ARTIGO DE REVISÃO

Toxoplasma gondii in small neotropical wild felids

Toxoplasma gondii em pequenos felinos silvestres neotropicais

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Abstract

In the last decade, studies on wildlife worldwide have discovered key epidemiological aspects of the sylvatic cycle of *Toxoplasma gondii*. However, despite the known role of wild felines as definitive hosts in the transmission and maintenance of this parasite, few studies have focused on the involvement of these animals. Brazil exhibits the largest number of wild felid species in the Americas, all of which have a critical conservation status. However, serological detections, epidemiological studies and some molecular characterizations of *T. gondii* have primarily used Neotropical felid populations that are maintained in captivity, which does not reflect the disease behavior in free-living conditions. A systematic review of the worldwide scientific literature was conducted focusing on toxoplasmosis in small Neotropical felids. This review covered a number of aspects, including the state of scientific research, parasite transmission in the wild, the genetic characteristics of isolates, the relationship between these genetic characteristics and the pathogenicity of the parasite, and the risk factors linked to conflicts with humans. The present review shows the relevance of studying these felid populations based on their frequent interactions with humans in peri-urban areas and the need for further comprehensive studies to establish the real significance of *T. gondii* in public and animal health in tropical and temperate regions.

Keywords: *Toxoplasma gondii*. Wild felids.Neotropical felids. Toxoplasmosis.

Resumo

Na ultima década, pesquisas em animais silvestres no mundo todo, tem demonstrado aspectos importantes na epidemiologia do ciclo silvestre de *Toxoplasma gondii*. No entanto, apesar do papel conhecido dos felinos silvestres como hospedeiros definitivos na transmissão e manutenção desse parasita, há poucos estudos sobre o envolvimento desses animais. O Brasil possui a maior quantidade de espécies de felinos silvestres do continente americano, todas em estado crítico de conservação. Porém, a detecção sorológica, pesquisas epidemiológicas e algumas caracterizações moleculares do *T. gondii* nestas espécies, utilizaram principalmente populações de felinos neotropicais mantidos em cativeiro, o que não reflete o comportamento da doença em condições de vida livre.Uma revisão sistemática da literatura cientifica mundial foi realizada focando a toxoplasmose em pequenos felinos neotropicais, abrangendo aspectos como o estado da pesquisa cientifica, transmissão do parasita na vida silvestre, características genéticas dos isolados e sua relação com a patogenicidade, além dos fatores de risco ligados aos conflitos com o homem. Esta revisão mostra a importância do estudo dessas populações de felinos, em função das frequentes interações com o homem em áreas peri-urbanas e a necessidade de estudos mais abrangentes, que estabeleçam a real importância do *T. gondii* no tangente á saúde pública e saúde animal nas regiões tropicais e temperadas.

Palavras-chave: *Toxoplasma gondii*. Felinos silvestres. Felinos neotropicais.Toxoplasmose.

Introduction

The ignorance of disease occurrence in wildlife populations has been discussed for decades, and a consensus acknowledging the insufficiency of data on the distributions of various agents has been reached

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among researchers. A recent study highlights the limited availability of data quantifying the relative risk for human health, particularly the risk of zoonotic diseases with interspecies transmission[1,2].

In the case of wild felids, some pathogens have been described, but little progress has been made toward understanding the natural history and especially the epidemiological interactions of wild felids with domestic felids and human populations. Given its widely known zoonotic characteristics, *Toxoplasma gondii* is a key agent that impacts public health[3].

Excluding *Puma concolor*, *Lynx rufus* in the United States and *Lynx canadensis* in Canada[4], all of the other Neotropical felid species are classified into different categories of risk[5] due to anthropogenic actions on biodiversity[6], particularly the only two South American endemic species (*Leopardus guigna* (kodkod) from Chile and *L. jacobita* (Andean cat) from the Andes mountain range. In this unfavorable scenario, there is little biological, ecological or infectiological knowledge on the twelve species of wild felids that inhabit the American continent.

Toxoplasmosis in small Neotropical felids

Theoretically, the 15 genera and 41 species of felids grouped into the subfamilies Felinae and Pantherinae, including the domestic cat, are definitive hosts of *T. gondii*[7]. Studies have shown the experimental and natural elimination of oocysts in six of the eight species of Brazilian Neotropical felids (Table 1): ocelot (*Leopardus pardalis*), margay (*L. wiedii*), oncilla (*L. tigrinus*), Geoffroy's cat (*L. geoffroyi*), colocolo (*Leopardus colocolo*), jaguarundi (*Puma yagouaroundi*), cougar (*P. concolor*) and jaguar (*Panthera onca*)[8,9,10].

The amount of *T. gondii* oocysts eliminated by cats in feces is high, but the diagnosis is difficult given the short period of excretion (approximately three weeks) and the fact that further eliminations may occasionally occur[11]. In wild felids, this elimination is sometimes associated with diarrheal episodes. In Belgium, a Siberian tiger had a 14-day diarrhea outbreak with a concentration of 200,000 oocysts/g of feces[12]. In addition, *Felis silvestris, Prionailurus bengalensis euptilura* and *Leopardus geoffroyi* in captivity displayed several

Table 1 - Elimination of *Toxoplasma gondii* oocysts by Neotropical wild felids

Species of Wild Felids	No. of Positives / No. Examined Animals	Infection	Author
Geoffroy's cat (*Leopardus geoffroyi*)	ND	N	a
	1 / 1	N	b
Colocolo (*Leopardus colocolo*)	ND	N	a
Ocelot (*Leopardus pardalis*)	2 / 2	E	c
	2 / 8	N	d
Jaguarundi (*Puma yagouaroundi*)	1 / 1	E	c
	ND	N	a
Cougar (*Puma concolor*)	1 / 1	E	e
	1 / 2	N	f
P. c. vancouverensis	1 / 16	N	g
Jaguar (*Panthera onca*)	1 / 25	N	d

References: a. Pizzi, Rico and Pessat[10]; **b.** Lukešová and Literák[13]; **c.** Jewell et al.[156]; **d.** Patton et al.[157]; **e.** Miller, Frenkel and Dubey[158]; **f.** Marchiondo, Duszynski and Maupin[159]; **g.** Aramini, Stephen and Dubey[14]
Abbreviations: N: Natural; E: Experimental; ND: No data available

Source: Modified from Elmore et al.[8]

diarrheal episodes, all of which included the elimination of oocysts[13]. However, little is known about the quantity and period of elimination of oocysts in wild animals. In *P. concolor*, the concentration was estimated to be in the range of $2.4x10^5$ to $12.5x10^6$ oocysts/g of feces[14].

The annual environmental contamination is estimated to be in the range of 94 to 4671 oocysts/m^2 of feces of naturally infected domestic felids[15]. However, higher levels can occur in wild felids based on the fact that some behavioral habits may contribute to oocyst dispersion. The reproduction of lions (*Panthera leo*) is programmed, and litters of cubs coexist in the same area. Thus, immediately following primary infection by *T. gondii*, these areas would receive large parasitic loads[16].

The defecation sites or latrines of Neotropical felids are considered areas of territorial marking and social gathering of adults and cubs[17] and concentrate two or more feces from different times of elimination, which indicates the repeated use of these sites. Most of these areas are found in middens and tree bases (68%) and between rocks (17%) and trails (15%), as shown by studies conducted on *L. geoffroyi* using 182 fecal samples collected in the Monte Deserto in Argentina[18] and 1,274 samples from 357 defecation sites in five natural parks (an average of 6.1 fecal samples were collected per site)[19]. Feces concentrated in an area that exhibits direct contact with susceptible animals would facilitate the transmission and maintenance of the sylvatic cycle of *T. gondii*[12,20,21].

The two classical transmission routes of *T. gondii* comprise the ingestion of viable tissue cysts found in nearly all warm-blooded animals and the contamination of food and water by the oocysts that are shed in felid feces.

The epidemiological impact of oocysts on the environment was recorded in Canada in 1995. Although the study of oocysts in the water reservoir was not successful, fecal samples from one *P. concolor* individual captured in the region and the analysis of the feces collected in the environment showed that this animal was directly responsible for the waterborne toxoplasmosis that affected the human population with the TgCgCa1 isolate[14,22,23].

Waterborne toxoplasmosis was reported in 39 of 600 American soldiers in Panamá[24] and in 155 inhabitants of Santa Isabel do Ivaí, Paraná, in Brazil[25]. The biological and molecular characteristics of the parasite isolated in the latter outbreak showed the presence of the regionally widespread BrI genotype (outbreak 1, outbreak 2 and TgCatBr85)[26]. The involvement of the atypical genotype GUY-2004-JAG (now called type 12)[27] as the cause of fatal toxoplasmosis in immunocompetent patients was confirmed in French Guiana[20]. All of these studies found an association between untreated water consumption, the presence of domestic and wild felids and serious clinical implications[7].

In the Americas, Neotropical felids were incorporated into pre-Columbian cultures through a mystical-religious relationship that still prevails in several Amerindian communities. Moreover, Neotropical felids, in addition to other wild animals, are part of Brazilian traditional medicine in zootherapeutic practices for the treatment of diseases[28-29] and are used as amulets[30] and food by indigenous communities in the Colombian Amazon and New Guinea[31]. Studies conducted in indigenous communities in Panama, Venezuela and the Brazilian Amazon[32,33,34,35,36,37,38,39,40] and recently in Columbian jungle army soldiers[41] concluded that, in the absence of domestic cats, the presence of wild felids is a risk factor linked to the transmission of toxoplasmosis.

Food chain and role in toxoplasmosis epidemiology

The impact of wildlife species on the transmission and epidemiology of toxoplasmosis has been the subject of many studies in the last decade. These studies

have aimed to establish the genetic diversity and sylvatic and/or domestic population structure of the parasite[42]. Several research studies involving the serology, molecular detection and isolation of *T. gondii* have been conducted in different orders of Brazilian mammals[9,36,43,44,45,46,47,48,49,50,51,52,53,54,55,56,57,58,59,60,61,62,63,64,65].Although debatable, these studies indicate that asexual reproduction in these intermediate hosts is responsible for the clonal expansion of *T. gondii* and sufficient for the maintenance of the parasitic cycle, which, in the absence of felids, traverses the food chain through carnivorism[66].

The infection rate by carnivorism is proportional to the prevalence of coccidia in preyed animals[3,16]. Theoretically, all species from different biological levels may contain parasitic cysts, but there are differences in prevalence according to the animal's biotic preference (strictly arboreal, arboreal and terrestrial or strictly terrestrial)[67].

There are large variations in the diet composition of Neotropical felids as a result of the biogeographical distribution of the fauna and climatic seasonality (Table 2)[68,69]. This feeding plasticity is reflected in the epidemiology of sylvatic cycle diseases. The ocelot (*L. pardalis*) is a generalist felid with a diet consisting of arboreal mammals under 100 g and likely larger species, including *Dasyprocta punctata* (Central American agouti), *Choloepus didactylus* (Linnaeus's two-toed sloth), Xenarthra and Neotropical primates (*Alouatta guariba clamitans*)[69,70,71,72,73,74,75]. The margay (*L. wiedii*) skillfully seeks marsupials, birds and reptiles[76,77]. Geoffroy's cat (*L. geoffroyi*) is an opportunistic terrestrial, arboreal and semiaquatic predator of small mammals (<400 g) and waterbirds (<200 g)[68,78,79]. The

Table 2 - Occurrence (percentage, %) of wild species preyed on by small Neotropical felids

Felid Species	Preyed Order or Class % (Reference)									
	Marsupials	Xenarthra	Rodentia	Primates	Carnivora	Reptiles	Artiodactyla	Birds	Lagomorpha	Invertebrates
Leopardus wiedii (Margay)	34.5[e] 18.2[l]	3.6[e]	18.2[e] 18.2[l] **80.7[f]			10.9[e] 9.1[l] 9.7[f]		29.1[e] 36.4[l] 3.2[f]	3.6[e]	9.1[l]
Leopardus tigrinus (Oncilla)	6.1[l] 2.3[m]		37.7[l] 83.3[m]		1.0[k]	2.0[l] 1.2[m]		29.6[l] 11.8[m]	1.5[l]	17.3[l]
Leopardus pardalis (Ocelot)	6.0[c] 18.5[d] 3.2[b] 16.8[l] 1.5[m]	6.0[c] 11.1[d] 31.5[b]	57.0[c] 25.9[d] 42.4[b] 50.1[l] 92.4[m]	7.0[c] 4.3[b]	3.2[b] 5.6[l]	18.5[d] 14.1[b] 3.0[m]		16.0[c] 14.8[d] 22.3[l] 3.0[m]	5.6[l]	
Leopardus geoffroyi (Geoffroy's cat)	1.7[a]	2.8[g] 0.8[n]	79.7[a] 86.2[o] 45.2[g] 58.3[h] 79.0[n]			4.4[a] 1.2[g] 14.5[i] 5.3[n]	0.9[n]	16.1[a] *39.4[g] 9.7[g] 7.3[h] 19.9[n]	1.2[a] 15.9[g] 1.7[h]	13.1[h] 6.0[n]
Leopardus colocolo (Colocolo)			92.0[i]			5.2[i]		2.7[i]		
Puma yagouaroundi (Jaguarundi)	33.3[e] 17.2[l] 4.8[m] 6.2[j]	0.8[m] 1.5[j]	8.3[e] 64.8[l] 77.6[m] 30.0[j]			16.7[e] 4.0[m] 13.5[j]	4.3[l] 1.5[j]	41.7[e] 10.4[m] 21.0[j]		8.6[l] 20.0[j]

References: a. Bisceglia et al.[18]; **b.** Moreno, Kays and Samudio Jr.[69]; **c.** Abreu et al.[70]; **d.** Martins, Quadros and Mazzolli[73]; **e.** Bianchi et al.[76]; **f.** Cinta-Magallón et al.[77]; **g.** Canepuccia, Martinez and Vassallo[78]; **h.** Pereira, Walker and Novaro[79]; **i.** García et al.[80]; **j.** Tófoli, Rohe and Setz[82]; **k.** Wang and MacDonald[150]; **l.** Rocha-Mendes et al.[160]; **m.** Silva-Pereira et al.[161]; **n.** Sousa and Bager[162]; **o.** Bisceglia et al.[163]

*Waterbirds; **Includes Soricomorpha (Soricidae)

oncilla (*L. tigrinus*) ingests rodents and some larger mammals, including *Bradypus variegatus* (brown-throated sloth)[75]. The colocolo's (*L. colocolo*) food habits are insufficiently recorded, although the rodent species *Lagidium viscacia*, *Phyllotis* sp. and *Ctenomys* spp. have been described as some of its prey[80,81]. The jaguarundi (*Puma yagouaroundi*) includes several species of birds and Didelphidae in its diet[76,82].

In some circumstances, the predator can become the prey. In fact, rare cases of a *Puma concolor* individual preying on *Leopardus pardalis*[83] and a *P. concolor* preying on *P.yagouaroundi*[73] as well as infrequent cases of cannibalism among *L. pardalis*[84] have been recorded.

The infection levels of prey animals are related to the species susceptibility, the environmental contamination by oocysts and the lifespan. Burrowing animals and terrestrial and/or arboreal mammals are more exposed to *T. gondii*, whereas species with a shorter lifespan have a lower probability of exposure to the agent[46,48].

Species with a high body mass have high titers of anti-*T. gondii* antibodies. In the infection of *Felis catus*, rodents, lagomorphs and birds have a higher impact on the prevalence of felids[85], with a lower titer of the reactive serum in areas with a high occurrence of birds. Males were found to be five times more likely to contract the parasite because females mostly eat small rodents, whereas males prey on all levels of the food chain and have larger territories.

Additionally, ethological changes in the intermediate host can significantly increase the predation rate by felids and other carnivorous animals, which ensures the parasite's transmissibility. In rodents, chronic infection with *T. gondii* affects the sensory, locomotor, spatial and defensive memory functions, which decreases anxiety and neophobic behavior (fear of novelty and of felid odor)[86,87] and thereby contributes to their predation by felids.

Seroepidemiology of *T. gondii* in wild Neotropical felids

Seroepidemiological studies of toxoplasmosis in wild felids show widespread and worldwide exposure to the parasite[3]. The first reports of the detection of antibodies against *T. gondii* in Brazil date from 1977. In the São Paulo Zoo, six of the nine *L. tigrinus* and five of the six *L. pardalis* individuals studied were found to be positive in the Sabin-Feldman test, although these individuals were found to be negative through the mouse bioassay[64].

Despite the little information available, serologic tests usually show good diagnostic agreement, as noted in domestic species. The study of 33 samples of naturally infected exotic wild animals indicated that the ELISA-IgG immunoassay performs better than the latex agglutination (LAT) and the hemagglutination inhibition (HI)[88] tests. The assessment of 88 Neotropical felid samples suggests that the sensitivity of LAT is lower than that of MAT (modified agglutination test)[89]. The analysis of the sera of captive Neotropical felids showed that results from the MAT and HI tests were in agreement in only eight positive (38.1%) and three negative (14.3%) samples of the 21 samples analyzed[90].

Prevalence studies in wild animals are scarce, and the data mostly correspond to zoos and wildlife protection centers in the Americas and other regions (Table 3). Two large-scale studies in Brazilian zoos[91,92] found 52.8% (253/481) and 59.6% (65/109) prevalences in *L colocolo*, *L. tigrinus*, *L. wiedii*, *L. pardalis*, *L geoffroyi* and *P. yagouaroundi* and concluded that feeding adult animals (>3 years old) raw meat that was frozen for less than seven days or road-kill carcasses are risk factors for the infection and persistence of *T. gondii* in conservation centers. Moreover, captured animals are three times more susceptible to infection than those born in captivity[93].

Table 3 – Studies on anti-*Toxoplasma gondii* antibodies in small Neotropical felids

Species	Common Name	Captivity		Wild		Country	Author
		No. of Positives / No. Tested	Diagnostic Test (Cutoff Point)	No. of Positives / No. Tested	Diagnostic Test (Cutoff Point)		
Leopardus geoffroyi	Geoffroy's cat			2/8	HI (≥16)	Bolivia	a
		10 / 12	MAT (≥20)			Brazil	b
		1 / 1	MAT (≥16)			Brazil	c
Leopardus wiedii	Margay	1 / 2	MAT (≥32)			Guatemala	d
		34 / 63	MAT (≥20)			Brazil	b
		4 / 4	IFAT (≥25)			Brazil	e
		10 / 17	MAT (≥16)			Brazil	c
Leopardus pardalis	Ocelot	5 / 6	SF (≥256)			Brazil	f
		1 / 1	IFAT (≥50)			United States	g
		1 / 1	IFAT (≥40)			Slovakia	h
				10/10	HI (≥16)	Bolivia	a
				3/3	MAT (≥25)	Brazil	i
		97 / 168	MAT (≥20)			Brazil	b
		4 / 5	IFAT (≥16)			Brazil	j
		6 / 8	MAT (≥16)			Brazil	k
		28 / 42	IFAT (≥25)			Brazil	e
		3 / 3	MAT (≥25)			Brazil	l
		10 / 14	MAT (≥16)			Brazil	c
				18/26	LAT (≥32)	Mexico	m
Leopardus tigrinus	Oncilla	6 / 9	SF (≥256)			Brazil	f
		1 / 1	IFAT (≥40)	1 / 1	KELA (≥48)	Bolivia	n
		66 / 131	MAT (≥20)			Slovakia	h
		22 / 35	IFAT (≥25)			Brazil	b
		15 / 22	MAT (≥16)			Brazil	e
						Brazil	c
Leopardus colocolo	Colocolo	1 / 8	MAT (≥20)			Brazil	b
		1 / 3	IFAT (≥25)			Brazil	e
Puma yagouaroundi	Jaguarundi	1 / 1	ELISA (≥64)			United States	o
		1 / 1	IFAT (≥40)			Slovakia	h
		1 / 1	IFAT (≥16)			Brazil	j
		49 / 99	MAT (≥20)			Brazil	b
		1 / 2	MAT (≥16)			Brazil	k
		10 / 25	IFAT (≥25)			Brazil	e
		2 / 3	MAT (≥16)			Brazil	c

References: a. Fiorello et al.[103]; **b.** Silva et al.[92]; **c.** Ullmann et al.[93]; **d.** Lickey et al.[98]; **e.** André et al.[91]; **f.** Sogorb, Jamra and Guimaraes[63]; **g.** Spencer, Higginbotham and Blagburn[164]; **h.** Sedlák and Bártová[165]; **i.** Whiteman[97]; **j.** Rivetti et al.[166]; **k.** Silva[90]; **l.** Minervino et al.[57]; **m.** Rendón-Franco et al.[96]; **n.** Deem, Davis and Pacheco[167]; **o.** Lappin et al.[88]

Abbreviations: ELISA Enzyme-Linked Immunosorbent Assay; IFAT: Indirect Fluorescent-Antibody Test; HI: Hemagglutination Inhibition Assay; MAT: Modified Direct Agglutination Test; SF: Sabin-Feldman [Dye] Test; KELA: Kinetics-Based Enzyme-Linked Immunosorbent Assay

Source: Modified from Dubey[3]

The difficulty in collecting samples from wild felids restricts the performance of further enhanced surveys, and population studies of toxoplasmosis are still scarce. A seroepidemiological study on *P. concolor* (76/346) and *L. rufus* (26/52), which was conducted in 15 countries in the Americas, showed that there were geographic differences: the highest *T. gondii* prevalence was found in South American wild

cougar females. Moreover, the geographic differences were found to be correlated with the type and susceptibility of prey[94]. Wild adult and female bobcats in the United States showed the highest prevalence with 83% (109/131) MAT-positive animals[95]. In Mexico, these variables were analyzed in 26 ocelot individuals, and an increased prevalence was found among males and sub-adults when the prevalence was assessed by LAT[96]. In Brazil, MAT seropositivity was recorded in all three captured *L. pardalis* individuals from Pará[97].

The co-infection of *T. gondii* with immunosuppressive agents occurs in domestic and wild felids[98]. Exotic captive felids in Thailand[99] were reactive to *T. gondii* and feline leukemia virus. In the United States, wild cougars and captive Pallas's cats reacted concomitantly to feline immunodeficiency virus[100,101]. In the Bolivian Chaco, the prevalence of *T. gondii* in wild *L. geoffroyi* and *L. pardalis* individuals that test positive for canine distemper virus, feline calicivirus and feline panleukopenia virus was 63.2%[102,103]. The sera of wild Brazilian *L. tigrinus* (2/2) and *L. pardalis* (1/1) reacted when tested for feline herpesvirus-1 (FHV-1), feline calicivirus (FCV), feline coronavirus (FCoV), feline parvovirus (FPV) and *Bartonella henselae*[104], which are infectious agents that were also detected in captive Neotropical felids from Brazilian zoos with prevalences of 19.6% FHV-1, 52.9% FCV, 68.6% FPV, 25.2% FCoV, 0.7% *Ehrlichia canis* and 50% *B. henselae*[105].

The presence of these agents in South American populations of wild felids concerns researchers who are attempting to understand the type of interactions that occur when populations of domestic cats overlap with wild populations and the role of these hosts in the spillover or spillback of feline immunosuppressive virus[106].

Clinical toxoplasmosis in wild felids

With the exception of *Lynx rufus*, there are no reports of clinical toxoplasmosis in the American continent that involve small wild Neotropical felids, and the reports available regard wild, exotic felids in captivity[3].

Infected wild felines are seropositive asymptomatic or exhibit unspecific signs of infection[107]. The infection severity is related to parasite virulence and genetic variability, host immune response[59] and co-infection with other immunosuppressive agents[108]. Neurological symptoms, including encephalitis, mydriasis, muscle atrophy, hind limb ataxia, pneumonia and myocarditis, occur in the generalized form[3], whereas atypical lesions, including retinal degeneration and necrosis of the lymph nodes of the digestive tract, are found in the severe forms[109,110].

The sand cat (*Felis margarita*) and Pallas's cat (*Otocolobus manul*)[108,111] are, thus far, the two most susceptible species, in which the congenital transmission of this parasite occurs and is associated with a high neonatal mortality (50-58%). The cubs of seropositive female Pallas's cats fail to acquire immunity at birth[112]. The explanation for this finding likely lies in co-evolution with *Toxoplasma* because domestic cats are not pets in Tibetan culture and extreme environmental conditions (temperature and altitude) preclude oocyst sporulation, which would limit host exposure to the agent and thus lead to immunity[101,113].

The affinity of *T. gondii* for the tissues and organs of infected animals is still unknown, and the preference of this parasite for the central nervous system is assumed based on mouse infection models, in which the number of cysts produced and their spatial location are not related to the inoculum concentration. However, there may be a relationship between the occurrence of cysts in specific brain areas and the host behavioral changes[114].

The distribution of *T. gondii* in experimentally infected cats was assessed using a mouse bioassay model in two studies[115,116]. In the first study, the isolation of the parasite was achieved in the heart (5/7), skeletal muscle and spinal cord (4/7) and brain (3/7);

in the second study, a greater presence was recorded in the tongue (9/9), heart (5/9), brain (4/9) and eyes (1/9). Subsequently, the density of *T. gondii* was shown to be lower in the brain (7/54) of naturally infected cats in Brazil, as demonstrated using the mouse bioassay; however, better results were found in the skeletal muscle (9/15) and heart (13/15) using the bioassay in cats[117].

Although the molecular detection of *T. gondii* using the B1 gene and a homogenate of the heart tissue, muscle or brain of the jaguarundi exhibited negative results, the isolation was successful in the bioassay using skeletal muscle, which indicates that this tissue exhibited a higher concentration of the parasite[118]. The authors emphasize the DNA amount of *T. gondii* present in the primary samples without replication in the mouse model[119].

Genetic diversity of *T. gondii* in wild felids

The traditional study of the virulence or pathogenicity of the infection in mice is insufficient to explain the marked differences between isolates resulting from polymorphisms in the parasitic genome. The polymorphisms were identified using multilocus PCR-RFLP genotyping and molecular markers[120,121,122], and their identification has enabled significant advances in the study of the population structure of *T. gondii*.

Typically, isolates from Europe and North America are classified into genetic strains type I, II and III[118]. The clonal structure characterized in different hosts from distant geographic regions displays a genetic divergence of less than 1% between strains[123]. A greater divergence is found in the virulence. In experimental infections, the type I strain results in a high lethality in mice with a rapid parasite replication. In contrast, the type II strain leads to chronic infection with a slow replication and the formation of tissue cysts, whereas the type III strain, although less frequent and with a low virulence, can cause the death of inoculated mice within a few weeks or months after inoculation[124].

Other studies propose a clonal structure consisting of the worldwide distribution of the SA1 and SA2 (South and Central America), RW (Europe, Asia, Africa and North America) and WW strains[125]. The genetic distances between isolates led to the hypotheses that *T. gondii* originated in South America, where it exhibits its greatest genetic variability, and that RW and WW populations were disseminated in the sixteenth century and appeared in the American continent soon after this dissemination.

The scenario is different in Brazil, where a high genetic diversity of *T. gondii* was evident using the molecular markers SAG1, SAG2, SAG3, BTUB, GRA6, c22-8, c29-2, L358, PK1, Apico and CS3. Upon the typification of 48 genotypes in 125 isolates of domestic animals, the clonal strains BrI, BrII, BrIII and BrIV were defined as the most frequent strains. Unlike in the rest of the world, these four strains, in addition to several other distinct and less prevalent strains, exhibited an epidemic population structure with little clonal expansion in Brazil[126].

The book "Toxoplasmosis of animals and humans"[3] describes the attempts of several researchers to isolate *T. gondii* in wild felids. Studies have shown that given the low parasitic load in the tissue or the collection of very small tissue fragments, the detection of this parasite using PCR was often not possible, despite some animals being seropositive for the agent[127]. A summary of the studies conducted is shown in table 4.

In the United States, the first viable isolate of *T. gondii* from *in situ* wild felids was prepared from the brain tissue of *L. rufus*, and, although it was not genetically characterized, this isolate exhibited a low virulence through the mouse bioassay[128]. Subsequently, in six *L. rufus* that were seropositive for *T. gondii* (MAT 25), five viable isolates of medium

Table 4 - *Toxoplasma gondii* isolates obtained from wild felids (both in the wild and in captivity) worldwide

Species	Condition	No. of Positives / No. Examined	Type of Sample	Detection	Genotyping (No. of samples)	Name of Isolate	Country	Author
Lynx rufus (Bobcat)	Wild	1 / 11	Brain	Bioassay	NA	NA	USA	a
Lynx rufus (Bobcat)	Wild	5 / 6	Heart	Bioassay SAG2	Genotype II (5)	NA	USA	b
Puma concolor vancouverensis (Puma)	Wild	2 / 2	Feces	Bioassay SAG1, SAG2, SAG3, BTUB, GRA6, c22-8, C29-2, L358, PK1, Apico.	Atypical recombinant genotype I-II-III (2)	TgCgCa1 TgCgCa2 Cougar2 Cougar COUG	Canada	c
Lynx rufus (Bobcat)	Wild	2 / 4	Brain Pectoral muscle Tongue	SAG1, GRA6, B1.	Atypical X (3) Genotype I (2) Genotype II (1) Recombinant II-III (1)	Type X	USA	d
Puma concolor (Puma)	Wild	5 / 26	Heart					e
Panthera onca (Jaguar)	Wild	1 / 1	Heart	GRA6, TUB2, W35, TgM-A, B18, B17	Atypical X (1)	Type X (type 12) GUY-2004-JAG	French Guiana	f
Felis silvestris silvestris (European wildcat)	Wild	4 / 12	Brain Lung	nSAG2, SAG3, BTUB, GRA6, c22-8, c29-2, L358, PK1, Apico	Genotype II (2) Genotype variant II	TgFsGER02 TgFsGER03 TgFsGER01	Germany	g
Panthera tigris (Tiger)	Captivity	1 / 1	Heart	GRA7, SAG2	Genotype II	NA	France	h
Felis margarita (Sand cat)	Captivity	4 / 4	Lung Heart Eye muscle Skeletal muscle Kidney Liver	Bioassay SAG1, SAG2, alt-SAG2, SAG3, BTUB, GRA6, c22-8, c29-2, L358, PK1, Apico	Atypical genotype (3) Genotype II (1)	TgSandCatUAE1 TgSandCatUAE2 TgSandCatUAE3 TgSandCatQA1	United Arab Emirates Qatar	i
Puma yagouaroundi (Jaguarundi)	Captivity	1 / 1	Heart Skeletal muscle Brain	Bioassay SAG1, SAG2, BTUB, GRA6, c22-8, c29-2, L358, PK1, Apico	Atypical genotype (1)	TgJagBr1	Brazil	j
Leopardus tigrinus (Oncilla)	Captivity	1 / 1	Brain Heart	Bioassay SAG1, SAG2, nSAG2, SAG3, BTUB, GRA6, c22-8, c29-2, L358, PK1, Apico, CS3	Atypical genotype (1)	Novo 5	Brazil	k

References: a. Walton and Walls[128]; **b.** Dubey et al.[118]; **c.** Dubey et al.[130]; **d.** Miller et al.[131]; **e.** Miller et al.[127]; **f.** Demar et al.[20]; **g.** Herrmann et al.[132]; **h.** Alerte[133]; **i.** Dubey et al.[109]; **j.** Pena et al.[59]; **k.** Vitaliano[134]

Source: Modified from Dubey[3]

virulence (18 to 31 days), as determined using the heart tissue bioassay, were obtained and typified as genotype II[119].

The atypical genotypes of wild Neotropical felids and their relationship with human toxoplasmosis were initially studied in Canada[14,129]. *T. gondii* oocysts

collected from *P. concolor* feces were inoculated in mice, which exhibited moderate virulence manifestation (9-16 days), and the subsequent bioassay in cats showed the fecal elimination of oocysts. A decade after cryopreservation, the isolate from sample B was typified by genotyping as recombinant I-II-III (TgCgCa2), whereas sample A differed from previous archetypes (TgCgCa1, Cougar2, Cougar or COUG)[130].

In situ, 30 wild felid samples were characterized in the United States using PCR-RFLP of gene B1 and the *loci* SAG1 and GRA6. Genotypes I and II were found in *P. concolor*, whereas recombinant II-III and atypical-*X* were found in *L. rufus* and in both species, respectively. This last genotype (atypical-*X*) is correlated with the contamination of coastal California and the introduction of toxoplasmosis into the region's seals[127,131].

Subsequently, this genotype was characterized in French Guiana in wild *Panthera onca* and was linked to toxoplasmosis in immunocompetent humans (GUY-2004-JAG) by sequencing using six microsatellite markers; the felid heart tissue bioassay caused the death of all of the mice (11 to 33 days after inoculation)[20]. In Germany, *T. gondii* DNA was detected in four primary brain and heart samples of *Felis silvestris silvestris*, three of which were characterized as genotype II (TgFsGER02, TgFsGER03) and one of which was found to be the type I allele variant in the *locus* Apico (TgFsGER01) using nine molecular markers. These findings are in agreement with the parasite's clonal distribution in Europe, which is predominantly type II[132].

In *ex situ* wild felids, the heart tissue homogenate from one *Panthera tigris altaica* of the Amneville zoo (France) was inoculated into mice. The isolate was classified as archetype II using the restriction enzymes Hha I in *locus* SAG2 and Mbo II and EcoRI in *locus* GRA7[133]. This archetype II was also isolated in a sand cat (*Felis margarita*) in Qatar (TgSandcatQA1), and others three atypical genotypes, which had been previously reported in dogs in Sri Lanka, were recorded in a study conducted in the United Arab Emirates (TgSandcatUAE1-3)[109].

In a study conducted in animals from Parque Dois Irmãos zoo in Recife, Pernambuco in Brazil[59], *T. gondii* was isolated for the first time in *P. yagouaroundi* using the mouse bioassay, and a new virulent genotype (TgJabBr1) was identified through molecular typing. Another isolate of *L. tigrinus,* which was obtained from the same zoo, was classified as NOVO 5, and the molecular virulence marker CS3 identified this sample as the type I allele, which corroborates the virulence results found in the bioassay (100% mortality and 17-day survival of inoculated mice)[134].

Wild felids in the sylvatic cycle of *Toxoplasma:* Implication on public health

In Europe and North America, the domestic cat (or other domestic or wild animals) is generally involved in the transmission of *T. gondii*. It is estimated that 80% of the immunocompetent human population is asymptomatic to classical infection with *T. gondii*, which is caused by clonal strain type II, and 15 to 20% of the immunocompetent human population exhibit fever and lymph node symptoms. A severe form can occur in primary-infected pregnant women and immunosuppressed patients infected with the type III strain, which displays variable virulence, or the highly virulent type I strain, which results in encephalitis, chorioretinitis, congenital infection and neonatal mortality[135,136,137].

In contrast, "Amazonian toxoplasmosis", which is also known as "wild rain forest toxoplasmosis", and "French Guiana toxoplasmosis", is the most severe form of the clinical disease in immunocompetent patients. In this cycle, wild felids and the majority of forest mammals and birds are intermediate hosts of the parasite. The transmission occurs either by inges-

tion of cysts present in the meat of these animals or by consumption of non-drinkable water contaminated by oocysts shed in the feces of felids[67].

In French Guiana, 44 primary-infected humans were recorded from 1997 to 2005 (seven children, two cases of mother and child and 33 patients unrelated to the epidemic). Three atypical, pathogenic genotypes of *T. gondii* were genotyped in this outbreak (GUY-2002-KOE, GUY-2003-MEL and RMS-2003-DJO)[138]. Two weeks after infection, the patients showed clinical signs of fever, mental changes, diarrhea, chorioretinitis and severe pulmonary compromise, which resulted in widespread toxoplasmosis with a mortality rate of 6.8%. The authors suggest that atypical genotypes are less adapted to the human immune system[139].

Although little information is provided, the studies reveal ample genetic diversity, which is related to the parasite's pathogenic characteristics in the host[119]. However, the effect on the ecosystem health is complex and poorly studied[140]. Studies are needed to clarify the movement of the parasite in the environment, which occurs through environmental contamination with oocysts eliminated by Brazilian wild felids[141] in areas where the contact between humans and domestic and wild animal has been increasing[20,142,143,144,145,146,147,148,149,150].

Despite some restrictions in habitat, all wild felid species display a wide distribution in the Neotropical zoogeographic region: from Southwest Texas in the United States to the southern tip of Argentina. In fact, the population of small Neotropical felids is estimated to be between 800,000 and 3 million individuals[151].

In Brazil, the number of encounters of wild felids with the human population has grown from sporadic to increasingly frequent. In 2012, at least 57 events were recorded using the Google alerts tool; these events involved ocelots (24), cougars (20), oncillas (9) and jaguars (4) in urban centers and rural areas and included attacks on humans and road-kills.

Low- and high-traffic highways are critical barriers to the movement of wildlife between different biomes and thus attractive places for felids because these are easy places to find road-kill. The probability that a wild felid will be found on a road is seven times higher than the probability of finding a wild felid in the interior of forests[152].

Studies of wildlife road-kill on Brazilian roads reveal alarming data. In Santa Catarina (BR-116, BR-282 and BR-470), 257 individuals (five *L. tigrinus*, four *P. yagouaroundi* and one *L. wiedii*)[153] were run over. In the province of Serrana de Cáceres - MT (BR 070), traffic collisions with 211 individuals, including *P. concolor*, *L. pardalis*, *P. yagouaroundi* and *L. colocolo*, were recorded throughout the course of one year[154]. In the southern region of Brazil, the mortality of native species in BR-101 and RS-389 was 869; these included 92 species and a single specimen of *L. tigrinus*[155]. The numbers may be higher for wild felids because some injured animals flee into the woods and other carnivorous animals may even carry the carcasses from the site in which the animal was run over.

Final considerations

Some questions should be answered. a) Is the risk of transmission of wild isolates in urban centers equal to that described in forest regions? b) What is the probability that *T. gondii* isolates originating from wild felids would circulate in urban areas? c) How significant is the involvement of these isolates in the disease epidemiology? Moreover, from the predation standpoint, an additional question should be addressed. d) What is the true role of wild felids in the sylvatic cycle of toxoplasmosis: environmental contamination by oocysts or the conservation and genetic exchange of the parasite?

Accordingly, knowledge of the role of wild felids in the epidemiology of *T. gondii* is relevant for the introduction of control techniques and to the study of the parasite dynamics in the sylvatic cycle.

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