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Review article

All about toxoplasmosis in cats: the last decade

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ABSTRACT

Toxoplasma gondii infections are common in humans and animals worldwide. Toxoplasmosis continues to be of public health concern. Cats (domestic and wild felids) are the most important host in the epidemiology of toxoplasmosis because they are the only species that can excrete the environmentally resistant oocysts in feces. Cats can excrete millions of oocysts and a single cat can spread infection to many hosts. The present paper summarizes information on prevalence, persistence of infection, clinical signs, and diagnosis of *T. gondii* infections in domestic and wild cats for the past decade. Special emphasis is paid to genetic diversity of *T. gondii* isolates from cats. Review of literature indicates that a unique genotype (ToxoDB genotype #9 or Chinese 1) is widely prevalent in cats in China and it has been epidemiologically linked to outbreaks of clinical toxoplasmosis in pigs and deaths in humans in China; this genotype has rarely been detected in other countries. This review will be of interest to biologists, parasitologists, veterinarians, and public health workers.

1. Introduction

Toxoplasma gondii infections in cats continue to be a public health and veterinary concern. Cats are the most important animals in the epidemiology of toxoplasmosis because they are the only hosts that can excrete the environmentally resistant oocysts. Several reviews indicate that *T. gondii* infections are common in cats worldwide (Dubey and Beattie, 1988; Dubey, 2010; Ding et al., 2017; Rahimi et al., 2015; Calero-Bernal and Gennari, 2019; Amouei et al., 2019; Montazeri et al., 2020). There are many unanswered questions concerning feline toxoplasmosis, especially how often cats excrete oocysts and how good is immunity to re-excretion of oocysts. The present review summarizes worldwide information on the prevalence of clinical and subclinical infections, diagnosis, control, and molecular epidemiology of toxoplasmosis in domestic and wild felids for the past decade. This information should be of interests to veterinarians, parasitologists, biologists, and public health workers.

2. Methods of review

Papers cited in PubMed, in reviews by others, and in the collection of one of us (J.P.D.) were consulted in original. Additionally, help of international collaborators were sought to make the review inclusive of all papers published. This review is divided in two parts, domestic cats and wild felids. Literature cited starts from 2009. A few references before 2009 were also cited for introduction or because they were not included in Dubey (2010).

3. Domestic cats

3.1. Prevalence

3.1.1. Serologic prevalence

T. gondii antibodies were found worldwide as previously reported (Dubey and Beattie, 1988; Dubey, 2010) and this trend has continued in the last decade (Table 1). In general, the seropositivity increases with the age of the cat, indicating post-natal transmission of *T. gondii*. Antibodies to *T. gondii* have been detected in most cats after weaning (6 to 10 weeks). It is possible that in some young cats, the low antibody titers represented maternally transferred antibodies. Maternally transferred antibodies disappear in the cat by 12 weeks of age (Dubey, 2010).

Prevalence of *T. gondii* infection varies according to the lifestyle of cats. It is generally higher in feral cats that hunt for their food than in domestic cats. Much is dependent on availability of food. Seroprevalence to *T. gondii* varied among countries, within different areas of a country, and within the same city (Table 1). The reasons for

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Table 1
Seroprevalence of *T. gondii* antibodies in domestic cats (*Felis catus*) (2009-2020).

Location	Region	Source	No. tested	No. positive	% positive	Test	Cut-off (reciprocal titer)	Remarks	Reference
Albania	Tirana	Stray	146	91	62.3	IFAT	100	Age	Silaghi et al. (2014)
Algeria	Algiers	Stray	96	48	50.0	MAT	6	Age	Yekkour et al. (2017)
Angola	Luanda	Owned	102	4	3.9	MAT	20	Age	Lopes et al. (2017)
Argentina	Buenos Aires	Owned	513	116	22.6	IFAT	25	Age, outdoor access, hunting habit	López et al. (2011)
Australia	Sydney	Owned	417	162	39.0	ELISA	-	Age, fed raw meat, hunting	Brennan et al. (2020)
Brazil	3 biomes	Stray	29	24	82.8	IFAT	16	-	Furtado et al. (2015)
Brazil	Acre	Owned	89	22	24.7	IFAT	64	-	de Souza et al. (2015)
Brazil	Bahia	Owned	28	14	50.0	IFAT	64	-	de Oliveira et al. (2019)
Brazil	Bahia	Owned and stray	231	105	45.4	IFAT	64	Area; associated with FIV in owned cats.	Munhoz et al. (2017)
Brazil	Fernando de Noronha	Stray	118	70	59.3	IFAT, MAT	16, 25	-	Costa et al. (2012)
Brazil	Fernando de Noronha	Stray and owned	348	248	72.2	IFAT	16	-	Magalhães et al. (2017)
Brazil	Fernando de Noronha	Stray	31	18	58.0	IFAT	16	-	Melo et al. (2016)
Brazil	Maranhão	Owned with outdoor access	200	101	50.5	IFAT	40	Outdoor access	Braga et al. (2012)
Brazil	Mato Grosso do Sul	Owned	50	2	4.0	IFAT MAT	64 16	Coinfection with *Leishmania* spp. in 2 cats	Braga et al. (2014)
Brazil	Mato Grosso do Sul	Owned and stray	151	49	32.5	IFAT	40	*Leishmania* infection	de Sousa et al. (2014)
Brazil	Paraíba	Owned and stray	201	88	43.8	IFAT	16	Age, hunting habit	Feitosa et al. (2014)
Brazil	Paraná	Owned	282	46	16.3	IFAT	16	-	Cruz et al. (2011)
Brazil	Paraná	Owned	2	2	100.0	IFAT	1:1024	Outbreak of clinical toxoplasmosis in goats	Neto et al. (2018)
Brazil	Pernambuco	Owned	35	9	25.7	IFAT	16	-	Arraes-Santos et al. (2016)
Brazil	Piauí	Shelter	102	0	0	ELISA	ImmunoComb	-	Teixeira et al. (2016)
Brazil	Rio de Janeiro	Owned	108	6	5.6	IHA	16	Use of litter boxes	Bastos et al. (2014)
Brazil	Rio de Janeiro	Owned	213	14	6.6	IFAT[3]	64	Cats with sporotrichosis	Barros et al. (2015)
Brazil	Rio de Janeiro	Stray; shelter	372	36	9.7	MAT	20	Shelter. Excellent correlation between neat serum and filter paper elutes	Bolais et al. (2017)
Brazil	Rio de Janeiro	Shelter and stray	433	95	21.9	IHA IFAT	ToxoTest-HAI® 64	-	Pereira et al. (2018)
Brazil	Rio Grande do Norte	Stray	53	28	52.8	MAT	25	-	Fournier et al. (2014)
Brazil	Rio Grande do Sul	Owned	245	93	37.9	IFAT	64	-	Pinto et al. (2009)
Brazil	Santa Catarina	Owned	300	43	14.3	IFAT	64	Age, outdoor access/rural area	Rosa et al. (2010)
Brazil	São Paulo	Stray	386	63	16.3	IFAT	64	Age. *Leishmania* spp. antibodies in 2 cats.	Cardia et al. (2013)
Brazil	São Paulo	Stray	70	11	15.7	IFAT	64	Age, outdoor access, hunting habit, homemade food and raw milk. *Leishmania* 4.2%	Coelho et al. (2011)
Brazil	São Paulo	Shelter	59	46	78.0	ELISA	-	Raman spectroscopy tested as a new test	Duarte et al. (2010)
Brazil	São Paulo	Zoonosis control center/ Shelter	251	21	20.3	IFAT	16	*Leishmania* infection, if already infected with FIV	Sobrinho et al. (2012)
Chile	San Carlos	Owned	60	29	48.3	ELISA	ImmunoComb	Age	Toro et al. (2015)
Chile	Southern	Owned	65	44	67.6	MAT	25	-	Barros et al. (2018)
China	-	-	97	25	25.8	ELISA	-	-	Jiang et al. (2015)
China	Beijing	Stray	64	37	57.8	MAT	20	-	Qian et al. (2012)
China	Beijing	Owned and shelters	45	16	35.6	ELISA	Shenzhen	-	Zhu et al. (2012)
China	Beijing	Owned and shelters	45	11	24.4	MAT	25	-	Zhu et al. (2012)
China	Guangzhou	Owned and stray	206	52	25.2	ELISA	CIVTEST	Stray	Zhang et al. (2009)
China	Guizhou	Stray	19	12	63.1	ELISA	-	-	Li et al. (2015)
China	Henan	Owned	843	178	21.1	ELISA	Combined company	Mixed breed, area, age	Wang et al. (2017a)
China	Henan	Owned	28	2	7.1	MAT	25	7% of 35	Yang et al. (2017)
China	Jiangsu	Stray	64	16	25.0	ELISA	Shanghai Ding Biological Technology	*T. gondii* more prevalent in lungs and heart than liver and spleen	Hou et al. (2018)
China	Jiangsu	Stray	116	24	20.7	ELISA	Combined company	Stray	Liu et al. (2014)
China	Lanzhou	Owned and stray	185	40	21.6	ELISA	-	-	Cai et al. (2015)
China	Lanzhou	Stray and owned	362	70	19.3	MAT	25	Stray, age	Cong et al. (2016)
China	Lanzhou	Owned and stray	221	47	21.3	MAT	25	Stray	Wu et al. (2011)

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Table 1 (*continued*)

Location	Region	Source	No. tested	No. positive	% positive	Test	Cut-off (reciprocal titer)	Remarks	Reference
China	Northeastern/ Eastern	Stray and owned	1141	176	15.4	IHA	64	Stray, *Dirofilaria*	Kang et al. (2016)
China	Shandong	Owned	180	39	21.6	IHA	64	Age	Cong et al. (2018)
China	Shanghai	Stray	145	17	11.7	ELISA	CIVTEST	Circulating antigen 11.7% of 145, DNA in 5.	Wang et al. (2012)
China	Xuzhou	Stray	41	17	41.5	ELISA	-	-	Fu et al. (2014)
China	Heilongjiang	Pets	352	69	19.6	IHA	1:64		Qiu et al. (2020)
	Jilin		235	43	18.2				
	Liaoning		267	51	19.1				
Egypt	Giza	Stray	158	154	97.5	MAT	5	-	Al-Kappany et al. (2010b)
Egypt	Giza	Stray	180	172	95.5	MAT	5	-	Al-Kappany et al. (2011)
Estonia	Tartu	Owned and shelter	490	298	60.8	MAT	40	Age, breed, area and outdoor access	Must et al. (2015)
Ethiopia	Addis Ababa	Stray	36	33	91.7	MAT	25	-	Dubey et al. (2013c)
Ethiopia	Addis Ababa	Stray	48	41	85.4	MAT	25	-	Tiao et al. (2013)
Finland	-	Finland	1121	461	41.1	MAT	40	Breed, age. Higher in Birman and Ocicats.	Must et al. (2017)
Finland	Helsinki	Owned and shelter	490	237	48.4	MAT	40	Age, feeding habits, breed, reproduction issues	Jokelainen et al. (2012)
France	Eastern Rural	Owned	861	454	52.7	MAT	40	Age,	Afonso et al. (2010)
France	Central/ Eastern	Stray	29	19	65.5	MAT	48	Climate and landscape characteristics	Afonso et al. (2013)
Honduras	-	Feral	12	4	33.3	IFA	32	-	McCown and Grzeszak (2010)
Iran	Ahvaz	Stray	100	54	54.0	MAT	25	Age	Hamidinejat et al. (2011)
Iran	Ahvaz	Owned	198	49	24.8	ICHA	-	Age	Mosallanejad et al. (2011)
Iran	Ahvaz	Stray	100	39	39.0	MAT[4]	25	Age	Mosallanejad et al. (2017)
Iran	Garmsar	Stray	107	69	64.5	ELISA	In-house	Age	Tehrani-Sharif et al. (2015)
Iran	Kerman	Stray and owned	140	45	32.1	MAT	20	Age; FIV positive cats were more likely to be infected with *T. gondii*.	Akhtardanesh et al. (2010)
Iran	Kerman	Stray	108	3	2.7	IFAT	16	-	Derakhshan and Mousavi (2014)
Iran	Mashhad	Stray	159	94	59.1	ELISA	IDVET	Age	Khodaverdi and Razmi (2019a)
Iran	Sari	Stray	100	16	16.0	LAT	64	Age, weight	Sharif et al. (2009)
Iran	Shiraz	Stray	145	120	82.8	MAT	20	Area. Nested PCR positivity - see Table 5	Asgari et al. (2018)
Iran	Urmia	Owned	50	15	30.0	ELISA	64	IgM-30%; IgG 8%	Javadi et al. (2010)
Iran	Urmia	Owned and stray	130	46	35.4	MAT	20	-	Raeghi et al. (2011)
Iraq	Babylon, Najaf, Diwanyia	Stray	90	41	45.5	LAT	2	58% in rural versus 38.9% in urban cats	Al-Ramahi et al. (2010)
Iraq	Military bases	Stray	207	63	30.4	LAT	32	-	Switzer et al. (2013)
Ireland	Dublin and adjacent regions	Owned and stray	83	28	33.7	ELISA	In-house	*Bartonella*	Juvet et al. (2010)
Italy	Florence	Stray	50	22	44.0	MAT	20	-	Mancianti et al. (2010)
Italy	Lombardy	Stray	203	62	30.5	IFAT	64	-	Spada et al. (2012)
Italy	Milan	Stray	78	17	21.8	IFAT	64	-	Spada et al. (2013)
Italy	Milan	Stray	82	24	29.3	IFAT	64	-	Spada et al. (2016)
Italy	Perugia	Owned	78	33	42.3	IFAT	64	-	Veronesi et al. (2017)
Italy	Rome	Owned and kennels	115	44	38.3	MAT[b]	20	-	Macrì et al. (2009)
Italy	Rome	Owned and kennels	115	45	39.1	IFAT	20	-	Macrì et al. (2009)
Japan	Amami Oshima Island	Stray	1363	123	9.0	GLIPS	-	Area	Matsuu et al. (2017)
Japan	Tokachi	Owned	419	73	17.4	LAT	32	Recombinant antigen ELISA compared with LAT	Abdelbaset et al. (2017)
Japan	Tokachi	Owned	353	57	16.1	LAT[2]	32	Breed, age, neuter status, outdoor access, hunting habits	Salman et al. (2018)
Japan	Tokyo	Shelter	337	20	5.9	LAT	64	-	Oi et al. (2015)
Japan	Tokyo	Shelter	104	7	6.7	LAT	64	-	Oi et al. (2015)
Korea	2 Provinces	Owned and stray	182	23	12.6	ELISA	IDVET	-	Chong et al. (2011)
Korea	9 major cities	Owned and stray	150	6	4.0	ELISA	In-house	No owned cat sample was positive	Kim et al. (2017)
Korea	Urban and rural	Stray	112	56	50.0	ELISA	In-house	-	Hwang et al. (2017)
Korea	Daejeon	Stray	118	7	5.9	ELISA	IDVET	-	Park et al. (2014)

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Table 1 (*continued*)

Location	Region	Source	No. tested	No. positive	% positive	Test	Cut-off (reciprocal titer)	Remarks	Reference
Korea	Seoul	Owned	437	10	2.2	ELISA	In-house	Cats adopted from shelters or vet clinics had higher prevalence	Hong et al. (2013)
Korea	Seoul	Stray and owned	152	11	7.2	ELISA	In-house	No positive samples from owned cats	Lee et al. (2010)
Korea	Seoul	Stray	456	69	15.1	ELISA	In-house	-	Lee et al. (2011)
Latvia	Urban areas	Shelter and owned	242	125	51.6	ELISA	50	Age, outdoor access	Deksne et al. (2013)
Mexico	Colima	Stray	48	14	29.2	ELISA	In-house	-	Rico-Torres et al. (2015)
Mexico	Durango	Shelter	150	14	9.3	MAT	25	*T. gondii* isolated from 5 cats (Table 3)	Dubey et al. (2009d)
Mexico	Yucatan	-	220	202	91.8	ELISA	-	No. of cats per household and low body condition were associated with reactivated chronic infection	Castillo-Morales et al. (2012)
Mexico	Yucatan	Owned	50	50	100.0	ELISA	In-house	Backyard cats	Jimenez-Coello et al. (2013)
Netherlands	Utrecht	Owned	450	91	20.2	ELISA	In-house	Age, hunting habit, stray before adoption, presence of dog in the house	Opsteegh et al. (2012)
New Caledonia	French territory Nouméa	Shelter	8	4	50.0	ELISA	IDVET	-	Roqueplo et al. (2011)
Nigeria	Maiduguri	Owned and stray	105	38	36.2	LAT	64	Stray	Kamani et al. (2010)
Nigeria	Southwestern	Animal market	226	10	4.4	MAT	20	-	Ayinmode et al. (2017)
Norway	Nationwide	Owned	478	196	41.0	DAT	40	Age, breed, sex.	Sævik et al. (2015)
Pakistan	Potohar Plateau	Owned	420	111	26.4	ELISA	IDVET	Age, area. *T. gondii* IgM antibodies in 3.5% of cats	Ahmad et al. (2014)
Panama	4 regions	Owned	120	30	25.0	ELISA	IDVET	Area	Rengifo-Herrera et al. (2017)
Peru	Lima	Owned	154	17	11.0	IHA	NM	Hunting, feeding habits (those fed raw meat had higher titers)	Cerro et al. (2014)
Philippines	Cebu	Owned and stray	104	44	42.3	LAT	-	Use of litter tray and contact with other animals	Ybañez et al. (2019)
Philippines	Manila	Stray and owned	60	28	46.7	LAT	15 IU/mL	-	Advincula et al. (2010)
Philippines	Manila	Stray	30	14	46.7	ELISA	Immunocomb	-	Reyes et al. (2013)
Poland	3 regions	owned	15	12	81.3	MAT	40	-	Sroka and Szymańska (2012)
Poland	Olsztyn	Owned	135	89	65.9	MAT	40	-	Michalski et al. (2010)
Poland	Southwestern	Owned	208	143	68.8	IFAT	128	Age, sex, outdoor access. IgM in 21%	Sroka et al. (2018)
Portugal	-	Owned	79	18	22.7	MAT [1]	20	-	Fernandes et al. (2019)
Portugal	Lisbon	Owned	215	44	20.5	MAT	40	Age	Esteves et al. (2014)
Portugal	Lisbon	Stray	423	187	44.2	MAT	20	Age	Waap et al. (2012)
Portugal	Madeira Island	Owned	141	43	30.5	ELISA	-	3.5% positive for *D. immitis*	Neves et al. (2020)
United Arab	Emirates Qatar	Stray	4	1	25.0	MAT	25	-	Dubey et al. (2010)
Romania	Cluj-Napoca	Owned	236	111	47.0	ELISA	50	Age, outdoor access	Györke et al. (2011)
Romania	Western	Stray	173	115	66.4	ELISA	IDVET	Area; 62.8% of 137 Timiş region; 80.6% of 36 Azad region	Darabus et al. (2011)
Russia	Daursky reserve	Stray	61	9	14.7	EIA	Chema-Medica/ Vector-Best	-	Pavlova et al. (2016)
Russia	Kazan	Stray	99	39	39.3	LAT	32	-	Shuralev et al. (2018)
Russia	Lipetsk	Stray	224	38	16.9	ELISA	-	-	Solomatina and Bespalova (2018)
Russia	Perm Krai	Circus	16	2	12.5	ELISA	Vektor-Best	-	Sivkova and Neprimerova (2017)
Qatar	Urban and suburban areas	Stray	495	406	82.0	MAT	25	Prevalence higher on summer season	Boughattas et al. (2017)
Saudi Arabia	Al-Ahsa	Owned and stray	156	98	62.8	ELISA	Shenzhen	Prevalence of 90% in stray cats versus 2% in pets	Al-Mohammed (2011)
South Africa	Eastern Cape	owned	109	35	22.9	LAT	64	Age	Tagwireyi et al. (2019)
South Africa	Johannesburg	Owned	102	18	17.6	ELISA	IDEXX	-	Lobetti and Lappin (2012)
Saudi Arabia	Riyadh	Owned and stray	200	52	26.0	ELISA	CHEKIT	Age, stray, breed	Mohammed et al. (2019)
South Africa	Western Cape	Stray	159	59	37.1	IFAT	100	Age	Hammond-Aryee et al. (2015)
Spain	Madrid	Stray,pets	585	189	32.3	IFAT	80	36.9% stray, 33.3% farm, 25.5% pets	Miró et al. (2004)
Spain	Madrid	Persian	20	2	10.0	IFAT	100	-	Miró et al. (2011)
Spain	Madrid	Stray	346	185	53.4	MAT	40		Miró et al. (2014)
Spain	Central	Stray	356	86	24.2	DAT	80	Sex, age, area and year of collection	Montoya et al. (2018)

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Table 1 (*continued*)

Location	Region	Source	No. tested	No. positive	% positive	Test	Cut-off (reciprocal titer)	Remarks	Reference
Spain	Ibiza	Shelter	105	58	55.2	MAT	20	-	Sherry et al. (2011)
Spain	Madrid	Persian	20	2	10.0	IFAT	100	-	Miró et al. (2011)
Spain	Majorca	Stray	59	50	84.7	MAT	25	Age	Millán et al. (2009a)
Sri Lanka	Colombo	Owned and stray	86	26	30.2	MAT	25	Age, feeding habits and stray had higher prevalence	Kulasena et al. (2011)
Taiwan	Taipei	Owned	100	10	10.0	ELISA	-	-	Fuh et al. (2013)
Thailand	Bangkok/ Chiang Mai	Stray	86	4	4.6	LAT	128	-	Buddhirongawatr et al. (2016)
Thailand	Bangkok	Stray	1490	72	4.8	Dye test	16	Area	Jittapalapong et al. (2010)
Thailand	Bangkok	Owned	348	35	10.1	MAT	25	-	Sukhumavasi et al. (2012)
Thailand	Western	Owned	36	3	8.3	LAT	64	-	Arunvipas et al. (2013)
Turkey	Ankara	Owned and stray	129	86	66.6	Dye test	16	Stray, hunting habit	Yücesan et al. (2019)
Turkey	İzmir	Stray	1121	384	34.2	IFAT	16	Healthy and deceased cats. Seroprevalence higher in dead cats.	Can et al. (2014)
				400	35.6	ELISA	IDVET		
Turkey	Kars	Owned	100	65	65.0	Dye test	16	-	Ercan and Kirmizigül (2019)
Turkey	Kars	Owned and stray	102	45	44.1	Dye test	16	Area	Erkiliç et al. (2016)
United Kingdom	Scotland	Owned and shelter	52	10	19.2	ELISA	64	-	Bennett et al. (2011)
USA	California	Stray	736	134	18.2	IFAT	160	-	VanWormer et al. (2013)
USA	Colorado California	Stray	272	3	1.1	ELISA	-	-	Bevins et al. (2012)
USA	Illinois	Stray	18	6	33.0	IFAT	25	Cats were more present on building sites than forest	Fredebaugh et al. (2011)
USA	Iowa	Stray	140	42	30.0	ELISA	IDEXX	Age	Palerme et al. (2019)
USA	Minnesota	Owned	16	9	56.2	MAT	25	Cats from farms	Verma et al. (2016)
USA	Nationwide	Owned	458	33	7.2	ELISA	64	43 states + DC	Bayliss et al. (2009)
USA	Ohio	Stray	200	103	51.5	MAT	25	-	Ballash et al. (2015)
USA	Pennsylvania	Stray	210	41	19.5	MAT	25	-	Dubey et al. (2009a)
USA	Virginia	Owned	232	63	27.1	IFAT	25	-	Hsu et al. (2011)
West Indies	Grenada	Owned and stray	176	51	29.0	MAT	25	-	Dubey et al. (2009b)
West Indies	St. Kitts	Stray	96	71	73.9	MAT	10	-	Dubey et al. (2009c)

DT = Dye test
ELISA = Enzyme-Linked Immunosorbent Assay
IFAT = Indirect fluorescent antibody test
IHA = Indirect hemagglutination
LAT = Latex agglutination test
MAT = Modified agglutination test
NM = Not mentioned
[1] = IHAT also done, with 16 (18%) cats positive using 1:80 cutoff.
[2] = IFA and Western blot had same results.
[3] = IHA also done with 16 cut-off.
[4] =ELISA also done with 30.0% of positive samples

Table 2
Association between FIV, FeLV, *Bartonella* and *T. gondii* infection in cats.

Country	No. of cats	*T. gondii* (%)	FIV (%)	FeLV (%)	*Bartonella* sp. (%)	Others (%)	Reference
Albania	146	62.3	ND	ND	0.6	*Leishmania infantum* 0.6 Anaplasma 2.1 Haemotropic mycoplasmas 30.8	Silaghi et al. (2014)
Brazil	213	6.6	5.6	16.4	ND	-	Barros et al. (2015)
Brazil	108	5.6	1.8	7.4	ND	-	Bastos et al. (2014)
Brazil	231	45.4	6.0	3.0	ND	*Neospora caninum* 21.6	Munhoz et al. (2017)
Brazil	251	20.3	5.6% of 302	1% of 302	ND	*Leishmania* spp. 21.8% of 302	Sobrinho et al. (2012)
China	362	19.3	9.1	11.3	ND	*Dirofilaria immitis* 3.0	Cong et al. (2016)
China	1141	15.4	ND	ND	ND	*Dirofilaria immitis* 1.9, *Cystoisospora felis* 9.9	Kang et al. (2016)
Egypt	240	47.0	27.0	2.0	ND	-	Abdou et al. (2013)
Egypt	180	95.5	33.9% of 174	4.6% of 174	58.9% of 178	*Dirofilaria immitis* 3.4% of 174	Al-Kappany et al. (2011)
Ethiopia	48	85.4	0 of 41	0 of 41	11.0% of 46	-	Tiao et al. (2013)
Germany	146	62.3	ND	ND	0.7	*Neospora caninum* 10.3 Anaplasma spp. 2.1 *Mycoplasma hae*mophilis-2.1 *Leishmania* spp. 0.7	Silaghi et al. (2014)
Grenada, West Indies	75 (pets)	30.6	0	9.0	50.6		Dubey et al. (2009b)
	101 (feral)	27.7	0	22.0	52.4		
Korea	118	5.9	ND	ND	18.6	-	Park et al. (2014)
Korea	117	50.0	ND	ND	50.0	Hemoplasma 47.9	Hwang et al. (2017)
Kuwait	240	19.6	23.9% of 218	2.8% of 218	ND	-	Abdou et al. (2013)
Iran	140	32.1	19.2	14.2	ND	Diseased cats-risk factor	Akhtardanesh et al. (2010)
Iraq	207	30.4	ND	ND	15.0	*Bartonella clarridgeiae* 12.6	Switzer et al. (2013)
Ireland	83	33.7	ND	ND	26.5	-	Juvet et al. (2010)
Italy	203	30.5	6.6% of 316	3.8% of 316	ND	-	Spada et al. (2012)
Italy	100	21.8% of 78	5	4	ND	-	Spada et al. (2013)
Italy	90	31.7	ND	ND	28.0	-	Spada et al. (2016)
Portugal	141	30.5	ND	ND	ND	*Dirofilaria immitis* 3.5 No *Leishmania* spp.	Neves et al. (2020)
Russia	55	14.7	ND	ND	ND	-	Pavlova et al. (2016)
Scotland	52	19.2	ND	ND	15.4	-	Bennett et al. (2011)
South Africa	102	17.6	ND	ND	23.5	-	Lobetti and Lappin (2012)
Spain	105	20.9	16.7	ND	ND	*Leishmania* 15.4	Miró et al. 2004
Spain	356-632	24.2% (of 356)	7.9% (of 632)	6.3% (of 632)	ND	*Leishmania infantum* 4.8% of 249	Montoya et al. (2018)
Spain	105	55.2	20.9	16.2	ND	*Leishmania infantum* 13.2	Sherry et al. (2011)
Spain	20	10.0	0.0	0.0	ND	*Leishmania* spp. 15.0	Miró et al. (2011)
Thailand	348	10.1	20.1% of 746	24.5% of 746	ND	*Dirofilaria immitis* 4.6	Sukhumavasi et al. (2012)
USA	458	7.2	ND	ND	19.0	-	Bayliss et al. (2009)
USA	210	19.5	ND	ND	25.7	-	Dubey et al. (2009a)
USA	140	30.0	ND	ND	ND	*Dirofilaria immitis* 6.4	Palerme et al. (2019)
USA	123	16.2	4.8	0.8	58.5	-	Powell et al. (2010)
USA	232	27.1	ND	ND	ND	-	Hsu et al. (2011)

ND = Not done.

these variations are many, so no generalizations should be made. It is noteworthy that the seroprevalence of *T. gondii* in cats in Thailand (Jittapalapong et al., (2010) is relatively low (4.8% of 1490) and in accordance with 7-11% prevalence in previous surveys (reviewed in Dubey, 2010). This maybe attributable to the lifestyle of cats. Most people in Thailand are Buddhist and vegetarians and cats are abundant around Buddhist Temples. This contrasts with cats in Egypt with a very high prevalence (Al-Kappany et al., 2011). In a study of backyard cats in Mexico, all 50 cats were seropositive and 23 of 30 backyard pigs were also seropositive (Jimenez-Coello et al., 2013).

Breed of the cat has been seldom examined as risk factors (Table 1). A study from Finland found that Birman and Ocicats had a statistically significant higher prevalence than five other breeds (Jokelainen et al., 2012; Must et al., 2017). In another report from Estonia, not being a pure breed had a high-risk factor (Must et al., 2015).

Concurrent infections with certain feline pathogens can affect *T. gondii* infections in cats. *Bartonella* spp. are bacterial zoonotic pathogens that can cause cat scratch disease, endocarditis, and several other syndromes in humans. *Leishmania* spp. another protozoan can cause disease in cats and humans. Feline immunodeficiency virus (FIV) is a retrovirus related to human immunodeficiency virus (HIV) and is known to cause immunosuppression in cats. Feline leukemia virus (FeLV), is related to human leukemia virus, and can also cause immunosuppression in cats. *Dirofilaria immitis,* a metazoan, can also be fatal in cats. Although these infections can modify the clinical outcome of infection, there is no evidence that they affect the seropositivity of *T. gondii* in cats. Data summarized in Table 2 show that many asymptomatic *T. gondii*-infected cats had these concurrent infections.

It is not possible to compare results in Table 1 because of the sample size, age of cats, and the serological tests used. There is little

Table 3
Comparison of serological tests for toxoplasmosis in cats.

Country	No. of sera	Serological assays				Remarks	Reference
		MAT (%)	IFA (%)	ELISA (%)	Others (%)		
Brazil	59	ND	ND	46 (78.0)	Raman Spectroscopy	-	Duarte et al. (2010)
Brazil	433	ND	71 (16.3)	ND	IHA 53 (12.2)	-	Pereira et al. (2018)
China	185[b]	39 (21.0)	Done together with MAT; same results	40 (21.6) GRA7-ELISA	ND	Excellent correlation between 2 tests	Cai et al. (2015)
China	145	ND	ND	17 (11.7) by ELISA (Ab) and 8 (5.5) by ELISA (Cag)	ND	2 samples also positive for Nested PCR	Wang et al. (2012)
China	45	11 (24.4)	ND	16 (35.5)	ND	Moderate agreement	Zhu et al. (2012)
Estonia	200	120 (60.0)	ND	114 (57.0)	ND	Good correlation	Galat et al. (2019)
Iran	100	39 (39.0)	ND	30 (30.0)	ND	PCR on blood 8 (8.0)	Mosallanejad et al. (2017)
Italy	115	44 (38.2)	45 (39.1)	ND	ND	Excellent correlation	Macrì et al. (2009)
Korea	182	ND	ND	21 (11.5)	TgRDT[a] 23 (12.6)	Excellent correlation	Chong et al. (2011)
Portugal	89	23 (26.0)	ND	ND	IHA 16 (18.0)	Poor correlation	Fernandes et al. (2019)
Romania	203	99 - 1:40 (48.7)	123-1:32 (60.5)	ID.VET 102 (50.2)	USAMV[c] 123 (60.5); ImComb 118 (58.1); RIVM 95 (46.7)	Good correlation	Györke et al. (2011)
Turkey	1121	ND	383 (34.1)	399 (35.5)	ND	In-house ELISA standardized with ID.VET ELISA Excellent correlation	Can et al. (2014)

[a]Rapid diagnostic test - rSAG1-loaded.
[b]Out of 190 sera 39 were positive both by MAT and IFA - 5 sera with discrepant results were excluded.
[c]USAMV = University of Agricultural Sciences and Veterinary Medicine - in-house ELISA; ImmunoComb (Biogal-Galed Labs, Israel); National Institute for Public Health and the environment (RIVM); IDVET-Grables, France.
ND = not done.

information available comparing different tests in sera from naturally exposed cats (Table 3). We are not aware of any validation of serological tests in cats using isolation of the parasite as a guide. In a study of 137 feral cats from Egypt, serologic and isolation data were compared. All cat sera were tested by the MAT starting with 1:5 dilution and tissues (brain, heart, tongue; together or pooled) of all cats were bioassayed in mice, irrespective of serology. Viable *T. gondii* was isolated from 115 (84.0%) of 133 seropositive cats; one of these cats had a MAT titer of 1:5 (Al-Kappany et al., 2010a, Al-Kappany et al., 2010b). In another study of cats from Brazil, *T. gondii* was isolated from 36 of 49 seropositive cats and 1 of 4 seronegative cats (Dubey et al., 2004b).

The MAT and IFA were the most often tests used to detect antibodies to *T. gondii* in cat sera and the results are comparable (Table 3). The MAT is simple, easy to perform, is not host-specific, and is available commercially (DAT, BioMerieux). The MAT is considered specific and no cross reaction have been documented with antigens of other microbes (Dubey et al., 1995a; Dubey 2010). The commercially available IHAT and LAT are less sensitive and less specific compared with MAT (Fernandes et al., 2019). The ELISA are easy to perform but need special equipment and the specificity and sensitivity depend on the antigen used (Chong et al., 2011; Gyorke et al., 2011; Cai et al., 2015; Abdelbaset et al., 2017; Galat et al., 2019). Combination of different recombinant antigens was found useful in the feline toxoplasmosis versus single antigen (Abdelbaset et al., 2017). Rapid serologic tests have been developed to detect *T. gondii* antibodies in cats, but they need further evaluation (Duarte et al., 2010; Chong et al., 2011; Jiang et al., 2015).

3.1.2. Isolation of viable T. gondii in tissues of cats

T. gondii was isolated from tissues of naturally infected cats by bioassay in mice or cell culture (Table 4). Of the 112 cats from Egypt whose tissues were bioassayed in mice individually, *T. gondii* was isolated from the hearts of 83 (74.1%), tongues of 53 (47%) and brains of 36 (32.1%) (Al-Kappany et al., 2010a, b). Thus, *T. gondii* was more prevalent in muscles than in the brain of cats.

3.1.3. Detection of T. gondii DNA in tissues of cats

T. gondii DNA has been reported in as many as 90% of 96 cats (Table 5). Because most of these studies did not perform bioassay to isolate viable parasites, epidemiological or clinical significance of *T. gondii* present DNA in blood is unknown.

3.1.4. Prevalence of T. gondii oocysts in cats

Data from past decade are summarized in Table 6. Prevalence varied with the method of detection. By microscopic examination, *T. gondii*-like oocysts were detected in <1% of cats. However, microscopic examination alone cannot distinguish between *T. gondii* and *Hammondia hammondi* oocysts in cat feces. The most complete data are available from Germany and other European countries. These samples were initially tested commercially and the samples with *T. gondii*-like oocysts were further evaluated for *T. gondii* and *Hammondia* infections using bioassays and PCR designed to distinguish *T. gondii* from *H. hammondi* (Herrmann et al., 2010; Schares et al., 2008; Schares et al., 2016). *H. hammondi* oocysts were common in cat feces (Table 7). Of the 105 cat feces positive microscopically for *T. gondii* oocysts, only 46 were PCR positive; 34 turned out to be *H. hammondi* and 4 were *T. gondii* confirmed by bioassay (Herrmann et al., 2010). The sampled cats are likely to be pets and relatively well cared for. These investigations have provided valuable information concerning ages and season of oocyst excretion and on the genetic characteristics of the *T. gondii* isolates. *T. gondii* oocysts are difficult to distinguish from *H. hammondi* and bioassay is needed for confirmation (Dubey et al., 2013d)

Compared with microscopical method, *T. gondii* DNA was isolated more frequently from cat feces, and in some instances the results are

Table 4
Isolation of viable *T. gondii* from tissues of domestic cats (2009-2020).

Country	Region	No. tested	No. antibody positive (test, cut-off)	Bioassay in mice	No. of samples (designation)	Genotype (ToxoDB genotype # - number of samples)	Reference
Argentina	Buenos Aires	ND	ND	oocysts	**3** (TgCat1Arg, TgCat2Arg, TgCat14-1Arg)	#2 (Type III) -3	Bernstein et al. (2018)
Brazil	Rio Grande do Norte	45	-	Many	0	-	Fournier et al. (2014)
Brazil	Fernando de Noronha	1	1 (MAT,1:25)	B, H, M	**1** (TgCatBrFN1)	#3 (Type II) -1	Silva et al. (2017)
Brazil	Fernando de Noronha	31	18 (IFA,1:16)	B, D, H	**2** (TgCatBrPE01,02)	#146 -2	Melo et al. (2016)
China	Guangdong	34	27 (MAT,1:40)		**17** (TgCtPRC2, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17; TgCtPRC1, 3)	#9 -15 #18 -2	Dubey et al. (2007a); Shwab et al. (2014)
China	Guangdong	ND	ND	ND	**8** (TgC1-8)	#9 -8	Zhou et al. (2009); Shwab et al. (2014)
China	4 regions	89	ND	B, H, T	**14** (TgCtys1,2; TgCtwh1-8; TgCtgd1,2; TgCtsx1,2)	#9 -14 See Wang et al. (2013) (Note: 2 of these 14 samples initially designated as genotype Chinese 2 were corrected as Chinese 1)	Chen et al. (2011); Wang et al. (2013a)
China	Beijing	64	37 (MAT,1:20)	B, H, T of 23	**11** (TgCatBj1-11)	#9 -11	Qian et al. (2012)
China	Guizhou	17	ND	B	**5** (TgCtgy 1-5)	#9 -5	Wang et al. (2013b)
China	Hubei, Shandong, Jiangsu	105	ND	B, H	**19** (TgCtwh9, 10, 11, 12, 14, 19, TgCtxz2, 4, 6, TgCtsd1, 2, 3, 4, 5, TgCtxz1, TgCtxz 3,5,7,8)	#9 -14 #205 -4 #10 (Type I) -1	Wang et al. (2013a)
China	Jiangsu	41	17 (MAT,1:25)	B, H, T	11	ND	Fu et al. (2014)
China	Guizhou	19	12 (ELISA)	B	**2** (TGGZ4,5)	#9 -2	Li et al. (2015)
China	Central	42	21 (MAT,1:25)	H, T	**8** (TgCatCHn1-3, TgCatCZg1-5)	#9 -6 #2 -1 #17 -1	Yang et al. (2015)
China	Henan	28	2 (MAT,1:25)	H	1 (TgCatCHn4)	#9 -1	Yang et al. (2017)
China	ND	ND	ND	ND	**9** (Wh10, Wh13, Xz34, Xz38, Xz7, Xz9, Xz37, Xz39, Xz40)	#9 -4 #205 -5	Cheng et al. (2017)
Colombia		116	42 (MAT,1:40)		**16** (TgCtCo2,7, TgCtCo14, TgCtCo12,13, TgCtCo1, TgCtCo4,10,11, TgCtCo5x, TgCtCo5,6, TgCtCo3,9, TgCtCo15, TgCtCo8)	#10 -2 #14 -1 #18 -2 #28 -1 #38 -3 #40 -1 #61 -2 #62 -2 #101 -1 #128 -1 Note: one of these cats had two different genotypes	Dubey et al. (2006); Rajendran et al. (2012); Cañón-Franco et al. (2014)
Egypt	Giza	137		B, H, T			

(*continued on next page*)

Table 4 (*continued*)

Country	Region	No. tested	No. antibody positive (test, cut-off)	Bioassay in mice	No. of samples (designation)	Genotype (ToxoDB genotype # - number of samples)	Reference
			137 (MAT,1:25)		**115** (TgCatEg1,2,3,4,5,8,9,10,12,14,16,20,21,23,25,26,28,29,30,31,32,33,38,39,41,42,44,45,46,49,51,52,54,56,59,60,63,64,68,75,76,77,78,79,81,85,90,91,96,97,98,99,101,103,104,107,109,112, 113, TgCatEg6,11,13,15,17,19,22,24,35,36,37,43,47,48,50,58,61,62,66,69,70,71,72,73,74,80,82,83,84, 86,87,92,93,94,95,100,102,105,108,110,111,114, TgCatEg7,18,34,65, TgCatEg88, TgCatEg53,67, TgCatEg57, TgCatEg27,40,89,106)	#3 (Type II variant) -59 #1 (Type II) -2 #2 (Type III) -42 #20 -4 #168 -1 #169 -2 #176 -1 mixed -4	Al-Kappany et al. (2010a); Al-Kappany et al. (2010b)
Ethiopia	Addis Ababa	36	33 (MAT,1:25)	H	**33** (TgCatEt2b,3b,6a,7a,7b,13a,13b,24a,26a, TgCatEt4a,6b,9b,10a,14a, TgCatEt1a,3a,5a,9a,12a,16a,17a,19a,21a,28a,TgCatEt 11a,11b,15a,18a,20a,22a,23a,25a,27a)	#1 (Type II) -9 #2 (Type III) -5 #3 (Type II variant) -10 #20 -9 (see Table 5)	Dubey et al. (2013a); Dubey et al. (2013b)
Iran	Mashhad	31	NA	B	1	Type II based on 5 PCR-RFLP markers	Khodaverdi and Razmi (2019b)
Iran	2 Provinces	4	2 (MAT,1:25)	B	2	Type II based on 5 microsatellite markers	Zia-Ali et al. (2007)
Mexico	Durango	8	6	B, H	**6** (TgCatMx2,3,4,5, TgCatMx1, TgCatMx1b)	#9 -4 #74-1 #155 -1	Dubey et al. (2009d)
Mexico	Colima	48	14 (ELISA)	Several tissues of 10 cats	1 (TgCatMe1)	#28 -1 DNA detected in tissues of 8 cats	Rico-Torres et al. (2015)
Mexico	Quintana Roo	11	ND	Blood, H, D	2 (TgCatMxQR1, 5)	ToxoDB genotypes uncertain	Valenzuela-Moreno et al. (2019)
Portugal	Lisbon	423	187 (MAT,1:25)	B of 56, M of 15 (bioassay in cell culture)	**35** (15 B and 10 M from 20 cats)	ND	Waap et al. (2012)
Portugal	Lisbon	164 15	Seropositive	B M	17 ND	Of 164 cats, 18 isolates obtained from bioassay in mice, five microsatellite markers used for genotyping 17 of the samples, revealed 16 type II strains, one type I potentially be a recombinant strain.	Vilares et al. (2014)
West Indies	St. Kitts	10	Seropositive	B, H, T	7 (TgCatStK2,3a,4,6, TgCatStK1, TgCatStK3b, TgCatStK7)	#2 (Type III) -4 #141 -1 #1 (Type II) -1 #13 -1	Dubey et al. (2009c)
Turkey	Izmir	100	Yes	B, H	22 (TgCatTr-Izmir1,2,3, 5,6,7,8,9, 11,12,13, 15,16,17,18,19,20,21,22, TgCatTr-Izmir110,14, TgCatTr-Izmir4)	Genotyped by 15 microsatellite markers. Type II -19 Type III -2 Africa 1 -1	Can et al. (2014)
USA	Illinois	8	(MAT,1:25)	Isolated before 2009	8 (TgCatUS2, 3, 4, 5, 6; TgCatUS1, TgCatUS8, TgCatUS7)	#4 -5 #1 -1 #3 -1 #8 -1	Dubey et al. (1995b); Mateus-Pinilla et al. (1999); Dubey et al. (2011)
USA	Mississippi	1		Isolated before 2009	1 (TgCatMs1)	#5 -1	

(*continued on next page*)

Table 4 (*continued*)

Country	Region	No. tested	No. antibody positive (test, cut-off)	Bioassay in mice	No. of samples (designation)	Genotype (ToxoDB genotype # - number of samples)	Reference
USA	Pennsylvania	3	2 (MAT,1:25)	H	2 (TgCatUs12,13)	#216 -2	Dubey et al. (2004c); Dubey et al. (2011) Dubey et al. (2014a)
USA	New York	3	2 (MAT, 1:25)	B, H (only heart positive); no oocysts in feces	2 (TgCatUs10,11)	#1 (clonal Type II)	Dubey et al. (2014b)
USA	California	166	ND	B (in cell culture)	14 (Fc4, 5, 6, 7, 8, 9, 10, 11, 12; Fc1, 13, 14, 15, 16)	Feral cat samples genotyped by 6 PCR-RFLP markers. #1 -9 #3 -5 (see Table 5)	VanWormer et al. (2014)

B = brain, D = diaphragm, H = heart, M = muscle, T = tongue, ND = No data.

alarming (Mancianti et al., 2010; Ould Ahmed Salem et al., 2017; Veronesi et al., 2017); in these reports *T. gondii* DNA was detected in many as 20% of asymptomatic cats. One of the drawbacks of DNA detection is prevention of contamination and the results do not distinguish between dead and live oocysts.

3.2. Clinical infections and oocyst excretion

Cats of any age or any breed and either sex can die of toxoplasmosis. Although any organ may be involved by *T. gondii*, pneumonitis is the most common finding and it can be rapidly fatal (reviewed in Dubey, 2010). Of the 31 cases of clinical toxoplasmosis in cats reported for the past decade, concomitant infections/immunosuppressive conditions were present in 11 cats (Table 8). Clinical presentations included jaundice, anorexia, vomiting, paresis, and dermatitis. Ocular lesions were not mentioned in any of these cats (Table 8). However, ocular fundic examination should be a routine part of the examination of febrile cats. In a study of 104 cases of uveitis, antibodies to *T. gondii* were detected in 19 sick (18.3%) versus 1 (5.3%) of healthy cats (Powell et al., 2010). However, serologic tests should be used only as an aid for diagnosis because the antibody titers may not be different than in healthy population. In another study of 14 seropositive cats that were clinically evaluated, 11 had neurological signs, 5 cats had uveitis, and 4 had diarrhea; *T. gondii* oocysts were detected in feces of 3 but the method of diagnosis was not stated. Aspartate aminotransferase (AST) and alanine aminotransferase (ALT) enzymes were elevated in three cats (Bastan and Bas, 2018). In another study from Romania, uveitis was diagnosed in 19 (86.4%) of 22 cases of suspected clinical toxoplasmosis in cats (Cucos et al., 2015).

In three of the 31 cats, diagnosis was made by finding tachyzoites in biliary contents of 3 cats (Lo Piccolo et al., 2019; De Tommasi et al., 2014), in dermal nodule aspirate of 2 cats (Caporali et al., 2018), lung aspirate of 1cat (Murakami et al., 2018), tracheal wash of 1 (Evans et al., 2017), and CSF of 1 cat (Hu et al., 2016).

Two of these 20 cats listed in Table 8 were excreting *T. gondii* oocysts. One of these cats, had diarrhea and was excreting as many as 1 million oocysts in feces (Dubey and Prowell, 2013). The cat was treated with clindamycin and discharged from the hospital in good condition. *T. gondii* oocysts were detected in feces of a cat 10 days before onset of clinical signs (Jokelainen et al., 2012).

3.3. Genetic types of *T. gondii* in domestic cats

T. gondii infections are common in humans, livestock and in companion animals but clinical disease is relatively rare. Why some individuals become ill or even die of toxoplasmosis is mostly unknown. Differences in molecular characteristics of *T. gondii* is a factor in pathogenesis of clinical toxoplasmosis. Until 20^{th} century, little was known of genetic types of *T. gondii*. In general, only a few lineages of *T. gondii*, namely type II, type III, and type 12 and Chinese I are frequently identified (Dubey et al., 2011; Khan et al., 2011; Liu et al., 2014). Type II strains are the predominant type prevalent in humans in North America, Africa, and Europe. Similarly, Type III strains are most prevalent in animals. Type 12 are most prevalent in wildlife in USA. Chinese 1 (ToxoDB genotype #9, haplogroup 13) is the most prevalent in China. Using PCR-RFLP markers 278 variations (ToxoDB PCR RFLP genotypes) have been found (Su and Dubey, 2020).

The types of strains prevalent in cats is most important in the epidemiology of the parasite because they are the only hosts that can excrete the environmentally resistant oocysts and can directly transmit the parasite to humans and livestock. The frequencies of major genotypes identified in cats (Tables 4,9,10) agree with global pattern of *T. gondii* distribution (Shwab et al., 2014). New information has emerged concerning molecular epidemiology of *T. gondii* infection in cats in China, Brazil and Colombia. Data from each country are summarized in Table 9. Genotypes from cats from different continents are summarized

Table 5
Detection of *T. gondii* DNA in tissues or blood of cats.

Country	Region	No.	Tissue[a]	No. positive (%)	Remarks	Reference
Algeria	Algiers	96	H	87 (90.6)	529bp	Yekkour et al. (2017)
Brazil	Rio Grande do Norte	62	Several	5 (8.0)	B1 gene. 4 of 5 cats had MAT titers of 25-12800	Fournier et al. (2014)
China	Guizhou	19	B	10 (52.6)	529bp.	Li et al. (2015)
China	Henan	36	B	5 (13.9)	2 - ToxoDB#9	Qian et al. (2015)
China	Yunnan	175	B, H, Li, T	44 (25.1)	B1 gene. DNA 14.5% of 175 B, 10.9% of 164 Li, 14.2% of 175 heart, 15.7% of 25 tongue. 16 DNA by 10 PCR-RFLP typed 11 - ToxoDB#9 1 - ToxoDB#1 (Type II) 1 - ToxoDB#3 (Type II variant) 1 - ToxoDB#20 2 - ToxoDB#225	Tian et al. (2014)
China	Shanghai	35	B	2 (5.7)	Nested PCR, 5.8SrRNA gene	Wang et al. (2012)
Iran	-	29 seropositive	Several	20 (68.9) - 9 tissues positive	B1 gene	Asgari et al. (2018)
Iran	-	100	B	8 (8.0)	B1 gene	Mosallanejad et al. (2017)
Mexico	-	10 seropositive	several	8 (80.0)	B1 gene, DNA positive B in 5, H in 2, Li in 2, Lu in 2, M in 6, Sp in 5	Rico-Torres et al. (2015)
Portugal	Lisbon	164	B	82 (50.0)	*SAG2*	Vilares et al. (2014)
USA	California	166	B, T	49 (30.0)	B1 gene	VanWormer et al. (2014)

[a] B = brain, D = diaphragm, H = heart, K = kidney, Li = liver, Lu = lung, Sp = spleen, T = tongue, M = skeletal muscle.

in Table 10. In China, more than 90% of strains were ToxoDB genotype #9–this type has not been linked in Europe and is rare in Americas. Genotype #9 has been found to severe illness in pigs and humans in China (Dong et al., 2018). It is noteworthy that the strains from wildlife have caused fatal illness in cats (Dubey and Prowell, 2013; Crouch et al., 2019).

3.4. Experimental infections in cats

3.4.1. Immunization of cats to prevent oocyst excretion

Oral inoculation of cats with 30 bradyzoites of a chemically induced mutant of *T. gondii* (T-263) can induce protective immunity to oocyst excretion (Freyre et al., 1993). The mechanism of prevention of oocyst excretion by T-263 strain is unknown. Recently, schizonts, mature microgamonts and macrogamonts of T-263 were identified in cats, indicating that fertilization is likely to be interfered (Dubey, 2017). It has been suggested that T-263 likely harbors multiple mutations (Ramakrishnan et al., 2019). More recently, a genetically engineered mutant, HAP2KO, was produced (Ramakrishnan et al., 2019). Oral inoculation of cats with HAP2KO live tissue cysts led to the excretion of abnormal oocysts (oocysts did not sporulate) but cats became immune to oocyst excretion (Ramakrishnan et al., 2019). This remarkable finding may lead to a successful vaccine for cats. In another study, ablation of the AAH genes resulted in reduced infection in cats, lower oocyst yields, and decreased rates of sporulation (Wang et al., 2017b).

Infections with killed whole *T. gondii* or recombinant proteins have been unsuccessful to prevent excretion of *T. gondii* oocysts following challenge with tissue cysts (see Dubey, 2010). Attempts to immunize cats with crude or recombinant rhoptry proteins (rROP) by rectal or nasal routes were also unsuccessful in preventing excretion of oocysts (Zulpo et al., 2012, 2017).

For vaccine development, it is desirable to standardize the methods for oral infection with *T. gondii.* Most authors used tissue cysts for oral infection. However, a tissue cyst may contain few to hundreds of bradyzoites. Cornelissen et al. (2014) reported that infection with 50 free bradyzoites consistently induced oocyst excretion in cats and confirmed the results reported earlier (Dubey, 2001).

3.4.2. Immunity to re-excretion of T. gondii oocysts

How often cats excrete oocysts in their lifetime is unknown, and it is impossible to simulate natural conditions for experimental infections in cats. Soon after the discovery of *T. gondii* oocyst in cat feces in 1970, immunity to re-excretion was studied in experimentally infected cats (Dubey and Frenkel, 1974). Cats that had excreted oocysts did not re-excrete after challenge within 2-3 months after primary infection. We are aware of only 2 studies that investigated oocyst excretion in the laboratory for more than 2 years (Dubey, 1995; Zulpo et al., 2018). In the experiment conducted in colony-raised cats in USA, 4 of 9 cats re-excreted oocysts after challenge with *T. gondii* after homologous or heterologous strains, 77 months after primary infection. There was no evidence of anamnestic antibody response and antibody had remained elevated for 6 years in the absence of reinfection (Dubey, 1995). Recently, a study in Brazil reported that protection to re-excretion of *T. gondii* oocysts had waned progressively from 1 to 3 years (Zulpo et al., 2018). At 12 months, 1 of 3 cats re-excreted oocysts after challenge and 2 of 2 cats re-excreted oocysts when challenged with heterologous *T. gondii* strains at 3 years.

With respect to oocyst re-excretion there are no data on naturally infected cats. However, naturally exposed cats did excrete oocysts after feeding them tissue cysts in the laboratory. In a study from USA (Dubey et al., 1970), 7 of 12 adult feral seropositive cats with dye test titers of 1:4-1:128 and 4 of 6 dye test positive cats in Germany (Piekarski and Witte, 1971) excreted *T. gondii* oocysts after feeding tissue cysts. It is noteworthy that the dye test is considered the most specific serological test for *T. gondii* and even a titer of 1:2 is considered specific. These data indicate that cats might re-excrete oocysts. In the study from Ethiopia,

Table 6
Prevalence of *T. gondii*-like oocysts in feces of domestic cats (2009-2020).

Country	Area	No. tested	Grams of feces	Method				Total positive (%)	Reference
				Direct	Bioassay	Molecular			
						PCR positive (gene)	Genotyping		
Argentina	Buenos Aires	3	NS	3	3	3 (TOX5-TOX8)	10 RFLP markers, all ToxoDB#2 (Type III)	3	Bernstein et al. (2018)
Brazil	Rio de Janeiro	54	NS	0	ND	ND	ND	0	Bastos et al. (2014)
Canada	Nationwide	636	5	0	ND	ND	ND	0	Villeneuve et al. (2015)
China	Kunming	115	NS	5	yes	5 (Tox4, 5)	Type II based on *GRA6* and *SAG2*	5 (4.0)	Liang et al. (2016)
China	Henan	360	5-10	ND	1	ND	Genotyped ToxoDB#1 (Type II)	1 (0.3)	Yang et al. (2015)
Colombia	Armenia	140	5	0	ND	25 (B1)	6 of 24 samples positive for ROP18 revealed atypical genotypes	25 (17.8)	Zamora-Vélez et al. (2020)
Denmark	22 Pig farms	52	4	0	ND	0 (529bp)	ND	0	Nielsen et al. (2019)
Egypt	Sharkia Province	100	2-10	2	ND	2 (B1)	ND	2 (2.0)	Abd El-Ghany and Merwad (2012)
Ethiopia	Addis Ababa	36	1-10	1	7	ND	ND	7 (19.4)	Dubey et al. (2013c)
Finland	Helsinki	131	10	2	ND	1 (529bp)	ND	1 (0.7)	Jokelainen et al. (2012)
Finland	Helsinki	1 clinical	10	1	ND	ND	ND	1 (100.0)	Jokelainen et al. (2012)
Germany and other European countries (2004-2006)		24106	Various	74	ND	26 (*T. gondii* (Oligo1/Oligo4, Tox5/Tox-8, Tox4/Tox5) and *H. hammondi* (HhamITS/CT1),	18 isolates typed, (15 ToxoDB#3 (Type II variant), 2 mixed genotypes, 1 not fully genotyped)	26 (0.11) PCR Tg positive, 22 (0.09) PCR Hh positive	Schares et al. (2008); Herrmann et al. (2010)
Germany (2007-2008)		18259	Various	Direct	Partially (n = 4)	46 (*T. gondii* -Tox5/Tox8, Tox4/Tox5 and *H. hammondi* (Hham34 F/Hham3R)	ND	46 (0.25) PCR Tg positive, 4 (0.02) bioassay Tg positive, 34 (0.19) PCR Hh positive	Herrmann et al. (2010) excluding data from the previous study Schares et al. (2008)
Germany (2007-2011, data of Herrmann et al., 2010 included)		61224	Various	105	Partially (n = 4)	84 (*T. gondii* (Tox5/Tox8, Tox4/Tox5) and *H. hammondi* (Hham34 F/Hham3R), 50 isolates typed, excluding 18 from a previous study, including also 4 bioassay positives)	39 ToxoDB#3 (Type II variant), 3 ToxoDB#1 (Type II), 1 ToxoDB#2 (Type III), 1 mixed genotype, 6 not fully genotyped)	84 (0.14) PCR Tg positive, 61 (0.1) PCR Hh positive	Schares et al. (2016)
India	Kerla	313	ND	ND	ND	14 (B1)	ND	14 (4.4)	Latha and Hareendran (2018)
Iran	Shiraz	29 seropositive	NS	0	ND	7 (B1)	ND	7 (24.1)	Asgari et al. (2018)
Iran	Mashhad	159	1	4	ND	ND	ND	4 (2.5)	Khodaverdi and Razmi (2019a)
Iran	Mashhad	175	NS	4	ND	8 (B1)	ND	8 (4.5)	Khodaverdi and Razmi (2019b)
Iran	Northwest	103	NS	0	ND	ND	ND	0	Mohebali et al. (2019)
Iran	Ahvaj	198	1	0	ND	ND	ND	0	Mosallanejad et al. (2011)
Ireland	Dublin	271	3	2	ND	ND	ND	2 (0.7)	Garcia-Campos et al. (2019)
Italy	Tuscany	50	0	ND	ND	8 (B1)	0	8 (16.0)	Mancianti et al. (2010)
Italy	Tuscany	146	0.04	0	ND	15 (B1)	Limited data	15 (10.3)	Mancianti et al. (2015)
Italy	Umbria	77	NS	ND	ND	10 (B1)	ND	10 (13.0)	Santoro et al. (2017)
Italy	Milan	139	NS	0	ND	ND	ND	0	Spada et al. (2013)
Italy	Perugia	78	5	2	ND	16 (B1)	ND	16 (20.5)	Veronesi et al. (2017)
Japan	Tokyo	834	5	5	1	1 (B1)	TgCatJpTy1/k-3 strain designated in 2020; genotype Type II	5 (0.6)	Matsui et al. (1986); Masatani et al. (2020)
Japan	Tokachi	351	NS	1	ND	ND	ND	1 (0.3)	Salman et al. (2018)
Kenya	Kiambu	103	NS	13	8	ND	ND	8 (7.8)	Njuguna et al. (2017)
Korea	Gwangju	563	NS	5	ND	5 (Tox-5/Tox-8 and Hham34 F/Hham3R)	ND	5 (0.9)	Ahn et al. (2019)

(*continued on next page*)

Table 6 (*continued*)

Country	Area	No. tested	Grams of feces	Method				Total positive (%)	Reference
				Direct	Bioassay	Molecular			
						PCR positive (gene)	Genotyping		
Korea	Seoul	300	2	10	2	14 (B1)	Type II based on 2 *SAG5D* and *SAG5E*	14 (4.7)	Jung et al. (2015)
Korea	9 cities	150	NS	ND	ND	0 (TOX5)	ND	0	Kim et al. (2017)
Kuwait	Several areas	240	NS	5	ND	ND	ND	5 (2.1)	Abdou et al. (2013)
Mauritania	Nouakchott	100	NS	23	ND	ND	ND	23 (23.0)	Ould Ahmed Salem et al. (2017)
Pakistan	Lahore	470	0.5/0.2 for PCR	15	ND	11 (TOX)	ND	11 (2.3); *H. hammondi* 4	Nabi et al. (2018)
Poland	Southwestern	41	2	2	ND	ND	B1	1 (2.4)	Sroka et al. (2018)
Qatar	Doha	4652	NS	425-*T. gondii*-like	ND	ND	ND	425 (9.1) *T. gondii*-like	Abu-Madi and Behnke (2014)
Romania	Transylvania	414	NS	5	ND	ND	ND	5 (1.2)	Mircean et al. (2010)
Russia	Tatarstan	148	NS	5	ND	ND	ND	5 (3.3)	Shamaev et al. (2018)
Russia	Crimea	55	NS	12	ND	ND	ND	12 (21.8)	Lukyanova et al. (2017)
Saudi Arabia	Riyadh	200	NS	24	ND	ND	ND	24 (12)	Mohammed et al. (2019)
Spain	Central	459	NS	0	ND	ND	ND	0	Montoya et al. (2018)
Switzerland	Bern, Olten	252	NS	2	ND	1(TOX5)	ToxoDB genotype #3 using 10 RFLP markers	1 (0.4)	Berger-Schoch et al. (2011)
Switzerland	Several regions	664	NS	9	ND	4	ND	4 (0.6)	Zottler et al. (2019)
Thailand	Songkhla	254	NS	49	ND	19 (2 for 529bp and 17 for ITS-1)	Genotyping using 6 RFLP markers revealed 5 genotypes	19 (7.4)	Chemoh et al. (2016); Chemoh et al. (2018)
Turkey	Ankara	14	NS	3	ND	ND	ND	3 (21.4)	Bastan and Bas (2018)
USA	Hawaii	69	0.2	ND	ND	5 (GRA6, ITS1)	ND	5 (7.2)	Davis et al. (2018)
USA	Maryland	1 clinical	NS	1	1	ND	ToxoDB#4-10 RFLP markers	1	Dubey and Prowell (2013)
USA	Virginia	49	NS	ND	ND	3 (Tox4, 5; ToxF, R)	ND	3 (6.0)	Lilly and Wortham (2013)
USA	Oklahoma	846	1-5	1	ND	ND	ND	1 (0.1)	Nagamori et al. (2018)
USA	Virginia	275	1-2	3	ND	ND	ND	3 (1.0)	Taetzsch et al. (2018)
USA	California	452	NS	10	ND	3 (B1, ITS-1)	ND	3 (0.6); *H. hammondi* in 1	VanWormer et al. (2013)
West Indies	St. Kitts	51	1-5	ND	0	ND	ND	0	Dubey et al. (2009c)

ND = not done
NS = not stated

Table 7
Excretion of *T. gondii* and *H. hammondi* oocysts in feces of naturally infected cats in Germany and 15 other countries of Europe.

Period sampled (month, year)	No. of feces	Microscopical results (9-14 μm oocysts)	PCR positive	*T. gondii*	*H. hammondi*	Remarks	Reference
10-2004 to 11-2006	24,106	74	54	26	22	3 months to 17- year old excreting *T. gondii*[a,b]	Schares et al. (2008)
6-2007 to 12-2011	61,224	No data	224	84	61	No common infections of *H. hammondi* and *T. gondii*. Climatic factors significant[c]	Herrmann et al. (2010); Schares et al. (2016)
Total	85,330	No data	278	110	83		

[a] Ages known for 18 cats; 3 months (1), 4 months (2), 5 months (1), 6 months (1), 1 year (1), 1.5 years (1), 2 years (1), 3 years (1), 5 years (1), 8 years (1), 10 years (2), 11 years (1), 13 years (2),14 years (1), 17 years (1).
[b] Oocysts per gram of feces 13,400 (in a 3-month old cat) to 13,300,000 (in a 10-year old cat).
[c] *T. gondii* oocysts predominantly during summer and autumn while *H. hammondii* mainly autumn and winter.

36 cats were captured, bled, and held in captivity in cages for 12 days when they were euthanized for bioassay of tissues and feces for viable *T. gondii.* During captivity cats were fed cooked diet. Seven of these 36 cats were found excreting *T. gondii* oocysts as determined by mouse bioassay (Dubey et al., 2013c). In 1 of these cats 70 million oocysts were detected in rectal contents. Four of these cats had high antibody titers (MAT 1:1600 or higher). These data indicate either prolonged time of oocyst excretion or re-excretion from seropositive cats; cats usually excrete oocysts for less than 1 week.

Additionally, malnutrition (Ruiz and Frenkel, 1980), and concurrent infection with the feline coccidium, *Cystoisospora felis* can affect immunity to excretion of oocysts in cats. Excretion of millions of *T. gondii* oocysts by chronically infected cats, in the absence of *T. gondii* infection from outside, is most intriguing because *C. felis,* is usually non-pathogenic for cats (Chessum, 1972; Dubey, 1976). Immunosuppression by pharmacological doses of immunosuppressive drugs and coinfection with FIV or FeLV do not affect re-excretion of oocysts in cats (reviewed in Dubey, 2010). Prolonged administration of pharmacological doses of cyclosporine (7.5 mg/kg/day, orally for 126 days) did not lead to re-excretion of *T. gondii* oocysts (Lappin et al., 2015).

In conclusion, immunity to re-excretion of *T. gondii* oocysts in cats is good and cats seldom excrete oocysts after primary infection. However, there are no guaranties that a cat will not excrete oocysts more than once in life. Therefore, irrespective of the serological status of the cat, cat owners should take precautions while handling cat feces and to prevent infection in cats (Dubey, 2010).

3.4.3. Serological responses of experimentally infected cats

Sera from experimentally infected cats were used to evaluate the usefulness of SAG1-ELISA for the detection of *T. gondii* antibodies. For this, four kittens were inoculated intraperitoneally with 10,000 *T. gondii* tachyzoites of the NED strain (Hosseininejad, 2012). Antibodies were detected 8–10 days p.i. as assayed by the IFAT and titers increased to 1:512 at day 41 p.i. when the experiment was terminated. The results obtained with ELISA paralleled IFAT values (Hosseininejad, 2012).

3.4.4. Pathogenesis of congenital infection

Congenital toxoplasmosis is relatively uncommon (Dubey, 2010). Histological documentation of congenital infection in experimentally infected cats is difficult because of short gestation (2 months) and because queens cannibalize sick kittens (reviewed in Dubey, 2010). In a Brazilian study, 8 queens (4 with each isolate) were orally inoculated with tissue cysts of 2 cat-derived isolates of *T. gondii* (TgCatBr60, TgCatBr71) at 23-34 day of gestation (Sakamoto et al., 2009). Of the 4 queens inoculated with TgCatBr60, all had mild clinical signs, none aborted, but 1 had stillbirth. Two 10 -day old kittens from 1 queen were seropositive. The 4 queens inoculated with TgCatBr71, all also had mild clinical signs, but 2 queens aborted. Ten-day old kittens from 1 queen were seropositive. The kittens born to other queens were seronegative at 10 days of age. However, it is uncertain if the kittens had colostrally-derived antibodies or were infected with *T. gondii*. The queens developed IFA titers of 16 to 2048.

3.4.5. Lipid metabolism determines host specificity of T. gondii oocyst excretion in cats

Of all the hosts of *T. gondii*, only felids can excrete *T. gondii* oocysts (Frenkel et al., 1970). Felines are the only mammals that lack delta-6-desaturase activity in their intestines, which is required for linoleic acid metabolism, resulting in systemic excess of linoleic acid. In a remarkable discovery, it was determined that *T. gondii* sexual development occurs when cultured feline intestinal epithelial cells are supplemented with linoleic acid (Martorelli di Genova et al., 2019). Inhibition of murine delta-6-desaturase and supplementation of their diet with linoleic acid allowed *T. gondii* sexual development in mice. This mechanism of species specificity is the first defined for a parasite sexual cycle (Martorelli di Genova et al., 2019).

4. Other felids

T. gondii infections are common in wild felids, especially in zoos (Dubey, 2010; Cañón-Franco et al., 2013a,b).

4.1. Prevalence

4.1.1. Serologic prevalence

Virtually all captive wild felids become exposed to *T. gondii* (Table 11). Up to 100% of bobcats were found seropositive. Additionally, Bártová et al. (2018) from Czech Republic zoos detected antibodies to *T. gondii* by LAT (cut-off not stated) in 3 of 5 African lion (*Panthera leo*), 2 of 4 Amur leopard (*Panthera pardus orientalis*), 3 of 4 Asiatic lion (*Panthera leo persica*), 2 of 3 Bengal tiger (*Panthera tigris bengalensis*), 13 of 16 cheetah (*Acinonyx jubatus*), 1 of 1 Indochinese tiger (*Panthera tigris corbetti*), 2 of 4 jaguar (*Panthera onca*), 3 of 3 Jaguarundi (*Puma yagouaroundi*), 4 of 4 leopard (*Panthera pardus*), 1 of 1

Table 8
Clinical toxoplasmosis in cats (2009-2020).

Location (No. of cats)	Main observations	IHC*	PCR	Genetic typing	IMS** and notes	Reference
Australia (1)	A 10-year-old, female, with neurological signs-paresis. Vaccinated against FIV, FELV, FIPV. Spinal cord lesion at C6-T2 suspected. *T. gondii* IgG titer 1:512. Refractory to low dose of clindamycin treatment. Cat euthanized and necropsied. Lesions confined to spinal cord. Severe inflammation with *T. gondii* present.	Sc	ND	ND	No	Lindsay et al. (2010)
Australia (4)	**Cat 5:** A 4-year-old, male, neurological signs, dysphagia; disseminated toxoplasmosis. **Cat 6:** 7-year-old, jaundice, hepatic lymphoma, immunosuppressive treatment. **Cat 7**: 9-year-old, jaundice, dyspnea; disseminated toxoplasmosis with *T. gondii* in B, H, K, Li, P. **Cat 8**: 4-year-old, dyspnea, disseminated toxoplasmosis with *T. gondii* in several tissues	**Cat 5** - B, Sc, K **Cat 6** – Li **Cat 7** - B, Li **Cat 8** - A, Co, Lu	Yes	ToxoDB#3 in all 4 cats, from B in **cat 5,** Li from **cat 6**, Li from **cat 7**, and Lu from **cat 8**	**Cat 5** - No **Cat 6** – Yes, lymphoma **Cat 7** – Yes, FIV **Cat 8** – Yes, polyarteritis and corticosteroids	Brennan et al. (2016)
Brazil (1)	A 5-year-old, male, with dyspnea, died. Bronchopneumonia, hepatitis. *T. gondii* in Li, Lu, Sp	Lu	Lu	ToxoDB#10 (Microsatellite markers: Type I-variant)	Yes, myeloid leukemia, FeLV-positive	Pena et al. (2017)
Canada (1)	A 22-month-old male, lethargy, vomiting. Abdominal mass found by ultrasonography. Cat died. Liver and mesenteric lymph nodes enlarged. Severe necrosis of lymph node and hepatitis were associated with tachyzoites.	Li	ND	ND	No	Cohen et al. (2016)
Finland (6)	Retrospective study of 6 (0.5-2-year-old) postmortems diagnosed with generalized toxoplasmosis. Clinical signs found: dyspnea in 5, incoordination in 3, gross lesions in lungs of all 6. Pneumonia predominant lesion in all 6. **Viable *T. gondii* isolated from tissues of 2 cats. Oocysts detected in 1 cat.**	B of 5, Li of 6, Lu of 6, Sp of 5, Lm of 2, H of 5, M of 1, and K of none.	Yes	Viable *T. gondii* isolated from B and H of 1 cat, and B and Lu of 1. From frozen tissue of the remaining 4 cats. Type II by 6 microsatellite markers.	No	Jokelainen et al. (2012)
Germany (1)	A 9-year-old, female, anorexia, vomiting, elevated liver enzymes, hyperbilirubinemia, had received cyclosporine for immune-mediated thrombocytopenia. Ultrasound revealed thickened gallbladder and common bile duct wall. Tachyzoites found in bile aspirate. **Diagnosis confirmed antemortem by PCR.** Treated successfully with clindamycin but relapsed.	ND	Yes	ND	Yes	Lo Piccolo et al. (2019)
Germany (1)	A 12-year-old, female, with progressive neurological signs. Hypernatremia, azotemia and hyperglobulinemia. MRI revealed neural lesions. Histologically, granulomatous and necrotizing panencephalitis involving hypothalamus and pituitary gland with *T. gondii* tissue cysts and tachyzoites.	ND	ND	ND	Thyroid adenoma, meningioma	Weingart et al. (2016)
Italy (1)	Adult, male cat with diarrhea, lethargy, and skin nodules, up to 1 cm in diameter presented on neck, head, and ears. Aspirate from nodules revealed many tachyzoites. Cat had antibodies to *T. gondii* by IFAT with low titer. TEM and PCR examinations were confirmatory. **Antemortem** diagnosis.	Skin	Skin	ND	Yes, FIV, FeLV	Caporali et al. (2018)
Italy (1)	A 12-year-old, female, with hyperadrenocorticism, pituitary, *T. gondii* antibody titer 1:20 (IHA). Histologically necrosis and encephalitis with tachyzoites present in lesions.	B, P	ND	ND	Yes	Spada et al. (2010)
Italy (1)	A 1-year-old, female, suffering from jaundice was necropsied. Cholangio-hepatitis confirmed histologically. Tachyzoites detected in smears of biliary contents and confirmed by PCR on DNA from stained smears. Tachyzoites detected by transmission electron microscopy of liver.	ND	Yes	ND		De Tommasi et al. (2014)
Italy (1)	A 6-months-old, female, with diarrhea; neurological signs; treatment with clindamycin; cat died.	B	ND	ND	Yes, FIV, FIPV	Zandonà et al. (2018)

(*continued on next page*)

Table 8 (*continued*)

Location (No. of cats)	Main observations	IHC*	PCR	Genetic typing	IMS** and notes	Reference
Italy (2)	**Case 1**: A 4-year-old female; gait abnormality progressed to nonambulatory paraparesis; MRI examination revealed focal intramedullary spinal cord lesion at the level of T6-T9; IFAT for *T. gondii* IgG titer of 1:64;; cat euthanized and necropsied. **Case 2:** A 6-year-old male; gait abnormality in pelvic limbs, progressed to tetraparesis; IFAT for *T. gondii* IgG titer of 1:320; cat treated with clindamycin (20 mg/kg, Po) for 1 week with no improvement; Cat died. Histologically, necrosis and inflammatory lesions in the meninges and the neural tissue were found in both cats.	B, Sc of both cats	ND	ND	No	Alves et al. (2011)
Japan (1)	An 11-year-old, male, diagnosed **antemortem**, sneezing, tachypnea, nasal tumor, aspirate of lung nodules revealed *T. gondii* tachyzoites. Antibodies to *T. gondii* (LAT 1:256). Viable *T. gondii* isolated from lung aspirate in Vero cell culture. Cat treated with clindamycin (12 mg/kg for month. *T. gondii* not detected in tissues postmortem. FIV, FELV and FIP- negative	Lu, K, B	Yes	ToxoDB #2 (Type III)	Yes, lymphoma	Murakami et al. (2018)
South Africa (1)	A 10-year-old, female, with fever, abdominal pain, and severe bilirubinuria. FIV, FELV-negative, Jaundice, pneumonia, hepatitis main lesions. Pancreatic lymph nodes enlarged with severe parasitism.	Several tissues	Li, Li	No	No	Nagel et al. (2013)
Switzerland (1)	A 10-year-old, male, with fever, anorexia, vomiting, and diarrhea. Aspirate of mesenteric lymph nodes revealed tachyzoites. Cat died and was necropsied. Microscopically, there was disseminated toxoplasmosis with severe lesions in Li, and Lu. **Viable *T. gondii* isolated from liver by bioassay in mice and cell culture.**	ND	Several tissues	ToxoDB #3 (Type II variant)	No	Spycher et al. (2011)
United Kingdom (1)	A 2-year-old female with 18-month history of lameness on all 4 limbs. Myositis on histology but *T. gondii* not identified in sections. IAF IgG titer 1:1600. Marked clinical improvement in 3 days after medication with Clindamycin (19.2 mg/kg, PO,q24hours).Treated for 6 weeks.	ND	Muscle-negative	ND	No	Butts and Langley-Hobbs (2020)
USA (1)	A 6-month-old, male, with lethargy, anorexia, fever, and diarrhea. Numerous *T. gondii* oocysts were found in feces diagnosed **antemortem.** Cat became asymptomatic after treatment with clindamycin orally for 10 days and discharged. **Viable *T. gondii* isolated from oocysts.**	ND	Oocysts	ToxoDB #4	No	Dubey and Prowell (2013)
USA (1)	A 2-year-old, male, with **acute respiratory distress syndrome (ARDS)**. Cat had been medicated with cyclosporine for eosinophilic (fungal) dermatitis. Thoracic radiography revealed nodules in lungs. Tracheal wash revealed numerous *T. gondii* tachyzoites. Histological examination revealed disseminated toxoplasmosis in B, H, Li, and Lu.	ND	ND	ND	Yes, cyclosporine medication	Evans et al. (2017)
USA (1)	A 3-year-old, male, with tetraparesis. MRI revealed spinal cord lesion. **Tachyzoites detected in cytospin of Cerebro spinal fluid.**	ND	ND	ND	FeLV-positive	Hu et al. (2016)
USA (1)	An 8-year-old, male, with seizers. MRI detected a mass on olfactory bulb and rostral front lobe; a 0.5 cm mass was removed surgically. Histology revealed granuloma due to *T. gondii. T. gondii* antibodies IgM and IgG positive.	B	ND	ND	No	Pfohl and Dewey (2005)
USA (2)	2 of 5 littermate 8-week-old kittens died of acute toxoplasmosis, thought to be **postnatally acquired.** The queen and the dead kittens had antibodies to *T. gondii* while 3 asymptomatic kittens were seronegative. Histologic examination revealed enteritis with **enteroepithelial stages (schizonts)**, pneumonia and disseminated infection.	Several tissues	Li, Lu	ToxoDB #4 in both kittens	No	Crouch et al. (2019)

*IHC = Immunohistochemistry, **IMS = Immunosuppression or concurrent infections, FIV = Feline immunodeficiency Virus, FIPV = Feline Infectious Peritonitis Virus, FELV = Feline Leukemia Virus, A = Adrenal gland, B = Brain, Co = Colon, H = Heart, K = Kidney, Li = Liver, Lu = Lung, Lm = Lymph node, M = Muscle, P = Pancreas, Sc = Spinal cord, Sp = Spleen

Table 9
Distribution of *T. gondii* genotypes from domestic cats 2009-present

Country	Viable isolates	DNA	Total	TOXODB genotypes #1 (Type II-clonal, haplo-group 2)	#2 (Type III, haplo-group 3)	#3 (Type II variant, haplo-group 2)	#4 (haplo-group 12)	#5 (haplo-group 12)	#9 (Chinese 1, haplo-group 13)	#10 (Type I, haplo-group 1)	Other genotypes (Genotype# - number of samples)	Reference
Algeria		12	12	-	-	-	-	-	-	-	All Type II based on microsatellite markers of cat tissue samples.	Yekkour et al. (2017)
Australia	-	8	8	-	-	7	-	-	-	-	1 sample no data	Brennan et al. (2016)
Brazil	28	-	28	-	-	-	-	-	-	-	**13 ToxoDB genotypes**: (#6-5, #8-2, #11-2, #14-1, #19-3, #21-7, #42-2, #47-1, #80-1, #104-1, #119-1, #120 -1, #126-1)	Dubey et al. (2004b); Su et al. (2006); Shwab et al. (2014)
Brazil	2	-	2	-	-	-	-	-	-	-	ToxoDB #146-2	Melo et al. (2016)
Brazil	46	-	46	-	-	-	-	-	-	-	**20 ToxoDB genotypes:** (#6, (Type BrI)-8, #11 (Type BrII)-8, #8 (Type BrIII)-5, #19-1, #26-2, #34-4, #55-2, #56-2, #58-1, #65-1, #67-1, #85-1, #86-1, #92-1, #108-1, #111-1, #117-1, #121-1, #124-1, #136-1) Mixed infection-2	Pena et al. (2008); Shwab et al. (2014)
Brazil	1	-	1	-	-	-	-	-	-	1	-	Pena et al. (2017)
Brazil	1	-	1	-	-	1	-	-	-	-	-	Silva et al. (2017)
Canada	2	-	-	-	-	-	-	1	-	-	ToxoDB #130-1	Dubey et al. (2008); Dubey et al. (2011)
Colombia	16	-	-	-	-	-	-	-	-	2	**9 ToxoDB genotypes**: #14-1, #18-2, #28-1, #38-3, #40-1, #61-2, #62-2, #101-1, #128-1). Note: one of these cats had two different genotypes	Dubey et al. (2006); Rajendran et al. (2012); Cañón-Franco et al. (2014)
China	17	-	17	-	-	-	-	-	15	-	**1 ToxoDB genotype:** #18-2	Dubey et al. (2007a); Shwab et al. (2014)
China	8	-	8	-	-	8	-	-	-	-	-	Zhou et al. (2009)
China	14	-	14	-	-	-	-	-	14	-	Note: 2 of these 14 samples initially designated as genotype Chinese 2 were corrected as Chinese 1	Chen et al. (2011); Wang et al. (2013a)
China	11	-	11	-	-	-	-	-	11	-	-	Qian et al. (2012)
China	5	-	5	-	-	-	-	-	5	-	-	Wang et al. (2013b)
China	19	-	19	-	-	-	-	-	14	1	**1 ToxoDB genotype:** #205-4	Wang et al. (2013a)
China	28	-	28	-	-	-	-	-	28	-	Microsatellite typing revealed minor differences	Li et al. (2014)
China	0	16	16	1		1	-	-	11	-	**2 ToxoDB genotypes:** #225-2 #20-1	Tian et al. (2014)
China	-	2	2	-	-	-	-	-	2	-	-	Li et al. (2015)
China		2	2	-	-	-	-	-	2	-	-	Qian et al. (2015)
China	9	-	8	-	1	-	-	-	6	-	**1 ToxoDB genotype:** #17-1	Yang et al. (2015)
China	1	-	1	-	-	-	-	-	1	-	-	Yang et al. (2017)
China	9	21	9	-	-	-	-	-	4	-	**1 ToxoDB genotype:** 5- #205	Cheng et al. (2017)
Egypt	115	-	115	2	42	59	-	-	-	-	**4 ToxoDB genotypes:** #20-4, #168-1, #176-1, mixed -4#169-2,	Al-Kappany et al. (2010a)

(*continued on next page*)

Table 9 (*continued*)

Country	Viable isolates	DNA	Total	TOXODB genotypes #1 (Type II-clonal, haplo-group 2)	#2 (Type III, haplo-group 3)	#3 (Type II variant, haplo-group 2)	#4 (haplo-group 12)	#5 (haplo-group 12)	#9 (Chinese 1, haplo-group 13)	#10 (Type I, haplo-group 1)	Other genotypes (Genotype# - number of samples)	Reference
Ethiopia	33	-	33	9	5	10	-	-	-	-	**1 ToxoDB genotype:** #20-9	Dubey et al. (2013b)
Finland	2	3	5	-	-	5	-	-	-	-	-	Jokelainen et al. (2012)
Iran	1	-	-	-	-	-	-	-	-	-	Belong to Type II based on 5 PCR-RFLP markers	Khodaverdi and Razmi (2019b)
Iran	2	-	2	-	-	-	-	-	-	-	Both samples are Type II based on 5 microsatellite markers	Zia-Ali et al. (2007)
Germany	68	-	68	3	1	54	-	-	-	-	10 samples not fully typed	Herrmann et al. (2010)
Japan	2	-	-	1	1	-	-	-	-	-	-	Taniguchi et al. (2018)
Mexico	6	-	6	-	-	-	-	-	4	-	**2 ToxoDB genotypes:** #74-1 #155-1	Dubey et al. (2009d)
Mexico	1	-	-	-	-	-	-	-	-	-	**1 ToxoDB genotype:** #28-1	Rico-Torres et al. (2015)
Mexico	2	-	2	-	-	-	-	-	-	-	ToxoDB genotypes uncertain	Valenzuela-Moreno et al. (2019)
Puerto Rico	6	-	6	-	-	-	-	-	-	-	**4 ToxoDB genotypes:** #49-3, #112-1, #115-1, #118-1	Dubey et al. (2007b); Dubey et al. (2011)
Portugal	17	-	17	-	-	-	-	-	-	1	**Genotyped by 5 microsatellite markers**: Type II (ToxoDB #1 or #3) -16 samples. The type I sample maybe a recombinant strain	Vilares et al. (2014)
St Kitts, West Indies	7	-	7	1	4		-	-	-	-	**2 ToxoDB genotypes:** #13-1, #141-1	Dubey et al. (2009c) Dubey et al. (2016) Shwab et al. (2014)
Switzerland	1	-	1	-	-	1	-	-	-	-	-	Spycher et al. (2011)
Turkey	22	-	22	?	2	?	-	-	-	-	**Genotyped by 15 microsatellite markers**: Type II (ToxoDB #1 or #3) -19 samples. Africa 1 (ToxoDB #6) -1	Can et al. (2014)
USA (New York)	0	2	2	-	-	-	2	-	-	-	-	Crouch et al. (2019)
USA (Illinois)	8	-	8	1	-	1	5	-	-	-	**1 ToxoDB genotype:** #8-1	Dubey et al. (1995b); Mateus-Pinilla et al. (1999); Dubey et al. (2011); Shwab et al. (2014)
USA (Mississippi)	1	-	1	-	-	-	-	1	-	-	-	Dubey et al. (2004c); Dubey et al. (2011)
USA (Maryland)	1	-	1	-	-	-	1	-	-	-	-	Dubey and Prowell (2013)
USA (Pennsylvania)	2	-	2	-	-	-	-	-	-	-	**1 ToxoDB genotype:** #216-2	Dubey et al. (2014a)
New York	2		2	2	-	-	-	-	-	-		Dubey et al. (2014b)
USA (California)	14	0	14	9	-	5	-	-	-	-	Feral cat samples genotyped by 6 PCR-RFLP markers.	VanWormer et al. (2014)

*Type X, variant of Type II.

Table 10
Distribution of PCR-RFLP (ToxoDB) *T. gondii* genotypes from domestic cats from different continents/countries.

Continent/country	Total typed	Classic Types			ToxoDB				Reference
		I (Toxo DB#10)	II (ToxoDB#1 or 3)	III (ToxoDB#2)	#4	#5	#9	Others	
Africa									
Algeria	12	0	12	-	0	0	0	0	Yekkour et al. (2017)
Egypt	115	0	61	42	0	0	0	8, plus 4 mixed	Al-Kappany et al. (2010a)
Ethiopia	33	0	19	5	0	0	0	9	Dubey et al. (2013b)
Asia (Southeast)									
China	139	1	9	1	0	0	113	15	See Table 9
South America									
Brazil (mainland)	78	1	0	1	0	0	0	76	See Table 9
Colombia	16	2	0	0	0	0	0	14	Dubey et al. (2006)
Mexico	7	0	0	0	0	0	0	7	Dubey et al. (2009d); Rico-Torres et al. (2015)
Europe									
Germany	68	0	57	1	0	0	0	10 not fully typed	Herrmann et al. (2010); Herrmann et al. (2012)
Portugal	17	1	16	0	0	0	0	0	Vilares et al. (2014)
Turkey	22	0	19	2	0	0	0	1 (#6, Africa1)	Can et al. (2014)
Finland	5	0	5	0	0	0	0	0	Jokelainen et al. (2012)
Switzerland	1	0	1	0	0	0	0	0	Spycher et al. (2011)
Caribbean									
Puerto Rico	6	0	0	0	0	0	0	6	Dubey et al. (2007b); Dubey et al. (2011)
St Kitts, West Indies	7	0	1	4	0	0	0	2	Dubey et al. (2009c) Dubey et al. (2016) Shwab et al. (2014)
North America									
Canada	2	0	0	0	0	1	0	1	Dubey et al. (2008); Dubey et al. (2011)
USA	30	0	18	0	8	1	0	3	Crouch et al. (2019); Dubey et al. (2011); Dubey and Prowell (2013); Dubey et al. (2014a,b); VanWormer et al. (2014)

ocelot (*Leopardus pardalis*), 1 of Pallas's cat (*Otocolobus manul*),1 of 1 Persian leopard (*Panthera pardus saxicolor*), 1 of 2 serval (*Leptailurus serval*), 2 of 2 Siberian tiger (*Panthera tigris altaica*), and 11 of 16 Sumatran tiger (*Panthera tigris sumatrae*). In a follow up of this survey from Czech zoos, *T. gondii* antibodies were reported in 8 of 8 Bengal tigers, and 13 of 14 lions (Marková et al., 2019).

Using sera from jaguars from 10 Mexican zoos, Reynoso-Palomar et al. (2020) compared a commercials IgG ELISA (DRG International, USA) based on tachyzoite lysate antigen (TLA), and in-house ELISA with recombinant antigens SAG1 and GRA7. Forty samples were seropositive by commercial ELISA and excellent correlation was found with in-house ELISA combining SAG1 and GRA7 antigens (Reynoso-Palomar et al., 2020).

4.1.2. Isolation and genetic characterization of viable T. gondii from wild felids

Viable *T. gondii* has been isolated from several wild felids (Table 12). Genetic typing results showed dominance of ToxoDB genotype #5, which is common in wildlife in general (Dubey et al., 2011). Among the wild felids, the high isolation rate from bobcats from Mississippi, USA is noteworthy. These bobcats were from a very remote area with virtually no human contact. All 35 (100%) bobcats were

Table 11
Seroprevalence of *T. gondii* in wild felids (2009-2019).

Location	No. tested	No. positive	% positive	Test	Cut-off titer	Notes	Reference
***Panthera* spp. (tiger, lion, leopard, jaguar)**							
Tiger (Panthera tigris)							
Brazil	6	4	66.7	IFAT	1:40	-	André et al. (2010)
China	3	2	66.6	MAT	1:25	-	Yang et al. (2017)
China	10	8	80.0	MAT	1:25	Parasite isolated from 2, see Table 3	Yang et al. (2019)
India	20	2	10.0	ELISA	Wuhan Hi-tech	*	Moudgil et al. (2019)
Mexico	9	9	100.0	ELISA, IFA	1:40	C,6 positive by IFA 1:40	Gomez-Rios et al. (2019)
Mexico	5	4	80.0	MAT	1:25	C, includes 2 positive *P. tigris sumatrae*	Alvarado-Esquivel et al. (2013)
Russia	18	7	38.8	ELISA	Chema, Moscow	-	Naidenko et al. (2019)
Russia	4	4	100.0	ELISA	Vektor-Best	-	Sivkova and Neprimerova (2017)
Thailand	75	14	18.6	LAT	1:64	C	Buddhirongawatr et al. (2016)
Lion (*Panthera leo*)							
Brazil	9	5	55.5	IFAT	1:40	-	André et al. (2010)
Brazil	3	3	100.0	MAT	1:25	C 3	Marujo et al. (2017)
China	5	5	100.0	MAT	1:400		Yang et al. (2017)
India	20	2	10.0	ELISA	Wuhan Hi-tech	-	Moudgil et al. (2019)
Mexico	7	7	100.0	MAT	1:50	C	Alvarado-Esquivel et al. (2013)
Mexico	8	8	100.0	ELISA, IFA	1:40	C, 6 positive by IFA 1:40	Gomez-Rios et al. (2019)
Namibia	59	55	93.2	ELISA, immunoblot	In-house	Fr	Seltmann et al. (2020)
Portugal	4	3	75.0	MAT	1:25		Tidy et al. (2017)
Russia	4	4	100.0	ELISA	Vektor-Best	-	Sivkova and Neprimerova (2017)
Leopard (*Panthera pardus*)							
Brazil	1	1	100.0	IFAT	1:40	-	André et al. (2010)
Mexico	1	1	100.0	ELISA, IFA	1:40	C, also positive by IFA,1:320	Gomez-Rios et al. (2019)
Mexico	5	5	100.0	MAT	1:200	C	Alvarado-Esquivel et al. (2013)
Namibia	58	47	81.0	ELISA, immunoblot	In-house	Fr	Seltmann et al. (2020)
Portugal	1	1	100	MAT	1:25		Tidy et al. (2017)
Thailand	12	4	33.3	LAT	1:64	C	Buddhirongawatr et al. (2016)
Clouded leopard (*Pardofelis nebulosa*)							
Thailand	5	2	40.0	LAT	1:64	C	Buddhirongawatr et al. (2016)
African leopard (*Panthera pardus nimr*)							
UAE	7	6	85.7	MAT	1:25	-	Dubey et al. (2010)
Snow leopard (*Panthera unica*)							
Mongolia	20	4	20.0	ELISA	ABNOVA	-	Esson et al. (2019)
Jaguar (*Panthera onca*)							
Brazil	13	11	84.6	IFAT	1:40	-	André et al. (2010)
Brazil	31	31	100.0	MAT	1:25	-	Furtado et al. (2015)
Brazil	1	1	100.0	MAT	1:25	-	Pimentel et al. (2009)
Brazil	3	3	100	MAT	1:25		Marujo et al. (2017)
Mexico	12	12	100.0	ELISA, IFA	1:40	C, 9 positive by IFA,1:40	Gomez-Rios et al. (2019)
Mexico	52	40	76.9	ELISA		C, 10 zoos	Reynoso-Palomar et al. (2020)
Mexico	13	10	76.9	MAT	1:25		Alvarado-Esquivel et al. (2013)
***Lynx* spp. (bobcat, cougar, Eurosian lynx, polecat, carachal, puma, mountain lion, Florida panther)**							
Bobcat (*Lynx rufus*)							
Mexico	2	2	50.0	MAT	1:800	C	Alvarado-Esquivel et al. (2013)
USA	258	111	43.0	ELISA		Samples from California and Colorado	Bevins et al. (2012); Carver et al. (2016)
USA	22	16	72.7	IFAT	1:160	-	VanWormer et al. (2013)
USA	50	29	58.0	MAT	1:25	Fr, tissue fluids from frozen samples	Verma et al. (2016)
USA	35	35	100.0	MAT	1:200	Fr	Verma et al. (2017)
Canadian lynx (*Lynx canadensis*)							
Canada	84	12	14.0	MAT	1:25	Fr	Simon et al. (2013)
Eurasian lynx (*Lynx lynx*)							
Finland	337	290	86.1	MAT	1: 40	Fr	Jokelainen et al. (2013)
Portugal	2	1	50.0	MAT	1:25		Tidy et al. (2017)
Mexico	2	2	100.0	ELISA, IFA	1:40	C, 1 positive by IFA at 1:40	Gomez-Rios et al. (2019)
Russia	5	1	20.0	ELISA	Chema, Moscow	-	Naidenko et al. (2019)
Iberian lynx (*Lynx pardinus*)							
Spain	129	81	62.8	MAT	1:25	Fr, C	García Bocanegra et al. (2010)
Spain	26	21	80.7	MAT	1:25	-	Millán et al. (2009b)
Polecat (*L. pardinus*), Serval (*Leptailurus serval*), Genetta cat (*Genetta genetta*)							
Caracal (*Lynx caracal*)							
Mexico	1	1	100.0	ELISA, IFA	1:40	C	Gomez-Rios et al. (2019)
Namibia	15	10	66.7	ELISA, immunoblot	In-house	Fr	Seltmann et al. (2020)
UAE	6	5	83.3	MAT	1:25	-	Dubey et al. (2010)
African caracal (*Caracal algira*)							
UAE	1	1	100.0	MAT	1:200	-	Dubey et al. (2010)

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Table 11 (*continued*)

Location	No. tested	No. positive	% positive	Test	Cut-off titer	Notes	Reference
Serval (*Leptailurus serval*)							
Brazil	1	1	100.0	IFAT	1:40	-	André et al. (2010)
Genetta cat (*Genetta genetta*)							
Brazil	1	1	100.0	IFAT	1:40	-	André et al. (2010)
Puma (*Felis concolor*)							
Brazil	18	14	77.8	IFAT	1:40	-	André et al. (2010)
Brazil	3	3	100.0	MAT	1:25	-	Pimentel et al. (2009)
Brazil	3	1	33.3	MAT	1:25		Marujo et al. (2017)
Mexico	2	2	100.0	ELISA, IFA	1:40	C, negative by IFA,1:40	Gomez-Rios et al. (2019)
Mexico	4	4	100	MAT	1:25	C	Alvarado-Esquivel et al. (2013)
USA	202	151	75.0	ELISA		Samples from California and Colorado	Bevins et al. (2012); Carver et al. (2016)
USA	72	58	80.6	IFAT	1:160	-	VanWormer et al. (2013)
Cheetah (*Acinonyx jubatus soemmerringii*)							
Namibia	250	131	52.4	ELISA, immunoblot	In-house	Fr	Seltmann et al. (2020)
Portugal	1	1	100.0	MAT	1:25		Tidy et al. (2017)
Qatar	5	5	100.0	MAT	1:50	-	Dubey et al. (2010)
UAE	34	31	91.1	MAT	1:25	-	Dubey et al. (2010)
King cheetah (*Acinonyx jubatus rex*)							
Qatar	1	1	100.0	MAT	1:3200	-	Dubey et al. (2010)
Endangered cats (Pallas cat, sand cat, Arabian sand cat)							
Sand cat (*Felis margarita*)							
Europe, Middle East	87	47	54.0	IFAT and Immunoblot	1:100	C, 15 zoos	Lücht et al. (2019)
Arabian sand cat (*Felis margarita harrisoni*)							
Qatar	20	14	70.0	MAT	1:50	*T. gondii* isolated by mouse bioassay	Dubey et al. (2010)
Palla's cat (*Otocolobus manul*)							
Europe, Middle East	52	47	90.4	IFAT and Immunoblot	1:100	C, 22 zoos	Lücht et al. (2019)
Mongolia	19	1	5.3	LAT	1:16	Fr	Swanson et al. (2010)
Russia	16	2	12.5	ELISA	Chema-Medica	Fr	Naidenko et al. (2014)
Russia	22	2	9.1	ELISA		Fr	Pavlova et al. (2016)
European wild cat, African wild cat, Asian golden cat, fishing cat, flat- head cat, leopard cat, black-footed cat, Rusty spotted cat, little spotted cat, oncilla							
European wild cat (*Felis silvestris catus*)							
France	112	75	67.0	MAT	1:15	Fr	Afonso et al. (2013)
	47 Hybrids with domestic cats	31	65.9				
Spain	59	50	84.7	MAT	1:25	Fr	Millán et al. (2009a)
African wild cat (*Felis silvestris gordoni*)							
Qatar	1	1	100.0	MAT	1:1600	C	Dubey et al. (2010)
UAE	5	5	100.0	MAT	1:100		Dubey et al. (2010)
Asian golden cat (*Captopuma temminckii*)							
Europe, Middle East	2	1	50.0	IFAT and Immunoblot	1:100	C, 2 zoos	Lücht et al. (2019)
Thailand	4	3	75.0	LAT	1:64	C	Buddhirongawatr et al. (2016)
Fishing cat (*Prionailurus viverrinus*)							
Europe, Middle East	40	22	55.0	IFAT and Immunoblot	1:100	C, 15 zoos	Lücht et al. (2019)
Thailand	7	1	14.2	LAT	1:64	C	Buddhirongawatr et al. (2016)
Leopard cat (*Prionailurus bengalensis*)							
Thialand	30	3	10.0	LAT	1:64	C	Buddhirongawatr et al. (2016)
Black-footed cat (*Felis nigripes*)							
Europe, Middle East	15	4	26.7	IFAT and Immunoblot	1:100	C, 3 zoos	Lücht et al. (2019)
Rusty spotted cat (*Prionailurus rubiginosus*)							
Europe, Middle East	28	27	96.4	IFAT and Immunoblot	1:100	C, 3 zoos	Lücht et al. (2019)
Oncila (*Leopardus tigrinus*)							
Brazil	22	15	68.1	MAT	1:16		Ullmann et al. (2010)
Brazil	15	9	37.0	MAT	1:25	11 Fr, 4 C	Marujo et al. (2017)
Mexico	3	3	100.0	ELISA, IFA	1:40	C,2 IFA positive	Gomez-Rios et al. (2019)
South American small cats (Geoffroy's cat, ocelot, little spotted cat, margay, pampos cat, kodkod, jaguarundi)							
Geoffroy's cat (*Oncifelis onchofelis geoffroyi*)							
Brazil	1	1	100.0	MAT	1:16		Ullmann et al. (2010)
Europe, Middle East	33	16	48.5	IFAT and Immunoblot	1:100	C, 14 zoos	Lücht et al. (2019)
Ocelot (*Leopardus pardalis*)							
Brazil	42	28	66.7	IFAT	1:40	-	André et al. (2010)
Brazil	14	10	71.4	MAT	1:16		Ullmann et al. (2010)
Brazil	3	3	100	MAT	1:25		Minervino et al. (2010)
Brazil	4	2	50.0	MAT	1:25	4 Fr	Marujo et al. (2017)
Mexico	2	2	100.0	ELISA, IFA	1:40	C, negative by IFA, 1:40	Gomez-Rios et al. (2019)
Mexico	3	2	66.6	MAT	1:25	C	Alvarado-Esquivel et al. (2013)

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Table 11 (*continued*)

Location	No. tested	No. positive	% positive	Test	Cut-off titer	Notes	Reference
Mexico	26	18	69.0	LAT	1:32	Fr	Rendón-Franco et al. (2012)
Oncilla (*Lynx triginus*)							
Brazil	35	22	62.8	IFAT	1:40	-	André et al. (2010)
Brazil	22	15	68.1	MAT	1:16		Ullmann et al. (2010)
Europe, Middle East	9	6	66.7	IFAT and Immunoblot	1:100	C, 3 zoos	Lücht et al. (2019)
Mexico	3	3	100.0	ELISA, IFA	1:40	C, 2 positive by IFA, 1:40	Gomez-Rios et al. (2019)
Margay (*Leopardus wiedii*)							
Brazil	4	4	100.0	IFAT	1:40	-	André et al. (2010)
Brazil	17	10	58.8	MAT	1:16		Ullmann et al. (2010)
Europe, Middle East	19	9	47.4	IFAT and Immunoblot	1:100	C, 7 zoos	Lücht et al. (2019)
Pampa's cat (*Oncifelis colocolo*)							
Brazil	3	1	33.3	IFAT	1:40	-	André et al. (2010)
Jaguarundi (*Puma yagouaroundi*)							
Brazil	25	10	40.0	IFAT	1:40	-	André et al. (2010)
Brazil	3	2	66.6	MAT	1:16	-	Ullmann et al. (2010)
Europe, Middle East	9	5	55.6	IFAT and Immunoblot	1:100	C, 5 zoos	Lücht et al. (2019)
Mexico	2	2	100.0	ELISA, IFA	1:40	C, negative by IFA, 1:40	Gomez-Rios et al. (2019)
Mexico	2	1	50.0	MAT	1:25	C	Alvarado-Esquivel et al. (2013)
Far eastern wildcat (*Prionailurus bengalensis*)							
Russia	23	3	13.0	ELISA	Chema, Moscow	-	Naidenko et al. (2019)
Kodkod (*Leopardus guigna*)							
Chile	2	2	100.0	MAT	1:25	-	Barros et al. (2018)

C = Captive
Fr = Free-range

seropositive. Viable *T. gondii* was isolated from 21 of 35 bobcats and the isolation rate could have been much higher if the samples were not autolyzed. Several days elapsed between collection of tissues and their receipt in the laboratory for bioassays (Verma et al., 2017).

4.1.3. *Detection of T. gondii DNA from wild felids*

T. gondii DNA was detected in frozen tissues of 31 (34.4%) of 90 free range Neotropical wild felids in Brazil; in 9 of 22 jaguarundi (*Puma yagouaroundi*), 6 of 22 Geoffroy's cat (*Leopardus geoffroyi*), 8 of 28 oncilla (*Leopardus tigrinus*), 6 of 10 margays (*Leopardus wiedii*), 1 of 1 ocelot (*Leopardus pardalis*), and 1 of 7 Pampas cat (*Leopardus colocolo*) using the ITS1 (Cañón-Franco et al., 2013b). DNA from 3 isolates (1 from *Leopardus wiedii*, Lw#31Tn, 2 from *Puma yagouaroundi*, Py21Sm, and Py#56Br) were characterized by 10 RFLP markers as: ToxoDB#255 (Lw31Tn), #256 (Py21Sm) and #67 (Py#56) (Cañón-Franco et al., 2013a).

In USA, *T. gondii* DNA was isolated from 11 (41.0%) of 27 bobcats (*Lynx rufus*), and 10 (14.0%) of 73 mountain lions (*Puma concolor*) using the B1 gene (VanWormer et al., 2013). *T. gondii* from 9 bobcats and 7 mountain lions was partially characterized as genotype II or Type X.

In Germany, a study identified *T. gondii* DNA from brains of 4 of 12 European wild cat (*Felis silvestris silvestris*) (Herrmann et al., 2013). DNA from 3 strains was ToxoDB#3 using 9 RFLP markers (Table 13). In Slovakia, *T. gondii* DNA was detected from pepsin digested muscle of 1 of 3 Eurosian lynx (*Lynx lynx*) and 1 of 2 wild cat (*Felis sylvestris*) (Turčeková et al., 2019).

4.1.4. *Prevalence of T. gondii oocysts in wild felids*

Data on oocyst excretion in wild felids is limited (Table 13). Presence of *T. gondii* oocysts was confirmed by PCR in 1 of 16 bobcats and 1 of 51 mountain lions by VanWormer et al. (2013).

Table 12
Isolation and genetic characterization of viable *T. gondii* from wild felids.

Species	Location	No.	Serology	Bioassay	Isolate designation	ToxoDB PCR/RFLP Genotype –number of samples	Remarks	Reference
Bobcat (*Lynx rufus*)	USA (Georgia)	5		Isolated before 2009	TgCatGa 1-5	#5 (4 strains typed, TgCatGa 1-4), no data from TgCatGa5		Dubey et al. (2004a); Dubey et al. (2011); Shwab et al. (2014)
Bobcat (*Lynx rufus*)	USA (Alabama)	2	No data	Cell culture-brain	TgBobcatAL1,2	#5 -2	-	Yu et al. (2013)
Bob cat (*Lynx rufus*)	USA (Mississippi)	35 wild caught	MAT, all 1:200	*T. gondii* isolated from 21 bobcats (tongue, heart, brain) by bioassay in mice	TgBobcatMS1-21	#5 -18 #24 -2 #2 -1	DNA sequencing revealed mixed genotypes.	Verma et al. (2017)
Bobcat (*Lynx rufus*)	USA (Pennsylvania)	2	MAT, 1:100 both	*T. gondii* isolated by bioassay in mice from heart	TgBobcatPa1,2	#5 -1 #1 or #3 (Type II) -1	-	Dubey et al. (2015)
Puma (*Felis concolor*)	Mexico (Durango)	1 wild caught 5-year old Puma, roaming in city	MAT, 1:200	*T. gondii* isolated from heart but not brain by bioassay in mice	TgPumaMe1	#222 -1	Strain pathogenic to outbred mice	Dubey et al. (2013d)
Sand cat (*Felis margarita*)	United Arab Emirates	3	MAT, 1:3200	*T. gondii* isolated from liver and lung homogenate	TgSandcatQA1, TgSandcatUAE1, 3	#3 -1 (Type II) #20 - 2	TgSandcatUAE1 died of renal disease, not toxoplasmosis	Dubey et al. (2010)
Serval (*Leptailurus serval*)	China (Zhenghou Zoo)	1 dead captive serval, died of other causes	MAT, 1:200	Muscle from heart, diaphragm, leg pooled and bioassayed in mice	TgServalCHn1	#20 -1	Strain pathogenic to mice	Dong et al. (2019)
Tiger (*Panthera tigris*)	China (several zoos)	6	MAT, 1:200	Striated muscle	TgTigerCHn1,2	#9 -2	TgTigerCHn1- intermediate pathogenicity; TgTigerCHn2- pathogenic	Yang et al. (2019)

4.2. Clinical toxoplasmosis in wild felids

Reports of clinical toxoplasmosis in bobcats, Pallas's cats, and Sand cats up to 2009 were summarized previously (Dubey and Beattie, 1988; Dubey, 2010). In a clinical trial of clindamycin (10-12.5 mg/kg, PO, twice daily) from 7-10 days preparturtion until 3-4 weeks postparturition reduced mortality from 100% to 5.8% in Pallas kittens in a Scottish zoo; 1 of 17 kittens died on clindamycin therapy versus all 9 kittens born to queens without treatment died (Girling et al., 2020).

Pallas's cats and Sand cats are highly susceptible to clinical toxoplasmosis in captivity; nothing is known of clinical disease in the wild. In addition to congenital toxoplasmosis reported earlier from a facility in United Arab Emirates (UAE) (Pas and Dubey, 2008), four additional cases were noted in sand cats (nos.FM002, FM017, FM019, 3667). Cases FM002, FM07, and FM019 were from the Breeding Centre for endangered Arabian Wildlife, UAE and case 3667 was from Al Wabra Wildlife Preservation (AWWP), the State of Qatar (Dubey et al., 2010).

The Sand cat FM017 was euthanized because of poor health at 3 years old; its MAT titer was >1:3200, and *T. gondii* tissue cysts were found in brain, heart, ocular muscles and skeletal muscle, confirmed by IHC.

The cat FM019, 18-month-old, died of acute toxoplasmosis-associated hepatitis and pneumonitis acquired after birth; *T. gondii* was demonstrated in histological sections and confirmed by IHC. *T. gondii* DNA was found by PCR of extracted DNA from liver and lung tissues of this cat; it had a MAT titer of 1:1600.

The Sand cat FM002, 12-year old had ataxia of rear legs, was seropositive to *T. gondii,* and treated with Clindamycin for 1 month. Clinical signs improved. Three years later, the cat had age related complications and was euthanized. Viable *T. gondii* was isolated by bioassays in mice inoculated with its tissues; *T. gondii* was not found in histological sections of this cat.

A 7-year-old Sand cat (no.3657) from AWWP died of acute visceral toxoplasmosis with demonstrable *T. gondii* tachyzoites by IHC, and *T. gondii* DNA by PCR, and a MAT titer of >3200 (Dubey et al., 2010).

Acute toxoplasmosis was reported in 2 Persian leopards (*Panthera pardus saxicolor*) that died in Golestan National Park, Iran based on serological and histopathological findings (Namroodi et al. 2016). IgM antibodies (titers 1:80 and 1:160) were detected in peritoneal effusion fluids of both leopards. Additionally, tachyzoites were detected in peritoneal fluid and tissue cysts were found in their brains. Finding of tachyzoites in peritoneal fluid and absence of parasites in visceral tissues is an unusual finding.

5. Conclusions

Here, we have summarized worldwide prevalence of *T. gondii* infection in cats. The high prevalence of antibodies in cats is indicative of past infection and excretion of *T. gondii* oocysts in the environment. Compared to high seropositivity, *T. gondii* oocysts were not common. Microscopically, oocysts were detected in feces of around 1% of cats, but *T. gondii* DNA was more prevalent. Because the bioassays for viable *T. gondii* oocysts are tedious and hazardous, molecular markers/parameters are needed to distinguish viable and non-viable oocysts in cat feces. Because cats are the only hosts that can excrete *T. gondii* oocysts, further research is needed concerning a vaccine against oocyst excretion in cats. Some progress is being made in this direction by cultivation of sexual phase of the parasite in vitro.

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Declaration of Competing interest

No conflict of interest.

Table 13
Prevalence of *T. gondii* oocysts in wild felids.

Host	Location	No. of cats	Remarks	Reference
Bobcat (*Lynx rufus*)	USA	16	*T. gondii*-like oocysts in 2, **confirmed by PCR 1**	VanWormer et al. (2013)
Canadian lynx (*Lynx canadensis*)	Canada	84	No oocysts by direct microscopy	Simon et al. (2013)
Eurasian lynx (*Lynx lynx*)	Finland	167	No oocysts by direct microscopy	Jokelainen et al. (2013)
Mountain lion (*Puma concolor*)	USA	51	*T. gondii*-like oocysts in 2, **confirmed by PCR 1**	VanWormer et al. (2013)
Tiger (*Panthera tigris*)	China	141 feces	Feces of 1 cat was bioassay positive in mice but viable *T. gondii* not isolated	Yang et al. (2019)
Several species	Mexico	35	No oocysts by direct microscopy, **5 found by nPCR SAG1**	Gomez-Rios et al. (2019)

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