of undercooked infected meat or consumption of food and water contaminated with oocysts excreted in cat feces are the main sources of infection. Cats are everywhere and a single cat can excrete millions of oocysts that can remain viable in the environment for months under natural conditions (Dubey, 2010). Estimation of oocyst contamination of the environment is difficult because of low numbers present in soil or water (Lélu *et al.*, 2012). Wild and domestic birds are excellent sentinels of environmental contamination with *T. gondii* oocysts because herbivorous birds feed on the ground, and birds of prey consume hundreds of rodents and other small mammals yearly that are important intermediate hosts of *T. gondii* (Dubey *et al.*, 2020; Iemmi *et al.*, 2020). Migratory birds (penguins, geese and others) can transport the parasite across seas (Sandström *et al.*, 2013). Some species (turkeys, geese, ducks and ostriches) are part of food supply for humans. A study estimated that billions of birds are consumed by cats yearly (Loss *et al.*, 2013). Thus, there is great potential for the spread of *T. gondii* oocysts in the environment.

We recently reviewed the biology of *T. gondii* infections in chickens (*Gallus domesticus*) (Dubey *et al.*, 2020). Here, *T. gondii* infections in other avian species, including domestic turkeys, ducks, geese, ratites and other avian species, are reviewed.

Turkeys (*Meleagris gallopavo*)

Antibodies to *T. gondii* were detected from 11.0 to 89.8% of turkeys surveyed (Table 1). Using a kinetic recombinant antigen (GRA7 and GRA8) ELISA, *T. gondii* antibodies were detected in 387 (20.2%) of 1913 sera from 14 turkey farms in different areas of Germany (Koethe *et al.*, 2011). Seroprevalence varied greatly among farms and within the individual farms, depending on fattening cycles and season which turkeys were slaughtered. Seroprevalences were higher in turkeys slaughtered in summer *vs* in fall or winter (Koethe *et al.*, 2011).

A very high rate of infection was reported in a study from Iran (Sarkari *et al.*, 2014). Antibodies to *T. gondii* were found in 89.8% of turkeys (Table 1) and *T. gondii* DNA was detected in 61.6% of turkey tissues (Table 2). Viable *T. gondii* was isolated from the muscle of 5 wild hunted turkeys in the USA (Table 3).

Turkeys are considered resistant to clinical toxoplasmosis and there were no reports of clinical toxoplasmosis since 2009. Experimentally, turkeys inoculated intravenously with *T. gondii* tachyzoites or oocysts orally remained healthy, irrespective of the dose (Bangoura *et al.*, 2013; Zöller *et al.*, 2013; Hotop *et al.*, 2014; Maksimov *et al.*, 2018). A kinetic ELISA was developed based on a mixture of recombinant dense granule antigens GRA7 and GRA8 using sera from turkeys inoculated intravenously with Me49 tachyzoites; SAG1 antigen was not suitable in this ELISA using recombinant SAG1 (Koethe *et al.*, 2011). In a subsequent study, information on a large panel of 101 synthetic peptides was obtained on sera from 18 turkeys intravenously inoculated with tachyzoites of 3 strains of *T. gondii* (RH-Type I, Me49-Type II and NED-Type III). The authors concluded that by using selected peptides, it was possible to

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Table 1. Seroprevalence of *Toxoplasma gondii* in turkeys (*Meleagris gallopavo*)

Country	Area	Source	No. tested	No. positive	% Positive	Test	Cut-off	Remarks	Reference
Brazil	Pernambuco	28 Farms	204	21	11.0	MAT	1:25		Sá *et al.* (2016)
Egypt	Kafr El-Sheikh	Farms	17	5	29.4	IHA[a]	1:80		Harfoush and Tahoon (2010)
Germany	5 States	14 Farms, abattoirs	1913	387	20.2	ELISA-in house	1:50	Sex, season association	Koethe *et al.* (2011)
Iran	Fars	FR, abattoir	54	49	89.8	MAT	1:40	*T. gondii* DNA and isolation	Sarkari *et al.* (2014)
Iran	Shiraz	Farms, abattoir	9	1	11.1	MAT	1:20		Asgari *et al.* (2013)
Iraq	Ninevah	Farms	107	82	76.6	LAT[b]	1:20		Butty (2009)
Nigeria	Ondo, Osun, Oyo	Farms	320	13	4.1	MAT	1:20	Sex association	Ayinmode *et al.* (2017)
USA	Pennsylvania	Hunted	20	6	30.0	MAT	1:5	*T. gondii* isolated	Cerqueira-Cézar *et al.* (2019)

ELISA, enzyme-linked immunosorbent assay; FR, free-range; IHA, indirect haemagglutination assay; LAT, latex agglutination test; MAT, modified agglutination test (Dubey and Desmonts, 1987).
[a]IHA (Toxo-IHA Fumouze, Diagnostics, France).
[b]LAT (Toxo latex kit from Bio-kit-SA, Barcelona, Spain).

serotype strains up to 9 weeks post-inoculation (p.i.) (Maksimov *et al.*, 2018). Antibodies peaked at 5–7 weeks p.i., using the SAG1-ELISA, and the results varied with the *T. gondii* isolate. Similar results were obtained by the indirect fluorescent antibody assay (IFA) (Maksimov *et al.*, 2018).

In turkeys orally inoculated with oocysts, the parasite was widely disseminated in turkey tissues (Bangoura *et al.*, 2013). Inoculated turkeys were euthanized 6 or 12 weeks p.i. and parasite distribution was assessed by polymerase chain reaction (PCR); no difference was found with respect to 6 or 12 weeks p.i. Brain, heart and drumstick were most frequently infected tissues. The route of inoculation could affect the distribution of parasite DNA. In turkeys inoculated intravenously with tachyzoites, liver, pectoral muscle, heart and brain were affected in decreasing order (Zöller *et al.*, 2013). Judging from the histopathological results, the number of *T. gondii* in turkey tissues was low. Tissue cysts were found in imprints of 1 liver, and 2 pectoral muscles of turkeys parenterally inoculated with tachyzoites (Zöller *et al.*, 2013). By using magnetic-capture PCR and 100 g samples, most *T. gondii* were found in the brain and heart (Koethe *et al.*, 2015). Parasite burden was higher in the drumstick *vs* pectoral muscles.

Ducks (*Anas* spp.) and geese

Ducks are important for the economy of some countries, especially China. Ducks are a good source of meat and eggs for human consumption. To our knowledge, there are no reports of clinical toxoplasmosis in domestic ducks or geese, but antibodies are common (Tables 4 and 5).

Toxoplasma gondii DNA was found in 9 (7.8%) of 115 muscle samples from 115 ducks and 2 of 42 geese (4.7%) (Zou *et al.*, 2017). Viable *T. gondii* was isolated from tissues of ducks in China, France and Malaysia (Table 3).

Ostriches (*Struthio camelus*) and other ratites

Ratite meat is lean and its human consumption is increasing. Serologic data are summarized in Table 6. Antibodies to *T. gondii* were detected up to 80.0% of sera (Table 6).

Viable *T. gondii* was demonstrated in ostrich tissues. In a Brazilian report, *T. gondii* was detected in brains of ostriches and in soil samples from paddocks (da Silva and Langoni, 2016). Brain (25 g) samples of 38 seropositive and 20 seronegative ostriches were bioassayed in mice. *Toxoplasma gondii* was isolated from 14 seropositive but not from seronegative ostriches. All strains were apparently pathogenic for mice. *Toxoplasma gondii* DNA was found in peritoneal exudates of mice inoculated from tissues of 8 ostriches, and in brains of mice inoculated with 6 ostrich samples. Nothing was said concerning finding viable *T. gondii*. Of interest is the report of finding *T. gondii*-like oocysts microscopically in soil samples from 5 of 20 paddocks; all were confirmed by PCR. In repeat sampling, *T. gondii*-like oocysts were found microscopically in soil samples from 9 of 20 paddocks and results were confirmed by PCR. It should be noted that only a few oocysts are normally present in soil and their detection is a challenge (J.P.D. own observation).

In marked contrast to the Brazilian report, in a Chinese study, *T. gondii* DNA was not detected in any of the 293 hearts and 77 brains of ostriches (Feng *et al.*, 2017).

A study in Egypt found *T. gondii* DNA in the blood of 9 of 120 ostriches (El-Madawy and Metawea, 2013). These authors also tested tissues of 5 ostriches that had died of toxoplasmosis-like illness; *T. gondii* DNA was found in the brains of 5, hearts of 3 and leg muscle of 1 (El-Madawy and Metawea, 2013) (Comment J.P.D. – tissues of these ostriches should be examined histologically for verification of molecular results).

Other wild avian species

Data on *T. gondii* seroprevalence, viable parasite and DNA characterization are arranged by scientific order of birds, by region and chronologically in Tables 2, 3 and 7.

Carnivorous birds

Prevalence of *T. gondii* in carnivorous birds reflects the prevalence of the parasite in their prey. For example, owls consume hundreds of rodents yearly. In a recent survey of kestrels at an airport site in Italy, *T. gondii* antibodies were detected in 33.3% of kestrel trapped during 2016 and 14.3% of 91 kestrel during 2017; seroprevalence was lower in juveniles than in adults (Iemmi *et al.*, 2020). Based on the remnants of animals in the feces of kestrels, rodents were a major component of the kestrel diet (Iemmi *et al.*, 2020). In a large sample size of raptors in Spain, *T. gondii* antibodies were found in 51.0% of 96 common buzzard, 17.7% of 175 Griffon vulture and 17.0% of Spanish Imperial eagle (Cabezón *et al.*, 2011). Among the raptors, vultures are considered resistant to clinical toxoplasmosis

Table 2. Isolation of viable *Toxoplasma gondii* from wild bird by bioassay in mice and/or cats

Host	Country	Location	No. tested	Tissues	No. isolated	Strain designation	PCR-RFLP genotype (Toxo DB)	Notes	Reference
Accipitriformes									
Bald eagle (*Haliaeetus leucocephalus*)	USA	Alabama	1	B	1	TgBeAl	1 genotype: #5 (1, TgBeA1)		Yu *et al.* (2013)
Bald eagle (*Haliaeetus leucocephalus*)	USA	California	5	H	1	TgHlUs1	1 genotype: #1, Type II (1, TgHlUs1)		Dubey *et al.* (2011*a*), Shwab *et al.* (2014)
Common buzzard (*Buteo buteo*)	Turkey	Seferihisar, Manisa	25	B, H	9	TgBirdTr_Izmir4,6,7 TgBirdTr_Manisa1-3,5-7	Genotyped by microsatellites. 2 genotypes: Type II, ToxoDB #1 or #3 (6, TgBirdTr_Izmir4, TgBirdTr_Manisa2, TgBirdTr_Manisa3, TgBirdTr_Manisa6, TgBirdTr_Manisa7, TgBirdTr_Izmir7). Type III, ToxoDB #2 (1, TgBirdTr_Manisa1). Mixed types (2, TgBirdTr_Izmir6, TgBirdTr_Manisa5)		Karakavuk *et al.* (2018)
Ferruginous hawk (*Buteo regalis*)	USA	Colorado	7	B, H	1	TgBrCoUs1	1 genotype: #1 (1, TgBrCoUs1)		Dubey *et al.* (2010)
Red-shouldered hawk (*Buteo lineatus*)	USA	Alabama	1	B	1	TgRshAL	1 genotype: #10, Type I (1, TgRshAL)		Yu *et al.* (2013)
Red-tailed hawk (*Buteo jamaicensis*)	USA	Colorado	25	B, H	1	TgBjCoUs1	1 genotype: #1 (1, TgBjCoUs1)		Dubey *et al.* (2010)
Red-tailed hawk (*Buteo jamaicensis*)	USA	Wisconsin	1	H	1	TgBjUS1	1 genotype: #15 (1, TgBjUS1)		Dubey *et al.* (2011*a*), Shwab *et al.* (2014)
Roadside hawk (*Rupornis magnirostris*)	Brazil	Minas Gerais	7	B, H	1	TgWildBrMG1	1 genotype: #108 (1, TgWildBrMG1)		Rêgo *et al.* (2018)
Rough-legged hawk (*Buteo lagopus*)	USA	Colorado	4	B, H	1	TgBlCoUs1	1 genotype: #2, Type III (1, TgBlCoUs1)		Dubey *et al.* (2010)
Swainson's hawk (*Buteo swainsoni*)	USA	Colorado	13	B, H	2	TgBsCoUs1,2	2 genotypes: #1, Type II (1, TgBsCoUs2), #167 (1, TgBsCoUs1)		Dubey *et al.* (2010)
Anseriformes									
Canada geese (*Branta canadensis*)	USA	Maryland	Hunted	H	9	TgGooseUS1-9	5 genotypes #1 (1, TgGooseUS9), #2 (4, TgGooseUS3,5,6,7), #4 (2, TgGooseUS2,8), #266 (1, TgGooseUS1), #267 (1, TgGooseUS4)	One isolate by bioassay in cat	Verma *et al.* (2016)
Domestic duck (unspecified)	China	Chongqing	12	B, H, K, Li, Lu, Sp	1	ND	PCR (ITS-1)		Zhao *et al.* (2015)
Domestic duck (unspecified)	Malaysia	Peninsular	23	B, H	4	DK1-4	PCR-RFLP-partial genotyping data	Backyards of homes	Puvanesuaran *et al.* (2013)
Mallard duck (*Anas platyrhynchos*)	France	Hunted	2	H	1	ND	Microsatellite markers, 1 genotype: type II, ToxoDB, #1 or #3 (1, one isolate)	Wild	Aubert *et al.* (2010)

(*Continued*)

Table 2. (*Continued.*)

Host	Country	Location	No. tested	Tissues	No. isolated	Strain designation	PCR-RFLP genotype (Toxo DB)	Notes	Reference
Mallard duck (*Anas platyrhynchos*)	Malaysia	4 states	30 hunted	B, H	4	NS	ND	*T. gondii* DNA was detected by PCR-RFLP in tissues of inoculated mice	Puvanesuaran *et al.* (2013)
Mallard duck (*Anas platyrhynchos*)	Senegal	Saint-Louis	1	B, H	1	TgA117073	Genotyped by 15 microsatellite markers as Type II ToxoDB #1 or #3 (1, TgA117073)		Galal *et al.* (2019)
Muskovy duck (*Cairina moschata*)	Senegal	Dakar, Kedougou, Saint-Louis	15	B, H	11	TgA117015, 117017, 117018, 117025, 117032, 117038, 117041, 117054, 117060, 117061, 117070.	12 strains genotyped with 15 microsatellites 4 genotypes: Type II, ToxoDB #1 or #3 (3, TgA117038, 117041, 117054), Type III, ToxoDB #2 (1, TgA117015), Africa 1, ToxoDB #6 (1, TgA117070), Africa 4, ToxoDB #20 (6, TgA117017, 177018, 177025, 177032, 177060, 117061).		Galal *et al.* (2019)
Mute swan (*Cygnus olor*)	USA	Great lakes	14	H	3	TgSwanUs1-3	2 genotypes: #2 (2, TgSwanUs1,2), #216 (1, TgSwanUs3)		Dubey *et al.* (2013)
Charadriiformes									
Yellow-legged gull (*Larus michahellis*)	Turkey	Balçova	2	B, H	2	TgBirdTr_Izmir2,3	Genotyped by microsatellite. 2 genotypes: Type II, ToxoDB #1 or #3 (1, TgBirdTr_Izmir2). Type III, ToxoDB #2 (1, TgBirdTr_Izmir3)		Karakavuk *et al.* (2018)
Columbiformes									
Eared dove (*Zenaida auriculata*)	Brazil	Paraná	46	Several tissues	12	TgDoveBr1-12	Nine strains typed. 5 genotypes: #1 (4, TgDoveBr1,2,8,9), #6 (1, TgDoveBr7), #17 (1, TgDoveBr11), #65 (1, TgDoveBr12), #182 (2, TgDoveBr6,10)		de Barros *et al.* (2014)
Rock pigeon (*Columba livia*)	Mexico	Durango	7	B, H	1	TgPigeonMx1	PCR-RFLP ToxoDB genotype # 9 (1, TgPigeonMx1)	MAT 1:400	Alvarado-Esquivel *et al.* (2011), Shwab *et al.* (2014)
Rock pigeon (*Columba livia*)	Portugal	Lisbon	41	B	24	NS	Genotyping by SAG2 (26 type II, two type III, one type I) and 5 microsatellites markers (12 type II, two type III, one type I and one recombinant)		Waap *et al.* (2012), Vilares *et al.* (2014)
Rock pigeon (*Columba livia*)	Serbia	Belgrade	4	H	3	NS	529 bp, PCR-RFLP-incomplete		Marković *et al.* (2014)
Falconiformes									
American kestrel (*Falco sparverius*)	USA	Colorado	5	B, H	1	TgFsCoUs1	1 genotype: #157 (1, TgFsCoUs1)		Dubey *et al.* (2010)

Southern caracara (*Caracara plancus*)	Brazil	Minas Gerais	7	B, H	2	TgWildBrMG4,6	2 genotypes: #13 (1, TgWildBrMG6) #290 (1, TgWildBrMG4)		Rêgo *et al.* (2018)
Galliformes									
Double-spurred spurfowl (*Pternistis bicalcaratus*)	Senegal	Kedougou	4	B, H	1	TgA117077	Genotyped with 15 microsatellites. 1 genotype: Africa 1, ToxoDB #6 (1, TgA117077)		Galal *et al.* (2019)
Guinea fowl (*Numida meleagris*)	Brazil	Minas Gerais	2	B, H	1	TgNmBr1	1 genotype: # 1, type II (1, TgNmBr1)		Dubey *et al.* (2011*b*)
Guinea fowl (*Numida meleagris*)	Senegal	Kedougou	1	B, H	1	TgA117058	Genotyped with 15 microsatellites. 1 genotype: Type Africa 1, ToxoDB genotype #6 (1, TgA117058)		Galal *et al.* (2019)
Turkeys (*Meleagris gallopavo*)	USA	Pennsylvania	20 hunted	H, Sk	5	TgturkeyPa1-5 (designated here)	2 genotypes: #5 (4, TgturkeyPa1-4), #216 (1, TgturkeyPa5)	18NC0055-(TgturkeyPa1) 18-WITU-0002 (TgturkeyPa2) 18-WITU-0012 (TgturkeyPa3) 18-WITU-0015 (TgturkeyPa4) 18-WITU-0019 (TgturkeyPa5)	Cerqueira-Cézar *et al.* (2019)
Passeriformes									
Hawaiian crow (*Corvus hawaiiensis*)	USA	Hawaii	2	B, Li, Sp, Lu	2	TgHcUS1, 2	1 genotype: #177 (2, TgHcUS1, 2)		Work *et al.* (2000), Shwab *et al.* (2014)
Pelecaniformes									
Striated heron (*Butorides striata*)	Brazil	Pernambuco	2	B, H, Sk	1	TgButstBrPE1	1 genotype: #13 (1, TgButstBrPE1)		Silva *et al.* (2018*b*)
Piciformes									
Campo flicker (*Colaptes campestris*)	Brazil	Minas Gerais	1	B, H	1	TgWildBrMG3	1 genotype: #11 (1, TgWildBrMG3)		Rêgo *et al.* (2018)
Keel-billed toucan (*Ramphastos sulfuratus*)	Costa Rica	Zoo	1	Sk	1	TgRsCr1	1 genotype: #52 (1, TgRsCr1)		Dubey *et al.* (2009), Shwab *et al.* (2014)
Toco toucan (*Ramphastos toco*)	Brazil	Minas Gerais	3	B, H	1	TgWildBrMG2	1 genotype: #290 (1, TgWildBrMG2)		Rêgo *et al.* (2018)
Psittaciformes									
Peach-Faced Lovebird (*Agapornis roseicollis*)	Australia	Sydney	1 pet	B	1	AgapornisTg1	1 genotype: #3, Type II variant (1, AgapornisTg1)	*T. gondii* genotyping in B of the bird	Cooper *et al.* (2015)
Strigiformes									
Barn owl (*Tyto alba*)	Turkey	Konak	2	B, H	2	TgBirdTr_Izmir1,5	Genotyped by microsatellites. 2 genotypes: Type II, ToxoDB #1 or #3 (1, TgBirdTr_Izmir5), Type III, ToxoDB #2 (1, TgBirdTr_Izmir1)		Karakavuk *et al.* (2018)
Barn owl (*Tyto alba*)	USA	Colorado	1	B, H	1	TgTaCoUs1	PCR-RFLP ToxoDB genotype # 5	MAT<1:25	Dubey *et al.* (2010)
Barred owl (*Strix varia*)	USA	Alabama	1	B	1	TgSaUS1	1 genotype: #3, Type II variant (1, TgSaUS1)	MAT 1:50	Love *et al.* (2016)

(*Continued*)

Table 2. (*Continued.*)

Host	Country	Location	No. tested	Tissues	No. isolated	Strain designation	PCR-RFLP genotype (Toxo DB)	Notes	Reference
Eurasian eagle-owl (*Bubo bubo*)	Turkey	Salihli	2	B, H	1	TgBirdTr_Manisa4	Mixed types (1, TgBirdTr_Manisa4)		Karakavuk *et al.* (2018)
Tropical screech owl (*Megascops choliba*)	Brazil	Minas Gerais	4	B, H	1	TgWildBrMG5	1 genotype: #8 (1, TgWildBrMG5)		Rêgo *et al.* (2018)
Struthioniformes									
Ostrich (*Struthio camelus*)	Brazil	São Paulo	38	B	14	TgOsBr1,2	2 genotypes: # 161 (1, TgOsBr2), #206 (1, TgOsBr1)	Abattoirs	da Silva and Langoni (2016)
Suliformes									
Great cormorant (*Phalacrocorax carbo*)	Turkey	Çiğli	1	B, H	1	NS	ND		Karakavuk *et al.* (2018)

B, brain; H, heart; K, kidney; Li, liver; Lu, lung; Sk, skeletal muscle; Sp, spleen; NS, not stated; ND, no data; PCR, polymerase chain reaction; PCR-RFLP, Restriction fragment length polymorphism.

Table 3. *Toxoplasma gondii* DNA from tissues of wild birds

Host	Country	Region	No. tested	Tissue	No. positive	% Positive	Remarks and PCR (gene)	Genotyping	Reference
Accipitriformes									
Black kite (*Milvus migrans*)	Spain	Several	3	B	1	33.3	N-PCR (529 bp – TOX9,11 primers)	ND	Darwich *et al.* (2012)
Common buzzard (*Buteo buteo*)	Turkey	Bergama, Bornova, Çiğli, Kemalpaşa, Konak, Manisa Salihli, Saruhanli, Seferihisar, Turgutlu	25	B, H	23	92.0	RT-PCR, (529 bp – TOX-SE,AS primers). Tg isolated	15 Microsatellite markers – ToxoDB #1 or #3 in 6, #2 in 1 and mixed in 2	Karakavuk *et al.* (2018)
Eurasian sparrow hawk (*Accipiter nisus*)	Turkey	Bornova, Çiğli, Karabağlar, Salihli, Saruhanlı	5	B, H	4	80.0	RT-PCR, (529 bp – TOX-SE,AS primers).		Karakavuk *et al.* (2018)
Griffon vulture (*Gyps fulvus*)	Spain	Several	105	B	1	0.9	N-PCR (529 bp – TOX9,11 primers)	ND	Darwich *et al.* (2012)
Anseriformes									
Canada geese (*Branta canadensis*) Snow geese (*Chen caerulescens*)	Canada	Nunavik	156	B, G, H, Li, Sk	14	9.0	RT-PCR (529 bp – TOX9,11 primers), highest concentration of parasite DNA (tachyzoite equivalent) in H = 744, B = 300, Sk = 104, Li = 33, G = 8	PCR-RFLP using GRA6 – type II	Bachand *et al.* (2019)

Eurasian green-winged teal (*Anas crecca*)	Italy	NS	8	B, H	5	62.5	N-PCR (B1)	ND	Nardoni *et al.* (2019)
Eurasian teal (*Anas crecca*)	Italy	Tuscany	3	B	1	33.3	N-PCR (B1)	10 PCR-RFLP markers – genotype incomplete	Mancianti *et al.* (2013)
Falcated teal (*Falcated teal*)	China	Jilin	8	H or Lu	1	12.5	N-PCR (B1)	10 PCR-RFLP markers – ToxoDB genotype incomplete	Zhang *et al.* (2015)
Geese (unspecified)	China	Shandong	42	Sk	2	4.7	N-PCR (B1)		Zou *et al.* (2017)
Hawaiian geese (*Branta sandvicensis*)	USA	Hawaii	4	Li, Lu	4	100.0	ND	10 PCR-RFLP markers – ToxoDB genotype #261 (21729-Li,21774-Lu, 25022-Li), #262 (21850-Li) (DNA from frozen tissues of IHC confirmed toxoplasmosis)	Work *et al.* (2016)
Mallard (*Anas platyrhynchos*)	China	Jilin	25	H or Lu	5	20.0	N-PCR (B1)	10 PCR-RFLP markers – ToxoDB genotype incomplete	Zhang *et al.* (2015)
Mallard (*Anas platyrhynchos*)	China	Shandong	115	Sk	9	7.8	N-PCR (B1)	10 PCR-RFLP markers – ToxoDB genotype #9 in a duck	Zou *et al.* (2017)
Mallard (*Anas platyrhynchos*)	Czech Republic	Several	280	B, H, Sk	15	5.4	RT-PCR, (B1,529 bp), *Tg* genotyped	6 PCR-RFLP markers – 6 type II, 7 type III, 6 type II/III	Skorpikova *et al.* (2018)
Mallard (*Anas platyrhynchos*)	Italy	Tuscany	2	B	1	50.0	N-PCR (B1)	10 PCR-RFLP markers – genotype incomplete	Mancianti *et al.* (2013)
Northern shoveler (*Anas clypeata*)	Italy	Tuscany	2	B	1	50.0	N-PCR (B1)	10 PCR-RFLP markers – genotype incomplete	Mancianti *et al.* (2013)
Bucerotiformes									
Southern-Yellow-billed hornbill (*Tockus leucomelas*)	South Africa	Limpopo	4	B	1	25.0	PCR (B1 – Tg1,2 primers)		Lukášová *et al.* (2018)
Charadriformes									
Eurasian stone curlew (*Burhinus oedicnemus*)	Turkey	Çiğli	1	B, H	1	100.0	RT-PCR, (529 bp – TOX-SE,AS primers)		Karakavuk *et al.* (2018)
Little tern (*Sternula albifrons*)	Turkey	Çiğli	1	B, H	0	0	RT-PCR, (529 bp – TOX-SE,AS primers)		Karakavuk *et al.* (2018)
Woodcock (*Scolopax rusticola*)	Greece	Macedonia, Mesolonghi	86	B	4	4.7	PCR (529 bp – Tox -9upAu, Tox-11doAu primers)	ND	Moustakidis *et al.* (2017)
Yellow-legged gull (*Larus michahellis*)	Turkey	Balçova, Konak	2	B, H	2	100.0	RT-PCR, (529 bp – TOX-SE,AS primers). Tg isolated	15 Microsatellite markers – ToxoDB #1 or #3 in 1, #2 in 1	Karakavuk *et al.* (2018)
Ciconiiformes									
Black stork (*Ciconia nigra*)	Turkey	NS	1	B, H	1	100.0	RT-PCR, (529 bp – TOX-SE,AS primers)		Karakavuk *et al.* (2018)
White stork (*Ciconia ciconia*)	Turkey	Konak	1	B, H	1	100.0	RT-PCR, (529 bp – TOX-SE,AS primers)		Karakavuk *et al.* (2018)
Columbiformes									
Laughing dove (*Streptopelia senegalensis*)	South Africa	Limpopo	4	B	1	25.0	PCR (B1 – Tg1,2 primers)		Lukášová *et al.* (2018)

(*Continued*)

Table 3. (*Continued.*)

Host	Country	Region	No. tested	Tissue	No. positive	% Positive	Remarks and PCR (gene)	Genotyping	Reference
Mourning dove (*Zenaida macroura*)	USA	Tennessee	186	B	2	1.0	PCR (529 bp, TOX4,5 primers)		Ammar *et al.* (2020)
Red-eyed dove (*Streptopelia semitorquata*)	South Africa	Limpopo	5	B	1	20.0	PCR (B1 – Tg1,2 primers)	15 microsatellites markers – genotyping type II	Lukášová *et al.* (2018)
Rock pigeon (*Columba livia*)	Iran	Khuzestan	43	B, H	3	6.9	PCR (B1 – TG1,2 primers)	PCR-RFLP using GRA6, 1 type II and 2 type III	Khademvatan *et al.* (2013)
Rock pigeon (*Columba livia*)	Pakistan	Punjab	54	H, Sk	19	35.1	PCR (B1 – TOX4,5 primers)	ND	Nazir *et al.* (2018)
Rock pigeon (*Columba livia*)	Portugal	Lisbon	41	B	28	68.2	PCR (B1)	Genotyping by SAG2 (26 type II, 2 type III, 1 type I), and 5 microsatellites markers (12 type II, 2 type III, 1 type 1, 1 recombinant)	Vilares *et al.* (2014)
Rock pigeon (*Columba livia*)	Serbia	Belgrade	7	H	5	71.4	RT-PCR (529 bp)	6 PCR-RFLP markers – 2 type II and 1 type III	Marković *et al.* (2014)
Wood pigeon (*Columba palumbus*)	Italy	NS	1	B, H	1	100.0	N-PCR (B1)	ND	Nardoni *et al.* (2019)
Wood pigeon (*Columba palumbus*)	Turkey	Konak	1	B, H	1	100.0	RT-PCR, (529 bp – TOX-SE,AS primers)		Karakavuk *et al.* (2018)
Falconiformes									
Common kestrel (*Falcus tinnunculus*)	Italy	NS	3	B, H	2	66.6	N-PCR (B1)	ND	Nardoni *et al.* (2019)
Common kestrel (*Falco tinnunculus*)	Poland	Several	3	B, H, Li, Sk	1	33.3	PCR (B1)	5 PCR-RFLP markers – type II/III	Sroka *et al.* (2019)
Common kestrel (*Falco tinnunculus*)	Turkey	Konak	1	B, H	0	0	RT-PCR, (529 bp – TOX-SE,AS primers)		Karakavuk *et al.* (2018)
Eurasian jay (*Garrulus glandarius*)	Slovakia	Tatra National Park	2	Sk	1	50.0	PCR (TGR1E – TGR1E-1,2 primers)	PCR-RFLP using SAG2 – type III	Turčeková *et al.* (2014)
New Zealand falcon (*Falco novaeseelandiae*)	New Zealand	Palmerston	35	H, Li, Lu, Sp	2	5.7	N-PCR (Pppk-dhps)	7 PCR-RFLP markers – genotype incomplete	Mirza *et al.* (2017)
Northern goshawk (*Accipiter gentilis*)	Slovakia	Tatra National Park	2	Sk	1	50.0	PCR (TGR1E – TGR1E-1,2 primers)	PCR-RFLP using SAG2 – type II	Turčeková *et al.* (2014)
Peregrine falcon (*Falco peregrinus*)	Turkey	Çiğli	1	B, H	1	100.0	RT-PCR, (529 bp – TOX-SE,AS primers)		Karakavuk *et al.* (2018)
Galliformes									
Quail (*Coturnix coturnix*)	China	Shandong	390	Sk	25	6.4	N-PCR (B1)	10 PCR-RFLP markers – ToxoDB genotype #9 in 5	Cong *et al.* (2017*b*)
Turkeys (*Meleagris gallopavo*)	Iran	Fars	54	B, Sk, T	33	66.0	N-PCR (B1). Samples from abattoirs	ND	Sarkari *et al.* (2014)

Gruiformes									
Eurasian coot (*Fulica atra*)	China	Jilin	25	H or Lu	1	4.0	N-PCR (B1)	10 PCR-RFLP markers – ToxoDB genotype incomplete	Zhang *et al.* (2015)
Passeriformes									
Hooded crow (*Corvus cornix*)	Iran	Tehran	55	B	9	16.3	N-PCR (GRA6)	PCR-RFLP using GRA6 – type III	Abdoli *et al.* (2018)
Hooded crow (*Corvus cornix*)	Israel	Haifa	101	B	1	1.0	PCR (529 bp – TOX4,5 primers)	11 PCR-RFLP markers – type II	Salant *et al.* (2013)
House sparrows (*Passer domesticus*)	Brazil	Bahia, Pernambuco	40	B	10	10.0	N-PCR (ITS1)	ND	Gondim *et al.* (2010)
House sparrows (*Passer domesticus*)	Brazil	Pernambuco	10	B	3	30.0	N-PCR (B1)		Vilela *et al.* (2011)
House sparrows (*Passer domesticus*)	China	Lanzhou	39	B, H, Lu	11	28.2	N-PCR (B1)	9 PCR-RFLP markers – ToxoDB genotype #3 in 3 and a new type in 1	Cong *et al.* (2013)
House sparrows (*Passer domesticus*)	China	Several	22	Sk	1	4.5	N-PCR (B1)	10 PCR-RFLP markers – ToxoDB genotype #3	Huang *et al.* (2012)
House sparrows (*Passer domesticus*)	Iran	Khuzestan	64	B, H	17	26.5	PCR (B1 – TG1,2 primers)	PCR-RFLP using GRA6, 1 type II and 16 type III	Khademvatan *et al.* (2013)
House sparrows (*Passer domesticus*)	Iran	Tehran	200	B	17	8.5	LAMP, PCR (529 bp – B3,F3, TOX4,5 primers)	ND	Abdoli *et al.* (2016)
Magpie (*Pica pica*)	Italy	Tuscany	41	Bl, H	15	36.6	N-PCR (B1)	5 PCR-RFLP markers – 8 type II and 7 type III	Mancianti *et al.* (2020)
Magpie (*Pica pica*)	Slovakia	Tatra National Park	3	Sk	1	33.3	PCR (TGR1E – TGR1E-1,2 primers)	PCR-RFLP using SAG2 – type III	Turčeková *et al.* (2014)
Magpie (*Pica pica*)	Spain	Several	33	B	5	12.8	N-PCR (529 bp – TOX9,11 primers)	ND	Darwich *et al.* (2012)
Olive-backed pipit (*Anthus hodgsoni*)	China	Hunan	44	B	1	2.2	N-PCR (B1)		Liu *et al.* (2019)
Oriental skylark (*Alauda gulgula*)	China	Lanzhou, Tianshui	34	B	3	8.8	N-PCR (B1)	10 PCR-RFLP markers – type II variant in 2, ToxoDB genotype #3	Cong *et al.* (2014)
Starling (*Sturnus vulgaris*)	Iran	Khuzestan	39	B, H	5	12.8	PCR (B1 – TG1,2 primers)	PCR-RFLP using GRA6, 2 type II and 3 type III	Khademvatan *et al.* (2013)
Thrush nightingale (*Luscinia luscinia*)	Turkey	Konak	1	B, H	1	100.0	RT-PCR, (529 bp – TOX-SE,AS primers)		Karakavuk *et al.* (2018)
Tree sparrows (*Passer montanus*)	China	Hunan	131	B	11	8.4	N-PCR (B1)	10 PCR-RFLP markers – ToxoDB genotype #10 in 3 sparrows	Liu *et al.* (2019)
Tree sparrows (*Passer montanus*)	China	Several	35	Sk	1	2.8	N-PCR (B1)	10 PCR-RFLP markers – ToxoDB genotype #10	Huang *et al.* (2012)
Yellow-breasted bunting (*Emberiza aureola*)	China	Hunan	26	B	1	3.8	N-PCR (B1)		Liu *et al.* (2019)
Phoenicopteriformes									
Great flamingo (*Phoenicopterus roseus*)	Turkey	Konak	1	B, H	1	100.0	RT-PCR, (529 bp – TOX-SE,AS primers)		Karakavuk *et al.* (2018)

(*Continued*)

Table 3. (*Continued.*)

Host	Country	Region	No. tested	Tissue	No. positive	% Positive	Remarks and PCR (gene)	Genotyping	Reference
Psittaformes									
Black-headed gull (*Chroicocephalus ridibundus*)	Italy	NS	4	B, H	4	100.0	N-PCR (B1)	ND	Nardoni *et al.* (2019)
Black-headed gull (*Chroicocephalus ridibundus*)	Poland	Several	2	B, H, Li, Sk	1	50.0	PCR (B1)	5 PCR-RFLP markers type II/III	Sroka *et al.* (2019)
Strigiformes									
Barn owl (*Tyto alba*)	Turkey	Çiğli, Konak	2	B, H	2	100.0	RT-PCR, (529 bp – TOX-SE,AS primers). Tg isolated	15 Microsatellite markers – ToxoDB #1 or #3 in 1, #2 in 1	Karakavuk *et al.* (2018)
Eurasian eagle-owl (*Bubo bubo*)	Turkey	Kemalpaşa, Salihli	2	B, H	2	100.0	RT-PCR, (529 bp – TOX-SE,AS primers)	15 Microsatellite markers – mixed type in 1	Karakavuk *et al.* (2018)
Little owl (*Athene noctua*)	Turkey	Çiğli	1	B, H	1	100.0	RT-PCR, (529 bp – TOX-SE,AS primers)		Karakavuk *et al.* (2018)
Morepork (*Ninox novaeseelandiae*)	New Zealand	Palmerston	36	H, Li, Lu, Sp	3	8.3	PCR (Pppk-dhps)	7 PCR-RFLP markers – genotype incomplete	Mirza *et al.* (2017)
Struthioniformes									
Ostrich (*Struthio camelus*)	Brazil	São Paulo	38	B	25	65.7	PCR (529 bp and 18S rRNA – TOX4,5 and Tg18s48F,359R primers). Tg isolated	10 PCR-RFLP markers – ToxoDB #161 and #206 in 2	da Silva and Langoni (2016)
Ostrich (*Struthio camelus*)	Egypt	Ismailia	120	Bl	9	7.5	N-PCR (B1)	ND	El-Madawy and Metawea (2013)
Suliformes									
Australasian harrier (*Circus approximans*)	New Zealand	Palmerston	46	H, Li, Lu, Sp	4	8.7	PCR (Pppk-dhps)	7 PCR-RFLP markers – genotype incomplete	Mirza *et al.* (2017)
Baikal teal (*Anas formosa*)	China	Jilin	50	H or Lu	11	22.0	N-PCR (B1)	10 PCR-RFLP markers – ToxoDB genotype #9 in 2	Zhang *et al.* (2015)
Common pheasants (*Phasianus colchicus*)	China	Several	98	Sk	2	2.0	N-PCR (B1)	10 PCR-RFLP markers – ToxoDB genotype #3	Huang *et al.* (2012)
Common pheasant (*Phasianus colchicus*)	Czech Republic	Several	350	B, H, Sk	12	3.4	RT-PCR, (B1,529 bp), Tg genotyped	6 PCR-RFLP markers – 1 type II, 4 type III, 4 type II/III	Skorpikova *et al.* (2018)
Dalmatian pelican (*Pelecanus crispus*)	Turkey	Çiğli	1	B, H	1	100.0	RT-PCR, (529 bp – TOX-SE,AS primers)		Karakavuk *et al.* (2018)
Eurasian jays (*Garrulus glandarius*)	Spain	Several	23	B	5	21.7	N-PCR (529 bp – TOX9,11 primers)	ND	Darwich *et al.* (2012)
Eurasian siskin (*Carduelis spinus*)	China	Lanzhou	41	B	5	12.2	N-PCR (B1)	10 PCR-RFLP markers – type II variant in 2, ToxoDB #3	Cong *et al.* (2014)
Great cormorant (*Phalacrocorax carbo*)	Turkey	Çiğli	1	B, H	1	100.0	RT-PCR, (529 bp – TOX-SE,AS primers). Tg isolated		Karakavuk *et al.* (2018)

B, brain; Bl, blood; H, heart; G, gizzard; Li, liver; Lu, lung; Sk, muscle; Sp, spleen; Tg, *Toxoplasma gondii*; ND, not done; NS, not stated; PCR, polymerase chain reaction; N-PCR, nested PCR; RT-PCR, real-time PCR; PCR, polymerase chain reaction; PCR-RFLP, Restriction fragment length polymorphism.

Table 4. Seroprevalence of *Toxoplasma gondii* in domestic ducks

Country	Area	Source	No. tested	No. positive	% Positive	Test	Cut-off	Remarks	Reference
China	Chongqing	NS	635 – FR	84	13.3	MAT	1:25	Tg isolated. Location, type of raising AS	Zhao *et al.* (2015)
			527 – caged	35	6.6				
China	Guangzhou	Abattoirs	349	56	16.0	MAT	1:5	6 had MAT titers of 1:40 or higher	Yan *et al.* (2009)
China	Jilin	Farms	268	29	0.8	LAT[a]	1:64		Li *et al.* (2020)
China	Lanzhou	Abattoirs	111 – caged	7	6.3	MAT	1:5		Cong *et al.* (2012)
			223 – FR	31	13.9				
China	Liaoning	Farms	268	26	9.7	MAT	1:25		Wang *et al.* (2014)
China	Shenyang	Abattoirs	146 – caged	11	7.5	MAT	1:25		Yang *et al.* (2012)
			122 – FR	15	12.3				
Czech Republic	Several	Abattoirs	360	52	14.0	IFA	1:40		Bártová *et al.* (2009)
Egypt	Behera	Abattoirs	151	21	13.9	MAT	1:25		AbouLaila *et al.* (2011)
Egypt	Kafr El-Sheikh	Farms	58	32	55.0	IHA[a]	1:80		Harfoush and Tahoon (2010)
Egypt	5 regions	Market	142	15	10.5	ELISA		IHC 3 positive. Region AS	Ibrahim *et al.* (2018)
Germany	Lower Saxony	61 farms	2534	145	5.7	ELISA – SAG1	1:200	Protection AS to indoors kept animals	Maksimov *et al.* (2011)
Iraq	Al-Qadisiya	Farms	50	28	56.0	LAT[a]	1:2		Alkhaled *et al.* (2012)
Iran	Mazandaran	Market	87	40	46.0	MAT	1:20		Amouei *et al.* (2018)
Malaysia	Johor, Kedah, Melaka, Perak	Farms, FR	205	30	14.6	MAT	1:6	Tg DNA and genotyping	Puvanesuaran *et al.* (2013)
Poland	Lublin	Farms	33	7	21.2	MAT[a]	1:40		Sroka *et al.* (2010)
Senegal	Dakar, Saint-Louis	Households	306	16	5.2	MAT	1:20	Tg isolated	Galal *et al.* (2019)

NS, not stated; ELISA, enzyme-linked immunosorbent assay; IFA, indirect fluorescent antibody test; IHAT, indirect haemagglutination test; LAT, latex agglutination test; MAT, modified agglutination test (Dubey and Desmonts, 1987); FR, free range; Tg, *Toxoplasma gondii*; AS, association; IHC, immunohistochemical.
[a]IHA (Toxo-IHA Fumouze Diagnostics, France); LAT (PLASMATECH Co., UK); MAT (Toxo-Screen DA®, Biomerieux, Lyon, France). This is the same test as MAT.

Table 5. Seroprevalence of *Toxoplasma gondii* in domestic goose

Country	Area	Source	No. tested	No. positive	% Positive	Test	Cut-off	Remarks	Reference
China	Guangdong	Farms	274	41	14.9	MAT	1:5	–	Yan *et al.* (2011*b*)
China	Guangdong	Farms	520	9	1.7	MAT		Age, management	Wang *et al.* (2012)
China	Hainan	Farms	600	102	17.0	IHA[a]	1:64	Presence of cats, hygiene AS. Tg DNA and genotyping	Rong *et al.* (2014)
China	Jilin	Farms	379	50	13.2	IHA[a]	1:64		Li *et al.* (2020)
China	Liaoning	Farms	128	9	7.0	MAT	1:25		Wang *et al.* (2014)
China	Shenyang	Abattoirs	83 – caged	5	6.0	MAT	1:25		Yang *et al.* (2012)
			45 – FR	4	8.9				
Czech Republic	Bohemia, Olomouc	Abattoirs	178	77	43.0	IFA	1:40		Bártová *et al.* (2009)
Germany	Lower Saxony	13 farms	373	94	25.2	ELISA-SAG1	1:200	Protection AS to indoors kept animals	Maksimov *et al.* (2011)
Iran	Mazandaran	Market	5	5	100.0	MAT	1:20	–	Amouei *et al.* (2018)
USA	Maryland	Hunted	169	12	7.1	MAT	1:25	Canada geese, Tg isolated	Verma *et al.* (2016)

AS, association; FR, free-range; Tg, *Toxoplasma gondii*; ELISA, enzyme-linked immunosorbent assay; IFA, indirect fluorescent antibody test; IHA, indirect haemagglutination assay; MAT, modified agglutination test (Dubey and Desmonts, 1987).
[a]IHA kit (Lanzhou Veterinary Research Institute, Chinese Academy of Agricultural Sciences, Lanzhou, China).

Table 6. Seroprevalence of *Toxoplasma gondii* in ratites

Host	Country	Area	Source	No. tested	No. positive	% positive	Test	Cut-off	Remarks	Reference
Emus (*Dromaius novaehollandiae*)	Brazil	Goiás	Farm	16	8	50.0	MAT	1:25		Gallo *et al.* (2019)
Ostriches (*Struthio camelus*)	Brazil	Mato Grosso, Rio Grande do Sul, São Paulo	3 Farms	46	8	17.4	MAT	1:16		Almeida *et al.* (2013)
Ostriches (*Struthio camelus*)	Brazil	Rio de Janeiro	Abattoirs	20	16	80.0	MAT	1:25		Gallo *et al.* (2019)
Ostriches (*Struthio camelus*)	Brazil	São Paulo	Farms	195	28	14.3	MAT	1:16	MAT titer 1:16384 in 2 ostriches	Contente *et al.* (2009)
Ostriches (*Struthio camelus*)	Brazil	São Paulo	Abattoir, 4 farms	344	38	11.0	MAT	1:8	Tg DNA and parasite isolation, Water source, presence of non-ostrich feces AS	da Silva and Langoni (2016)
Ostriches (*Struthio camelus*)	China	Hebei, Henan	Abattoirs	315	20	6.4	MAT	1:25	Tg DNA and parasite isolation	Feng *et al.* (2017)
Ostriches (*Struthio camelus*)	Egypt	Ismailia	Farm	120	15	12.5	MAT	1:25	Tg DNA. 5 (4.2%) IgM positive	El-Madawy and Metawea (2013)
Rheas (*Rhea americana*)	Brazil	Espírito Santo, Goiás, São Paulo	Farm	68	18	26.5	MAT	1:25		Gallo *et al.* (2019)
Rheas (*Rhea americana*)	Brazil	Rio Grande do Sul, Santa Catarina	2 Farms	20	10	50.0	MAT	1:25		Almeida *et al.* (2013)

MAT, modified agglutination test (Dubey and Desmonts, 1987); AS, association; Tg, *Toxoplasma gondii*.

Table 7. Serologic prevalence of antibodies to *Toxoplasma gondii* in wild birds

Order, common name, (*scientific name*)	Country	Region	No. tested	No. positive	% Positive	Test	Cut-off	Notes	Reference
Accipitriformes									
Bald eagle (*Haliaeetus leucocephalus*)	Czech Republic	Zoos	1	1	100.0	LAT[a]			Bártová *et al.* (2018)
Bald eagle (*Haliaeetus leucocephalus*)	USA	Alabama	13	12	92.3	MAT	1:25		Love *et al.* (2016)
Bearded vulture (*Gypaetus barbatus*)	Spain	Several	15	6	42.8	MAT	1:25		Cabezón *et al.* (2011)
Black kite (*Milvus migrans*)	Portugal	Central, northern	1	1	100.0	MAT	1:20		Lopes *et al.* (2011)
Black kite (*Milvus migrans*)	Senegal	Dakar	2	2	100.0	MAT	1:20		Galal *et al.* (2019)
Black kite (*Milvus migrans*)	Spain	Several	17	5	29.4	MAT	1:25		Cabezón *et al.* (2011)
Bonelli's eagle (*Aquila fasciata*)	Spain	Several	9	1	11.1	MAT	1:25		Cabezón *et al.* (2011)
Booted eagle (*Hieraaetus pennatus*)	Spain	Southern	1	1	100.0	MAT	1:25		Cano-Terriza *et al.* (2015)
Broad-winged hawk (*Buteo platypterus*)	USA	Alabama	20	6	30.0	MAT	1:25		Love *et al.* (2016)
Cinereous vulture (*Aegypius monachus*)	Czech Republic	Zoos	11	7	64.0	LAT[a]	–		Bártová *et al.* (2018)
Cinereous vulture (*Aegypius monachus*)	Spain	Several	23	6	26.0	MAT	1:25		Cabezón *et al.* (2011)
Common buzzard (*Buteo buteo*)	Portugal	Central, northern	26	18	69.2	MAT	1:20		Lopes *et al.* (2011)
Cooper's hawk (*Accipiter cooperii*)	USA	Alabama	12	6	50.0	MAT	1:25		Love *et al.* (2016)
Crested goshawk (*Accipiter trivirgatus*)	Taiwan	Several	41	7	17.0	MAT[b]	1:40		Chen *et al.* (2015)
Eagle (*Aquila* spp.)	Mexico	Durango	2	1	50.0	MAT	1:25	Location AS	Alvarado-Esquivel *et al.* (2011)
Eurasian buzzard (*Buteo buteo*)	Italy	Northern	12	1	8.3	MAT[b]	1:40		Gazzonis *et al.* (2018)
Eurasian buzzard (*Buteo buteo*)	Spain	Several	96	49	51.0	MAT	1:25		Cabezón *et al.* (2011)
Eurasian griffon (*Gyps fulvus*)	Czech Republic	Zoos	4	3	75.0	LAT[a]	–		Bártová *et al.* (2018)
Eurasian sparrow hawk (*Accipiter nisus*)	Italy	Northern	2	1	50.0	MAT[b]	1:40		Gazzonis *et al.* (2018)
Golden eagle (*Aquila chrysaetos*)	Spain	Several	8	5	62.5	MAT	1:25		Cabezón *et al.* (2011)
Golden eagle (*Aquila chrysaetos*)	USA	Alabama	1	1	100.0	MAT	1:25		Love *et al.* (2016)
Griffon vulture (*Gyps fulvus*)	Israel	4 Areas	101	40	39.6	MAT	1:25		Salant *et al.* (2013)
Griffon vulture (*Gyps fulvus*)	Spain	Several	175	31	17.7	MAT	1:25		Cabezón *et al.* (2011)
Montagu's harrier (*Circus pygargus*)	Spain	Several	7	1	14.3	MAT	1:25		Cabezón *et al.* (2011)
Northern goshawk (*Accipiter gentilis*)	Portugal	Central, northern	3	3	100.0	MAT	1:20		Lopes *et al.* (2011)
Northern goshawk (*Accipiter gentilis*)	Spain	Several	5	2	40.0	MAT	1:25		Cabezón *et al.* (2011)
Osprey (*Pandion haliaetus*)	Spain	Several	7	2	28.5	MAT	1:25		Cabezón *et al.* (2011)

(*Continued*)

Table 7. (*Continued.*)

Order, common name, (*scientific name*)	Country	Region	No. tested	No. positive	% Positive	Test	Cut-off	Notes	Reference
Red kite (*Milvus milvus*)	Spain	Several	3	1	33.3	MAT	1:25		Cabezón *et al.* (2011)
Red-shouldered hawk (*Buteo lineatus*)	USA	Alabama	41	9	21.9	MAT	1:25		Love *et al.* (2016)
Red tailed hawk (*Buteo jamaicensis*)	USA	Alabama	71	22	30.9	MAT	1:25		Love *et al.* (2016)
Roadside hawk (*Rupornis magnirostris*)	Brazil	São Paulo	1	1	100.0	MAT	1:16		Gonçalves *et al.* (2013)
Serpent eagle (*Spilornis cheela*)	Taiwan	Several	43	20	46.5	MAT[b]	1:40		Chen *et al.* (2015)
Short-toed Snake-eagle (*Circaetus gallicus*)	Spain	Several	10	5	50.0	MAT	1:25		Cabezón *et al.* (2011)
Spanish Imperial eagle (*Aquila adalberti*)	Spain	Several	146	25	17.0	MAT	1:25		Cabezón *et al.* (2011)
Tawny eagle (*Aquilla rapax*)	Czech Republic	Zoos	1	1	100.0	LAT[a]	–		Bártová *et al.* (2018)
Western marsh-harrier (*Circus aeruginosus*)	Italy	Northern	2	1	50.0	MAT[b]	1:40		Gazzonis *et al.* (2018)
Western marsh-harrier (Circus *aeruginosus*)	Spain	Several	6	3	50.0	MAT	1:25		Cabezón *et al.* (2011)
Anseriformes									
Bar-headed goose (*Anser indicus*)	Spain	Córdoba	11	1	9.1	MAT	1:25		Cano-Terriza *et al.* (2015)
Barnacle goose (*Branta leucopsis*)	Europe	Russia, Svalbard, The Netherlands	1087	98	9.0	MAT[b]	1:40	See text	Sandström *et al.* (2013)
Black swan (*Cygnus atratus*)	Portugal	Zoo	7	1	14.3	MAT[b]	1:20		Tidy *et al.* (2017)
Canada goose (*Branta canadensis*)	Canada	Saskatoon	71	2	2.8	MAT[b]	1:40		Al-Adhami *et al.* (2016)
Canada goose (*Branta canadensis*)	Canada	Nunavik	148	16	10.8	MAT[a]	1:25		Bachand *et al.* (2019)
Canada goose (*Branta canadensis*)	Europe	The Netherlands	38	3	7.9	MAT[b]	1:40	See text	Sandström *et al.* (2013)
Common teal (*Anas crecca*)	Italy	Tuscany	41	3	7.3	MAT[b]	1:10	PCR positive in 1 seropositive	Mancianti *et al.* (2013)
Coscoroba swan (*Coscoroba coscoroba*)	Czech Republic	Zoos	2	1	50.0	LAT[a]			Bártová *et al.* (2018)
Domestic geese (*Anser anser*)	Europe	The Netherlands	161	13	8.1	MAT[b]	1:40	See text	Sandström *et al.* (2013)
Emperor goose (*Chen canagica*)	Spain	Southern	2	1	50.0	MAT	1:25		Cano-Terriza *et al.* (2015)
Eurasian green-winged teal (*Anas crecca*)	Iran	Mazandaran	20	12	60.0	MAT	1:20		Amouei *et al.* (2018)
Garganey (*Spatula querquedula*)	Senegal	Dakar	28	8	28.5	MAT	1:20		Galal *et al.* (2019)
Geese (*Anser* sp.)	Brazil	Paraná	149	27	18.1	IFA	1:25	Higher prevalence in animals from urban parks	Konell *et al.* (2019)

(*Continued*)

Table 7. (*Continued.*)

Order, common name, (*scientific name*)	Country	Region	No. tested	No. positive	% Positive	Test	Cut-off	Notes	Reference
Lesser snow geese (*Chen caerulescens*)	Canada	Karrak Lake Nunavut	121	43	36.0	IFA	1:20	Results higher than MAT[b] at 1:40 dilution	Elmore *et al.* (2014)
Lesser snow geese (*Chen caerulescens*)	Canada	Nunavut	233	66	28.3	ELISA			Elmore *et al.* (2015)
Lesser snow geese (*Chen caerulescens*)	Canada	Nunavik	8	2	25.0	MAT[a]	1:25		Bachand *et al.* (2019)
Ross's geese (*Chen rossi*)	Canada	Nunavut	234	76	32.4	ELISA			Elmore *et al.* (2015)
Mallard duck (*Anas brachyrhynchus*)	Europe	Denmark, Svalbard	573	59	10.2	MAT[b]	1:40	See text	Sandström *et al.* (2013)
Mallard duck (*Anas platyrhynchos*)	Mexico	Durango	2	1	50.0	MAT	1:25	Location AS	Alvarado-Esquivel *et al.* (2011)
Mallard duck (*Anas platyrhynchos*)	Iran	Mazandaran	20	9	45.0	MAT	1:20	–	Amouei *et al.* (2018)
Mallard duck (*Anas platyrhynchos*)	Italy	Tuscany	17	2	11.7	MAT[b]	1:10	PCR positive in 1 seropositive	Mancianti *et al.* (2013)
Mallard duck (*Anas platyrhynchos*)	Portugal	Zoo	4	3	75.0	MAT[b]	1:20		Tidy *et al.* (2017)
Mallard duck (*Anas platyrhynchos*)	Spain	Several	6	2	33.3	MAT	1:25		Cabezón *et al.* (2011)
Mallard duck (*Anas platyrhynchos*)	Spain	Southern	4	1	25.0	MAT	1:25		Cano-Terriza *et al.* (2015)
Mallard duck (*Anas platyrhynchos*)	Taiwan	Several	1	1	100.0	MAT[b]	1:40		Chen *et al.* (2015)
Mandarian duck (*Aix galericulata*)	Portugal	Zoo	6	3	50.0	MAT[b]	1:20		Tidy *et al.* (2017)
Mexican duck (*Anas diazi*)	Mexico	Durango	2	1	50.0	MAT	1:25	Location AS	Alvarado-Esquivel *et al.* (2011)
Mute swan (*Cygnus olor*)	USA	Northeastern	632	54	8.5	MAT	1:25	Tg isolated	Dubey *et al.* (2013)
Northern pintail (*Anas acuta*)	Spain	Several	1	1	100.0	MAT	1:25		Cabezón *et al.* (2011)
Orinoco (*Neochen jubata*)	Brazil	Goiás	41	35	85.3	IFA	1:20	*N. caninum* in 12.1%	André *et al.* (2019)
Paradise shelduck (*Tadorna variegata*)	Czech Republic	Zoos	1	1	100.0	LAT[a]	–		Bártová *et al.* (2018)
Ross's geese (*Chen rossi*)	Canada	Karrak Lake Nunavut	123	48	39.0	IFA	1:20	Results higher than MAT[b] at 1:40 dilution	Elmore *et al.* (2014)
Shoveller duck (*Anas clypeata*)	Italy	Tuscany	11	2	18.1	MAT[b]	1:10	PCR positive in 1 seropositive	Mancianti *et al.* (2013)
Sudanese duck (*Anas platyrhynchos*)	Egypt	Several	142	15	10.5	ELISA		Region AS. IHC	Ibrahim *et al.* (2018)
Swan goose (*Anser cygnoides*)	Portugal	Zoo	1	1	100.0	MAT[b]	1:20		Tidy *et al.* (2017)
Tundra swan (*Cygnus columbianus*)	China	Jiangxi	9	2	22.2	IHA[b]	1:64		Luo *et al.* (2017)
Wood duck (*Aix sponsa*)	Portugal	Zoo	7	2	28.6	MAT[b]	1:20		Tidy *et al.* (2017)
Bucerotiformes									
Eurasian hoopoe (*Upupa epops*)	Spain	Several	1	1	100.0	MAT	1:25		Cabezón *et al.* (2011)

(*Continued*)

Table 7. (*Continued.*)

Order, common name, (*scientific name*)	Country	Region	No. tested	No. positive	% Positive	Test	Cut-off	Notes	Reference
Cariamiformes									
Crested seriema (*Cariama cristata*)	Brazil	Minas Gerais, São Paulo	1	1	100.0	MAT	1:5		Vitaliano *et al.* (2014)
Charadriformes									
Audouin's gull (*Larus audouinii*)	Spain	Alboran Island	46	1	2.2	MAT	1:25	Age, food source, year AS	Cabezón *et al.* (2016)
Caracara (*Caracara plancus*)	Brazil	Pernambuco	115	6	5.2	MAT	1:25		Silva *et al.* (2018*a*)
Common kestrel (*Falco tinnunculus*)	Italy	Northern	18	1	5.5	MAT[b]	1:40		Gazzonis *et al.* (2018)
Common snipe (*Gallinago gallinago*)	Italy	Tuscany	8	2	25.0	MAT[b]	1:10		Mancianti *et al.* (2013)
Common snipe (*Gallinago gallinago*)	Pakistan	Punjab	4	1	25.0	LAT[b]	1:64	Age, health status AS	Naveed *et al.* (2019)
Yellow-legged gull (*Larus michahellis*)	Europe	France, Spain, Tunisia	988 nests	233	23.6	ELISA[b]		ELISA in 1122 egg yolk. Different prevalence between colonies AS	Gamble *et al.* (2019)
Yellow-legged gull (*Larus michahellis*)	Spain	Iberian Peninsula	479	109	22.8	MAT	1:25	Age, food source, year AS	Cabezón *et al.* (2016)
Ciconiiformes									
Black stork (*Ciconia nigra*)	Spain	Several	1	0	0	MAT	1:25		Cabezón *et al.* (2011)
White stork (*Ciconia ciconia*)	Spain	Several	64	9	14.1	MAT	1:25		Cabezón *et al.* (2011)
Columbiformes									
Dove (*Spilopelia* sp.)	Senegal	Dakar	1	1	100.0	MAT	1:20		Galal *et al.* (2019)
Eared dove (*Zenaida auriculata*)	Brazil	Paraná	206	46	22.3	MAT	1:16	Location AS. Tg isolated	de Barros *et al.* (2014)
Eurasian collared dove (*Streptopelai decaocto*)	Pakistan	Punjab	10	2	20.0	LAT[b]	1:64	Age, health status AS	Naveed *et al.* (2019)
Feral pigeon (*Columba livia var. domestica*)	Spain	Southern	142	13	9.2	MAT	1:25		Cano-Terriza *et al.* (2015)
Gray-fronted dove (*Leptotila rufaxilla*)	Brazil	Paraíba	5	1	20.0	MAT	1:25		Andrade *et al.* (2016)
Oriental turtle dove (*Streptopelia orientalis*)	Taiwan	Several	16	4	25.0	MAT[b]	1:40		Chen *et al.* (2015)
Picazuro pigeon (*Patagioenas picazuro*)	Brazil	Minas Gerais, São Paulo	3	1	33.3	MAT	1:5		Vitaliano *et al.* (2014)
Rock pigeon (*Columba livia*)	Brazil	São Paulo	126	0	0	MAT	1:5	Tg not isolated by bioassay of any of 126 pigeons	de Godoi *et al.* (2010)
Rock pigeon (*Columba livia*)	Brazil	São Paulo	120	1	0.8	IFA	1:20		de Sousa *et al.* (2010)
Rock pigeon (*Columba livia*)	Brazil	São Paulo	238	12	5.0	MAT	1:8	Tg not isolated	de Lima *et al.* (2011)
Rock pigeon (*Columba livia*)	China	Guangdong	275	24	8.7	MAT	1:5		Yan *et al.* (2011*a*)
Rock pigeon (*Columba livia*)	China	Several	963	104	10.8	IHA[b]	1:64	Age, gender AS	Zhang *et al.* (2019)

(*Continued*)

Table 7. (*Continued.*)

Order, common name, (*scientific name*)	Country	Region	No. tested	No. positive	% Positive	Test	Cut-off	Notes	Reference
Rock pigeon (*Columba livia*)	Egypt	Several	310	42	13.5	ELISA		IHC	Ibrahim *et al.* (2018)
Rock pigeon (*Columba livia*)	Israel	Several	495	20	4.0	MAT	1:5	Climate, population near to human settlement	Salant *et al.* (2009)
Rock pigeon (*Columba livia*)	Mexico	Durango	521	7	1.9	MAT	1:25	Location AS. Tg isolated	Alvarado-Esquivel *et al.* (2011)
Rock pigeon (*Columba livia*)	Portugal	Lisbon	1507	39	2.6	MAT[b]	1:20	Tg isolated in cell cultures seeded with 13 of 20 seropositive pigeons	Waap *et al.* (2012)
Rock pigeon (*Columba livia*)	Russia	Circus animals	28	10	35.7	ELISA[a]			Sivkova and Neprimerova (2017)
Rock pigeon (*Columba* livia)	Spain	Córdoba	142	13	9.2	MAT	1:25		Cano-Terriza *et al.* (2015)
Rock pigeon (*Columba* livia)	Taiwan	Several	62	1	1.6	MAT[b]	1:40		Chen *et al.* (2015)
Rock pigeon (*Columba livia*)	Turkey	Niğde	216	2	0.9	DT	1:16		Karatepe *et al.* (2011)
Rock pigeon (*Columba livia*)	USA	Colorado	129	5	3.9	MAT	1:25		Dubey *et al.* (2010)
Rock pigeon (*Columba livia*)	USA	Tennessee	1	1	100.0	MAT	1:32		Gerhold *et al.* (2017)
Spotted-necked dove (*Streptopelia chinensis*)	Taiwan	Several	17	5	29.4	MAT[b]	1:40		Chen *et al.* (2015)
Cuculiformes									
Coucal (*Centropus* sp.)	Senegal	Dakar	1	1	100.0	MAT	1:20		Galal *et al.* (2019)
Falconiformes									
Common kestrel (*Falco tinnunculus*)	Italy	Parma	238	62	26.1	MAT[b]	1:25	Age, year sampled, AS	Iemmi *et al.* (2020)
Common kestrel (*Falco tinnunculus*)	Spain	Several	13	4	30.7	MAT	1:25		Cabezón *et al.* (2011)
Crested caracara (*Caracara plancus*)	Brazil	Minas Gerais, São Paulo	2	1	50.0	MAT	1:5		Vitaliano *et al.* (2014)
Eurasian hobby (*Falco subbuteo*)	Italy	Northern	3	1	33.3	MAT[b]	1:40		Gazzonis *et al.* (2018)
Lesser kestrel (*Falco naumanni*)	Spain	Several	5	2	40.0	MAT	1:25		Cabezón *et al.* (2011)
Peregrine falcon (*Falco peregrinus*)	Spain	Several	4	1	25.0	MAT	1:25		Cabezón *et al.* (2011)
Yellow-headed caracara (*Milvago chimachima*)	Brazil	São Paulo	3	2	66.6	MAT	1:16		Gonçalves *et al.* (2013)
Galliformes									
Common quail (*Coturnix coturnix*)	China	3 Provinces	620	59	9.5	MAT	1:5		Cong *et al.* (2017*b*)
Common quail (*Coturnix coturnix*)	Mexico	Durango	7	1	14.2	MAT	1:25	Location AS	Alvarado-Esquivel *et al.* (2011)
Common quail (*Coturnix coturnix*)	Turkey	Niğde	144	0	0	DT	NS		Kiliç *et al.* (2017)
Guinea fowl (*Numida meleagris*)	Brazil	Minas Gerais	10	2	20.0	MAT	1:10	Tg isolated	Dubey *et al.* (2011*a*)

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Table 7. (*Continued.*)

Order, common name, (*scientific name*)	Country	Region	No. tested	No. positive	% Positive	Test	Cut-off	Notes	Reference
Guinea fowl (*Numida meleagris*)	Brazil	Rio de Janeiro	114	14	12.3	MAT	1:16		Ferreira *et al.* (2013)
Guinea fowl (*Numida meleagris*)	Senegal	Dakar	13	1	7.7	MAT	1:20	Tg isolated	Galal *et al.* (2019)
Hawaiian goose (*Branta sandvicensis*)	USA	Hawaii	94	26	27.6	MAT	1:25	48% in Molokai, 23% in Maui, and 21% in Kauai	Work *et al.* (2016)
Silver pheasant (*Laphura nycthemera*)	Portugal	Zoo	6	1	16.6	MAT[b]	1:20		Tidy *et al.* (2017)
Rock ptarmigan (*Lagopus muta*)	Canada	Saskatoon	25	1	4.0	MAT[b]	1:40		Al-Adhami *et al.* (2016)
Gruiformes									
Common coot (*Fulica atra*)	Spain	Several	1	1	100.0	MAT	1:25		Cabezón *et al.* (2011)
Common moorhen (*Gallinula chloropus*)	Pakistan	Punjab	5	1	20.0	LAT[b]	1:64	Age, health status AS	Naveed *et al.* (2019)
Common moorhen (*Gallinula chloropus*)	Spain	Several	1	1	100.0	MAT	1:25		Cabezón *et al.* (2011)
Eurasian coot (*Fulica atra*)	Iran	Mazandaran	10	5	50.0	MAT	1:20		Amouei *et al.* (2018)
Grey crowned crane (*Balearica regulorum*)	Portugal	Zoo	4	0	0.0	MAT[b]	1:20		Tidy *et al.* (2017)
Japanese crane (*Grus japonensis*)	Portugal	Zoo	2	1	50.0	MAT[b]	1:20		Tidy *et al.* (2017)
Rail (*Rallus* sp.)	Senegal	Dakar	2	1	50.0	MAT	1:20		Galal *et al.* (2019)
Otidiformes									
Great bustard (*Otis tarda*)	Spain	Several	7	1	14.2	MAT	1:25		Cabezón *et al.* (2011)
Passeriformes									
Ashy-throated casiornis (*Casiornis fuscus*)	Brazil	Bahia	1	1	100.0	MAT	1:25		Andrade *et al.* (2016)
Black drongo (*Dicrurus macrocercus*)	Pakistan	Punjab	9	1	11.1	LAT[b]	1:64	Age, health status AS.	Naveed *et al.* (2019)
Buff-browed foliage-gleaner (*Syndactyla rufosuperciliata*)	Brazil	São Paulo	7	4	57.1	MAT	1:5		Gennari *et al.* (2014)
Common babbler (*Turdoides caudatus*)	Pakistan	Punjab	2	1	50.0	LAT[b]	1:64	Age, health status AS.	Naveed *et al.* (2019)
Common myna (*Acridotheres tristis*)	Pakistan	Punjab	11	2	18.1	LAT[b]	1:64	Age, health status AS	Naveed *et al.* (2019)
Common raven (*Corvus corax*)	Spain	Northeast	113	91	80.5	MAT	1:25	Year sampled AS	Molina-López *et al.* (2012)
Creamy-bellied thrush (*Turdus amaurochalinus*)	Brazil	São Paulo	2	1	50.0	MAT	1:5		Gennari *et al.* (2014)
Curve-billed thrasher (*Toxostoma curvirostre*)	Mexico	Durango	2	1	50.0	MAT	1:25		Alvarado-Esquivel *et al.* (2011)
European goldfinch (*Carduelis carduelis*)	Spain	Several	1	1	100.0	MAT	1:25		Cabezón *et al.* (2011)
European starling (*Sturnus vulgaris*)	USA	Colorado	27	4	15.0	MAT	1:50		Dubey *et al.* (2010)
Formosan blue magpie (*Urocissa caerulea*)	Taiwan	Several	16	6	37.5	MAT[b]	1:40		Chen *et al.* (2015)
Golden-crowned warbler (*Basileuterus culicivorus*)	Brazil	São Paulo	12	2	16.7	MAT	1:5		Gennari *et al.* (2014)
Great-tailed grackle (*Quiscalus mexicanus*)	Mexico	Durango	18	5	27.8	MAT	1:25	Location AS	

(*Continued*)

Table 7. (*Continued.*)

Order, common name, (*scientific name*)	Country	Region	No. tested	No. positive	% Positive	Test	Cut-off	Notes	Reference
									Alvarado-Esquivel *et al.* (2011)
Hooded crow (*Corvus cornix*)	Israel	6 areas	101	48	47.5	MAT	1:25	Geographic location AS	Salant *et al.* (2013)
Hooded crow (*Corvus cornix*)	Italy	Pisa	120	4	3.3	MAT[b]	1.25		Mancianti *et al.* (2020)
House crow (*Corvus splendens*)	Israel	Eilat	16	2	12.5	MAT	1:25		Salant *et al.* (2013)
House crow (*Corvus splendens*)	Pakistan	Punjab	17	6	35.3	LAT[b]	1:64	Age, health status AS	Naveed *et al.* (2019)
House sparrow (*Passer domesticus*)	Brazil	Bahia, Pernambuco	293	3	1.0	IHA	1:32	Tg DNA	Gondim *et al.* (2010)
House sparrow (*Passer domesticus*)	Brazil	Pernambuco	151	91	60.3	IHA[a]	1:16	Tg DNA	Vilela *et al.* (2011)
House sparrow (*Passer domesticus*)	China	Lanzhou	313	39	12.4	MAT	1:5	Tg DNA in 11 tissues of 39 seropositive	Cong *et al.* (2013)
House sparrow (*Passer domesticus*)	Pakistan	Punjab	9	1	11.1	LAT[b]	1:64	Age, health status AS	Naveed *et al.* (2019)
Indian silverbill (*Lonchura malabarica*)	Pakistan	Punjab	4	2	50.0	LAT[b]	1:64	Age, health status AS	Naveed *et al.* (2019)
Jackdaw crow (*Corvus monedula*)	Israel	Ganei Yavne	5	2	40.0	MAT	1:25	–	Salant *et al.* (2013)
Java sparrows (*Lonchura oryzivora*)	China	Beijing, Shangqiu	350	120	34.3	MAT	1:20	Gender, colour AS	Huang *et al.* (2019)
Jungle babbler (*Turdoides striatus*)	Pakistan	Punjab	6	1	16.6	LAT[b]	1:64	Age, health status AS	Naveed *et al.* (2019)
Lesser woodcreeper (*Xiphorhynchus fuscus*)	Brazil	São Paulo	2	1	50.0	MAT	1:5		Gennari *et al.* (2014)
Magpie (*Pica pica*)	Italy	Pisa	651	41	6.2	MAT[b]	1:40		Mancianti *et al.* (2020)
Magpie (*Pica pica*)	Taiwan	Several	22	10	45.5	MAT[b]	1:40		Chen *et al.* (2015)
Pale-breasted thrush (*Turdus leucomelas*)	Brazil	São Paulo	1	1	100.0	MAT	1:5		Gennari *et al.* (2014)
Pied crow (*Corvus albus*)	Senegal	Dakar	2	2	100.0	MAT	1:20		Galal *et al.* (2019)
Plain antvireo (*Dysithamnus mentalis*)	Brazil	São Paulo	11	5	45.4	MAT	1:5		Gennari *et al.* (2014)
Red-crowned ant-tanager (*Habia rubica*)	Brazil	São Paulo	13	8	61.5	MAT	1:5		Gennari *et al.* (2014)
Red vented bulbul (*Pycnonotus cafer*)	Pakistan	Punjab	11	3	27.2	LAT[b]	1:64	Age, health AS	Naveed *et al.* (2019)
Ruby-crowned tanager (*Tachyphonus coronatus*)	Brazil	São Paulo	6	1	16.7	MAT	1:5		Gennari *et al.* (2014)
Rufous-bellied thrush (*Turdus rufiventris*)	Brazil	São Paulo	18	15	83.3	MAT	1:5		Gennari *et al.* (2014)
Rufous-breasted leaftosser (*Sclerurus scansor*)	Brazil	São Paulo	1	1	100.0	MAT	1:5		Gennari *et al.* (2014)
Rufous gnateater (*Conopophaga lineata*)	Brazil	São Paulo	15	6	40.0	MAT	1:5		Gennari *et al.* (2014)
Squamate antbird (*Myrmeciza squamosa*)	Brazil	São Paulo	4	3	75.0	MAT	1:5		Gennari *et al.* (2014)
White-browed warbler (*Basileuterus leucoblepharus*)	Brazil	São Paulo	5	1	20.0	MAT	1:5		Gennari *et al.* (2014)
White-eyed foliage-gleaner (*Automolus leucophthalmus*)	Brazil	São Paulo	14	3	21.4	MAT	1:5		Gennari *et al.* (2014)
White-lined tanager (*Tachyphonus rufus*)	Brazil	Bahia	16	1	6.2	MAT	1:25		Andrade *et al.* (2016)

(*Continued*)

Table 7. (*Continued.*)

Order, common name, (*scientific name*)	Country	Region	No. tested	No. positive	% Positive	Test	Cut-off	Notes	Reference
White-necked thrush (*Turdus albicollis*)	Brazil	São Paulo	5	5	100.0	MAT	1:5		Gennari *et al.* (2014)
White-shouldered fire-eye (*Pyriglena leucoptera*)	Brazil	São Paulo	11	4	36.4	MAT	1:5		Gennari *et al.* (2014)
White-spotted woodpecker (*Veniliornis spilogaster*)	Brazil	São Paulo	1	1	100.0	MAT	1:5		Gennari *et al.* (2014)
White-throated woodcreeper (*Xiphocolaptes albicollis*)	Brazil	São Paulo	2	1	50.0	MAT	1:5		Gennari *et al.* (2014)
White-vented myna (*Acridotheres javanicus*)	Taiwan	Several	1	1	100.0	MAT[b]	1:40		Chen *et al.* (2015)
White wagtail (*Motacilla alba*)	Pakistan	Punjab	11	1	9.0	LAT[b]	1:64	Age, health AS	Naveed *et al.* (2019)
Pelecaniformes									
Black-crowned night heron (*Nycticorax nycticorax*)	Taiwan	Several	2	2	100.0	MAT[b]	1:40		Chen *et al.* (2015)
Buff-necked ibis (*Theristicus caudatus*)	Brazil	Minas Gerais, São Paulo	2	2	100.0	MAT	1:5		Vitaliano *et al.* (2014)
Cattle egret (*Bubulcus ibis*)	Brazil	Fernando de Noronha	197	157	79.7	MAT	1:5		Costa *et al.* (2012)
Cattle egret (*Bubulcus ibis*)	Taiwan	Several	7	4	57.1	MAT[b]	1:40		Chen *et al.* (2015)
Eurasian spoonbill (*Platalea leucorodia*)	Spain	Several	81	5	6.2	MAT	1:25		Cabezón *et al.* (2011)
Grey heron (*Ardea cinerea*)	Spain	Several	5	3	60.0	MAT	1:25		Cabezón *et al.* (2011)
Malay night heron (*Gorsachius melanolophus*)	Taiwan	Several	21	5	23.8	MAT[b]	1:40		Chen *et al.* (2015)
Purple heron (*Ardea purpurea*)	Spain	Several	4	0	0	MAT	1:25		Cabezón *et al.* (2011)
Roseate spoonbill (*Platalea ajaja*)	Czech Republic	Zoos	6	1	16.6	LAT[a]	–		Bártová *et al.* (2018)
Phaethontiformes									
Red-billed tropic bird (*Phaeton aethereus*)	Brazil	Abrolhos Archipelago	25	7	28.0	MAT	1:5		Gennari *et al.* (2016*b*)
Phoenicopteriformes									
Lesser flamingo (*Phoenicopterus minor*)	Portugal	Zoo	3	1	33.0	MAT[b]	1:20		Tidy *et al.* (2017)
Piciformes									
Black vulture (*Coragyps atratus*)	Brazil	São Paulo	121	16	13.2	MAT	1:5		Gennari *et al.* (2017)
Black vulture (*Coragyps atratus*)	USA	Alabama	8	1	12.0	MAT	1:25		Love *et al.* (2016)
Crescent-chested puffbird (*Malacoptila striata*)	Brazil	São Paulo	3	2	66.7	MAT	1:5		Gennari *et al.* (2014)
Psittaformes									
Alexandrine parakeets (*Psittacula eupatria*)	China	Beijing, Weifang	61	4	6.5	MAT	1:5	Season AS	Zhang *et al.* (2014)
Black-goggled tanager (*Lanio melanops*)	Brazil	São Paulo	15	5	33.3	MAT	1:5		Gennari *et al.* (2014)
Black-headed gull (*Chroicocephalus ridibundus*)	China	Dianchi Lake	659	131	19.9	MAT	1:5		Miao *et al.* (2014)
Budgerigars (*Melopsittacus undulatus*)	China	Beijing, Weifang	202	18	8.9	MAT	1:5	Season AS	Zhang *et al.* (2014)

(*Continued*)

Table 7. (*Continued.*)

Order, common name, (*scientific name*)	Country	Region	No. tested	No. positive	% Positive	Test	Cut-off	Notes	Reference
Cockatiels (*Nymphicus hollandicus*)	China	Beijing, Weifang	22	3	13.6	MAT	1:5	Season AS	Zhang *et al.* (2014)
Lovebirds (*Agapornis* sp.)	China	Beijing, Weifang	26	1	3.8	MAT	1:5	Season AS	Zhang *et al.* (2014)
Rainbow lorikeet (*Trichoglossus haematodus*)	Czech Republic	Zoos	4	1	25.0	LAT[a]	–		Bártová *et al.* (2018)
Red-tailed Amazon parrot (*Amazona brasiliensis*)	Brazil	Paraná	51	0	0	IFA	1:16		Sato *et al.* (2020)
Turquoise-fronted Amazon (*Amazona aestiva*)	Brazil	São Paulo	71	7	10.0	MAT	1:16		Gonçalves *et al.* (2013)
Sphenisciformes									
Galapagos penguin (*Spheniscus mendiculus*)	Republic of Ecuador	Galapagos	298	7	2.3	MAT	1:50	Region AS	Deem *et al.* (2010)
Humboldt penguin (*Spheniscus humboldti*)	Czech Republic	Zoos	4	2	50.0	LAT[a]	–		Bártová *et al.* (2018)
Magellanic penguin (*Spheniscus magellanicus*)	Brazil	Bahia, Espírito Santo, Rio de Janeiro	145	18	12.4	MAT	1:20	Tg not isolated	Acosta *et al.* (2018)
Magellanic penguin (*Spheniscus magellanicus*)	Brazil	Espírito Santo, Santa Catarina, São Paulo	100	28	28.0	MAT	1:20	Captive	Gennari *et al.* (2016*a*, 2016*b*)
Magellanic penguin (*Spheniscus magellanicus*)	Chile	Magdalena Island	132	57	43.2	MAT	1:20		Acosta *et al.* (2019)
Struthioniformes									
Greater rhea (*Rhea americana*)	Portugal	Zoo	1	1	100.0	MAT[b]	1:20		Tidy *et al.* (2017)
Suliformes									
Brown booby (*Sula leucogaster*)	Brazil	Abrolhos Archipelago	19	9	47.4	MAT	1:5		Gennari *et al.* (2016*a*, 2016*b*)
Masked booby (*Sula dactylatra*)	Brazil	Abrolhos Archipelago	23	8	34.8	MAT	1:5		Gennari *et al.* (2016*a*, 2016*b*)
Flightless cormorants (*Phalacrocorax harrisi*)	Republic of Ecuador	Galapagos	258	6	2.3	MAT	1:50	Tg isolated	Deem *et al.* (2010)
Strigiformes									
Barn owl (*Tyto alba*)	Brazil	São Paulo	4	2	50.0	MAT	1:16		Gonçalves *et al.* (2013)
Barn owl (*Tyto alba*)	Spain	Several	45	6	13.3	MAT	1:25		Cabezón *et al.* (2011)
Barred owl (*Strix varia*)	USA	Alabama	54	25	46.2	MAT	1:25	Tg isolated	Love *et al.* (2016)
Burrowing owl (*Athene cunicularia*)	Brazil	Minas Gerais, São Paulo	5	1	20.0	MAT	1:5		Vitaliano *et al.* (2014)
Collard scops owl (*Otus bakkamoena*)	Taiwan	Several	74	20	27.0	MAT[b]	1:40		Chen *et al.* (2015)

(*Continued*)

Table 7. (*Continued.*)

Order, common name, (*scientific name*)	Country	Region	No. tested	No. positive	% Positive	Test	Cut-off	Notes	Reference
Common scops-owl (*Otus scops*)	Spain	Several	4	1	25.0	MAT	1:25		Cabezón *et al.* (2011)
Eastern screech owl (*Megascops asio*)	USA	Alabama	16	2	12.0	MAT	1:25		Love *et al.* (2016)
Eurasian eagle owl (*Bubo bubo*)	Portugal	Central, northern	3	1	33.3	MAT[b]	1:20		Lopes *et al.* (2011)
Eurasian eagle owl (*Bubo bubo*)	Spain	Several	144	98	68.0	MAT	1:25		Cabezón *et al.* (2011)
Grass owl (*Tyto capensis*)	Taiwan	Several	20	3	15.0	MAT[b]	1:40		Chen *et al.* (2015)
Great horned owl (*Bubo virginianus*)	USA	Alabama	28	13	46.4	MAT	1:25		Love *et al.* (2016)
Little owl (*Athene noctua*)	Italy	Northern	17	4	23.5	MAT[b]	1:40		Gazzonis *et al.* (2018)
Little owl (*Athene noctua*)	Spain	Several	19	3	15.7	MAT	1:25		Cabezón *et al.* (2011)
Long-eared owl (*Asio otus*)	Spain	Several	9	1	11.1	MAT	1:25		Cabezón *et al.* (2011)
Long-eared owl (*Asio otus*)	Taiwan	Several	4	1	25.0	MAT[b]	1:40		Chen *et al.* (2015)
Short-eared owl (*Asio flammeus*)	Taiwan	Several	11	1	9.0	MAT[b]	1:40		Chen *et al.* (2015)
Spotted owlet (*Athene brama*)	Pakistan	Punjab	9	3	33.3	LAT[b]	1:64	Age, health AS	Naveed *et al.* (2019)
Tawny owl (*Strix aluco*)	Italy	Northern	12	1	8.3	MAT[b]	1:40		Gazzonis *et al.* (2018)
Tawny owl (*Strix aluco*)	Portugal	Central, northern	5	1	20.0	MAT	1:20		Lopes *et al.* (2011)
Tawny owl (*Strix aluco*)	Spain	Several	38	5	13.6	MAT	1:25		Cabezón *et al.* (2011)

ELISA, enzyme-linked immunosorbent assay. Unless stated otherwise, ELISA=ELISA in-house; IFA, indirect fluorescent antibody test; IHA, indirect haemagglutination assay; LAT, latex agglutination test; MAT, modified agglutination test (Dubey and Desmonts, 1987); Tg, *Toxoplasma gondii*; AS, positive association; IHC, immunohistochemical.

[a]ELISA Vekto-Toxo antibodies kits (Vektor-Best, Russian Federation); IHA (ImmunoHAI-Toxoplasmose, Wama Diagnostic, São Carlos, SP, Brazil); WAMA Diagnosis. Imuno-HAI; LAT Pastorex toxo, Bio-Rad Laboratories s.r.o., Prague, Czech Republic; MAT (New Life Diagnostic LLC, Carlsbad, CA, USA).

[b]ELISA ID Screen Avian Toxoplasmosis Indirect (ID VET, France); IHA (Lanzhou Veterinary Research Institute, Chinese Academy of Agricultural Sciences, Lanzhou, China); LAT Latex agglutination test (Antec Diagnostic Products, Bridport, Dorset, UK); MAT (Toxo-Screen DA®, Biomerieux, Lyon, France). This is the same test as MAT.

and other microbial infections in general. In 2 large surveys, *T. gondii* antibodies were found in 17.7% of 175 *Gyps fulvus* in Spain (Cabezón *et al.*, 2011) but twice (39.6% of 101) more were infected in Israel (Salant *et al.*, 2013); the results are comparable because modified agglutination test (MAT) at the serum dilution of 1:25 was used in both studies. Finding of *T. gondii* DNA in tissues of 43 of 48 (89.6%) wild birds (mostly carnivorous) in Turkey suggests a very high prevalence of the parasite in local rodents (Karakavuk *et al.*, 2018). Of 281 raptors from a rehabilitation centre in the USA, 34.5% were seropositive with highest (46.0%) prevalence in Barred owl (Love *et al.*, 2016)

Viable *T. gondii* was isolated (Table 2) and DNA demonstrated (Table 3) from several species of carnivorous birds. The highest prevalence of DNA was in *Buteo buteo* from Turkey; 23 (92.0%) of 25 were infected (Table 3).

Experimental infection of crested caracara with *T. gondii*

An experiment on caracara in Brazil provided useful information. Caracaras are raptors/scavengers with wide distribution. Eight caracaras that could not be released from a rehabilitation centre were used in this experiment. They were serologically negative to *T. gondii* by IFA (cut-off 1:40). Five caracaras were fed rodent (*Calomys callosus*) infected with Me49 strain of *T. gondii*. The birds were euthanized 68 days p.i. Blood was collected for serological examination weekly or more often. Seroconversion occurred between 5 and 14 days p.i. The serological response was erratic. In 1 bird (No.6), transient antibody was observed on day 14 and then at 45 days p.i. The highest antibody titer was 1:650. Antibodies became undetectable at 68 days p.i. in 2 birds. By immunohistochemistry, *T. gondii* was detected in the hearts and muscles of all 5 caracaras and demonstrated by bioassay in the hearts of 2

Table 8. Clinical toxoplasmosis in wild birds

Host	Country	Observations	Diagnostic method	Remarks	Reference
Bar-shouldered dove (*Geopelia humeralis*)	France	A 6-year-old dove born in the zoo was found dead. Pneumonia was the main lesion and only lungs were studied histologically. Numerous tachyzoites were seen in lesions. Diagnosis was confirmed ultrastructurally	Histopathology and TEM	–	Rigoulet *et al.* (2014)
Black-footed penguin (*Spheniscus demersus*)	The Netherlands	3 captive penguins in a zoo died within a day after neurological signs were observed. All 3 had similar lesions. Liver, lungs, intestines, and brain had intralesional tachyzoites. Diagnosis confirmed by IHC and TEM	Histopathology, IHC, TEM	–	Ploeg *et al.* (2011)
Guinea fowl (*Numida meleagris*)	Brazil	Nine of 29 guinea fowl on a farm became ill and 6 died. Two guinea fowl were necropsied. Both birds had disseminated toxoplasmosis with intralesional *T. gondii*. One of the 2 sera tested had a MAT titer of 1:1280. Diagnosis was confirmed by IHC	Serology, histopathology, IHC	–	Vielmo *et al.* (2019)
Kereru (*Hemiphaga novaeseelandiae*)	New Zealand	2 kererus were found dead in a wildlife park. Pneumonia was the main lesion in both birds. Tachyzoites and tissue cysts were associated with lesions	Histopathology, IHC	Limited genotyping revealed atypical Type II	Howe *et al.* (2014)
Lovebird (*Agapornis roseicollis*)	Australia	A female pet bird developed ataxia 1 year after being caged. It had head tilt, tremors and was euthanized. The most important histologic findings were enlargement of spleen, encephalitis and cerebral haemorrhage	IHC, PCR	ToxoDB genotype #3 (Type II) DNA isolated from frozen brain sample	Cooper *et al.* (2015)
North Island brown kiwi (*Apteryx mantelli*)	New Zealand	A juvenile hand raised kiwi was found dead. Most important lesion was hepatitis with tissue cysts. Lesions were seen in other organs, but protozoa were not identified	Histopathology, IHC	Limited genotyping revealed atypical Type II	Howe *et al.* (2014)
North Island kaka (*Nestor meridionalis*)	New Zealand	1 kaka was found dead in wild. Most important lesion was hepatitis with tissue cysts. Lesions were seen in other organs, but protozoa were not identified	Histopathology, IHC	Limited genotyping revealed atypical Type II	Howe *et al.* (2014)
Valley quail (*Callipepla californica*)	Brazil	A captive raised quail recently acquired from another facility died suddenly with clinical signs of diarrhoea and dyspnoea. Disseminated toxoplasmosis involving most organs, many tachyzoites present	IHC, PCR, *T. gondii* DNA in many tissues	*T. gondii* DNA from kidney genotyped with 10 PCR-RFLP markers revealed ToxoDB genotype #87	Casagrande *et al.* (2015)

IHC, immunohistochemistry; PCR, polymerase chain reaction; TEM, transmission electron microscopy; PCR-RFLP, Restriction fragment length polymorphism.

birds. Three control caracaras not inoculated with *T. gondii* remained serologically negative to *T. gondii* (Vitaliano *et al.*, 2010).

Herbivorous/insectivorous birds

Seroprevalence varied depending on the geography, host and the habitat (Table 7). For example, in the ground feeding pigeon (*Columba livia*), seroprevalences varied from 1.6 to 35.7% (Table 7). In a large sample size of pigeons, a low prevalence (1.9% of 521) was reported; the pigeons were from Durango City, Mexico that has a dry climate (Alvarado-Esquivel *et al.*, 2011). This low prevalence is likely related to the effect of climate on oocyst survival. In another survey from cold climate, only 3.9% of pigeons from Colorado, USA were seropositive (Dubey *et al.*, 2010). *Toxoplasma gondii* antibodies were detected in 11.8% of 35 pigeons and 9.5% of 620 quails that were destined for human consumption in China (Cong *et al.*, 2012, 2017*a*). Finding of *T. gondii* DNA in the muscles of 6.4% of 390 quails indicates that the parasite was present in these birds destined for human consumption (Cong *et al.*, 2017*b*). Similarly, *T. gondii* DNA was detected in 5.4% of 280 wild ducks and 3.4% of 350 common pheasants hunted for human consumption in the Czech Republic (Skorpikova *et al.*, 2018).

Toxoplasma gondii infection in sea gulls and other scavenging birds indicates contamination of marine/lake waters with oocysts. In one study, 22.8% of 479 yellow-legged gulls (*Larus michahellis*) were seropositive to *T. gondii* (Cabezón *et al.*, 2016). In another investigation, *T. gondii* antibodies (assessed by ELISA) were detected in 233 of 1122 freshly laid *L. michahellis* eggs (Gamble *et al.*, 2019). The freshness of eggs was verified by immersion in water; such eggs do not float in water (Gamble *et al.*, 2019). The occurrence of *T. gondii* antibodies in 4 other species of sea birds (*Sula* spp. and *Phaeton* spp.) from Brazil (Gennari *et al.*, 2016*b*) and in 19.9% of 659 black-headed gulls (*Chroicocephalus ridibundus*) in China (Miao *et al.*, 2014) indicates that *T. gondii* infection is common in sea birds. *Toxoplasma gondii* oocysts from feline feces can be washed into sewage and freshwater run-off and contaminate marine waters. Antibodies to *T. gondii* were detected in 8.5% of 632 mute swans (*Cygnus olor*) from the USA and viable *T. gondii* was isolated from hearts of 3 (Dubey *et al.*, 2013). Mute swan is an invasive species present in US waters; infection in these hosts is indicative of oocyst contamination.

Reports of viable *T. gondii* and parasite DNA from tissues of wild birds are summarized in Tables 2 and 3, respectively.

Experimental infection of pigeons with T. gondii

Little information is available concerning the efficacy of different diagnostic methods for the detection of *T. gondii* infection in wild birds. A diagnostically useful experimental study was conducted in pigeons in Brazil (de Godoi *et al.*, 2010). Sixteen seronegative pigeons (*C. livia*) were inoculated orally with 50 oocysts of the *T. gondii* VEG strain and divided into 4 groups of 4 pigeons each and euthanized at 15, 30, 45 and 60 days p.i. One pigeon died of toxoplasmosis on day 23 p.i. and tissue cysts were found in its brain; other pigeons remained healthy. All pigeons were seronegative by the MAT (cut-off 1:5) and IFA (cut-off 1:4) before feeding oocysts and developed antibody titers of more than 1:4000 by both MAT and IFA. Tissues (brain, heart, muscle) were tested by bioassay in mice and by PCR. Viable *T. gondii* was isolated from 5 of 12 pigeons and DNA was detected by nested PCR in tissues of 7 of 12 pigeons. By serology and bioassay, none of the 160 naturally exposed pigeons were positive for *T. gondii* providing further evidence of the validity of serology (de Godoi *et al.*, 2010).

Migratory birds

Toxoplasma gondii infections in migratory birds are of epidemiological significance because the parasite can be transported with the host and the introduction of *T. gondii* in new geographic locations can disturb the equilibrium (Gennari *et al.*, 2014). For example, ToxoDB genotype #9 (Chinese 1) occurs mainly in China but has been occasionally found in other countries, including the USA and Mexico. Whether migratory birds could have transported the parasite is a possibility. Antibodies to *T. gondii* were detected in Magellanic penguins in Chile and these birds migrate throughout South American coastline (Acosta *et al.*, 2018, 2019).

A study of migratory and non-migratory geese revealed interesting results (Sandström *et al.*, 2013). A total of 2675 birds, both adults and juveniles, of 4 goose species (*Anser anser*, $n = 266$; *A. brachyrhynchus, n = 787*; *Branta canadensis, n = 79*; *B. leucopsis, n = 1543*) at Arctic brood-rearing areas in Russia and on Svalbard, and temperate wintering grounds in the Netherlands and Denmark (migratory populations) as well as temperate brood-rearing grounds (the Netherlands, non-migratory

Table 9. *Toxoplasma gondii* genotypes based on DNA directly from host tissue

Country	Host	No.	10 PCR-RFLP markers ToxoDB genotype	Reference
China	*Alauda gulgula*	2	#3	Cong *et al.* (2014)
China	*Anas formosa*	2	#9	Zhang *et al.* (2015)
China	*Anas* sp.	1	#9	Zou *et al.* (2017)
China	*Carduelis spinus*	2	#3	Cong *et al.* (2014)
China	*Coturnix coturnix*	5	#9	Cong *et al.* (2017*a*, 2017*b*)
China	*Passer domesticus*	1	#3	Huang *et al.* (2012)
China	*Passer domesticus*	4	#3 in 3 and possible new type in 1	Cong *et al.* (2013)
China	*Phasianus colchicus*	1	#3	Huang *et al.* (2012)
China	*Passer montanus*	1	#10	Huang *et al.* (2012)
China	*Passer montanus*	3	#10	Liu *et al.* (2019)
Israel	*Corvus cornix*	1	#1	Salant *et al.* (2013)
South Africa	*Streptopelia semitorquata*	1	#1 or #3 (15 microsatellites)	Lukášová *et al.* (2018)
USA	*Branta sandvicensis*	4	#261 in 3, #262 in 1	Work *et al.* (2016)

Table 10. Distribution of PCR-RFLP (ToxoDB) *Toxoplasma gondii* genotypes from wild birds from different continents/countries

Continent/country	Total typed	Classic types I ToxoDB #10	II ToxoDB #1 or #3	III ToxoDB#2	#4	#5	#6	#9	#11	#20	Others	
Africa												
Senegal	15		5	1			3			6		Galal *et al.* (2019)
Asia												
China	(22)[a]	4	9					8			1 Possible new type	See Table 9
Israel	(1)[a]		1									Salant *et al.* (2013)
Oceania												
Australia	1		1									Cooper *et al.* (2015)
Europe												
France	1		1									Aubert *et al.* (2010)
Turkey	9		7	2								Karakavuk *et al.* (2018)
Central America												
Costa Rica	1										1 (#52)	Dubey *et al.* (2009), Shwab *et al.* (2014)
South America												
Brazil	19		5				1		1		12 (#8-1, #13-2, #17-1, #65-1, #108-1, #161-1, #182-2, #206-1, #290-2)	da Silva and Langoni (2016), de Barros *et al.* (2014), Dubey *et al.* (2011*b*), Rêgo *et al.* (2018), Silva *et al.* (2018*a*, 2018*b*)
North America												
Mexico	1							1				Alvarado-Esquivel *et al.* (2011), Shwab *et al.* (2014)
USA	32(4)[a]	1	6	4	2	6					13 (#15-1, #157-1, #167-1, #177-2, #216-2, # 61-3, #262-1, #266-1, #267-1)	Cerqueira-Cézar *et al.* (2019), Dubey *et al.* (2010), Dubey *et al.* (2011*b*), Dubey *et al.* (2013), Love *et al.* (2016), Shwab *et al.* (2014), Verma *et al.* (2016), Yu *et al.* (2013)
Grand total	102	5	35	7	2	6	4	9	1	6	27	

[a]DNA from tissues. Twenty-seven of the 102 samples were DNA from bird tissues.

populations) were tested for *T. gondii* antibodies (MAT, 1:40). Only adult *B. leucopsis* were seropositive: *T. gondii* antibodies were found in 14.8% of 811 adults from Svalbard and 17.7% of 157 from Russia sampled during summer but not in any of the 456 juveniles sampled in summer (Arctic) and summer and winter in the Netherlands. Similar results were obtained with 3 other species of goose (Sandström *et al.*, 2013). The authors concluded that geese become infected postnatally at wintering groups.

In a study of migratory birds and resident Nearctic brown lemmings (*Lemmus trimucronatus*) from Arctic Canada, *T. gondii* infections were detected only in migratory geese (Table 1) and not in resident lemmings (Elmore *et al.*, 2015).

Clinical toxoplasmosis in wild birds

Little is known of clinical toxoplasmosis among wild birds in nature. Among all avian species, most severe toxoplasmosis has been reported in canaries (*Serinus canaria*), Hawaiian geese (*Branta sandvicensis*) and Hawaiian crows (*Corvus hawaiiensis*); reports between 1988 and 2009 were summarized previously (Dubey, 2010). In the past decade, few cases of fatal toxoplasmosis were documented in captive birds or those from National Parks (Table 8).

Hawaiian crows (*C. hawaiiensis*) and Nene goose (*B. sandvicensis*) are endangered native species in Hawaii. Nene is the largest extant terrestrial bird in Hawaiian Island and the official state bird (Work *et al.*, 2015). Of 300 Nene examined at necropsy, inflammatory conditions were found in 69 and 16.0% of these were thought to be toxoplasmosis (Work *et al.*, 2015). Thus, 11 geese died of toxoplasmosis. The presence of cats in colonies near the native bird sites is thought to be a source of *T. gondii* oocysts for the birds (Lepczyk *et al.*, 2020).

Two episodes of clinical toxoplasmosis were reported in guinea fowl in the USA and Brazil. An owner in Mississippi, USA lost 7 of 20 backyard guinea fowls. Birds were lethargic before death. Two dead birds were necropsied. Severe lesions of multifocal necrosis, fibrin exudation and inflammation of spleen, lung, heart and bone marrow were seen microscopically in 1 and mild lesions in the other guinea fowl. *Toxoplasma gondii* was identified histologically in tissues of both birds and the diagnosis was confirmed by PCR (Jones *et al.*, 2012).

The Brazilian outbreak of clinical toxoplasmosis was reported in guinea fowl on a chicken farm; the farm had 47 chickens (*G. domesticus*) and 29 guinea fowl (Vielmo *et al.*, 2019). Of these 76 birds, 22 (13 chickens and 9 guinea fowl) had clinical signs and 15 (9 chickens, 6 guinea fowl) died. Two guinea fowl were examined at necropsy and both had toxoplasmosis (Table 8).

Genetic diversity of *T. gondii* isolates

PCR-RFLP genetic data based on extraction of DNA from host tissue are summarized in Table 9 and from the live tachyzoites in Table 10. A total of 102 samples from birds were genotyped in this summary (Table 10), including 75 from viable *T. gondii* isolates (Table 2) and 27 from DNA extracted from tissues of birds (Table 10). Overall, genotype distribution follows the global patterns recognized previously (Shwab *et al.*, 2014; Su and Dubey, 2020), with ToxoDB genotypes #1 and #3 (collectively known as Type II), and genotype #2 (known as Type III) being dominant in Africa and Europe. Most genotypes identified in the Americas were diverse and different from those in the Old World. Of interest is the predominance of ToxoDB genotype #9 (Chinese 1) in China and its rare occurrence in Mexico (Alvarado-Esquivel *et al.*, 2011; Shwab *et al.*, 2014). Type I isolates (ToxoDB genotype #10) are considered rare worldwide. It was detected in a hunted turkey in 4 tree sparrows in China (Table 3). As this genotype is highly virulent to mice and relatively easy to isolate by bioassay, future study to obtain isolates for genotyping is needed to confirm the findings. Also, of interest is the finding of ToxoDB genotypes #4 and #5, together known as Type 12, in North America but their rare frequency from the rest of the world.

Conclusions

Here, we summarized seroprevalence, clinical disease, epidemiology and genetic diversity of *T. gondii* strains isolated from wild birds worldwide for the past decade. It is obvious that *T. gondii* infection in raptors is common and they are excellent sentinels to monitor *T. gondii* in rodents and small other animals. Detection of *T. gondii* antibodies in eggs offers a non-invasive sampling method. In one investigation, *T. gondii* antibodies (assessed by ELISA) were detected in 233 of 1122 freshly laid yellow-legged gulls (*L. michahellis*) eggs (Gamble *et al.*, 2019). Finding antibodies in sea gulls indicates contamination of fresh and marine waters with *T. gondii* oocysts. In general, *T. gondii* infection in herbivorous birds is a good measure of oocyst contamination in the environment. Genetic studies revealed low genetic diversity in Europe, Asia, Africa and the USA, but higher diversity of *T. gondii* in South America. A study of migratory and non-migratory geese at Arctic brood-rearing areas in Russia and on Svalbard, and temperate wintering grounds in the Netherlands and Denmark (migratory populations) revealed that geese become infected postnatally at wintering groups (Sandström *et al.*, 2013).

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