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Neosporosis in animals—The last five years

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ABSTRACT

Neospora caninum is a protozoan parasite of animals. Until 1988, it was misdiagnosed as *Toxoplasma gondii*. Since its first recognition in 1984 in dogs and the description of a new genus and species *Neospora caninum* in 1988, neosporosis has emerged as a serious disease of cattle and dogs worldwide. Abortions and neonatal mortality are a major problem in livestock operations and neosporosis is a major cause of abortion in cattle. This review is focused on current status of neosporosis in animals based on papers published in the last five years. Worldwide seroprevalences are tabulated. Strategies for control and prevention are discussed.

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1. Introduction

Neospora caninum is morphologically similar to *Toxoplasma gondii* but these parasite species are biologically different. Neosporosis, is primarily a disease of cattle and dogs and is not considered zoonotic whereas toxoplasmosis is a serious disease of humans, sheep, and many other warm-blooded animals. Although much has been published on the biology of *N. caninum* during the last 23 years since its discovery in 1988 (Dubey et al., 2002), neosporosis continues to be a major problem in cattle. In the present review we summarize information on neosporosis in animals for the past 5 years.

2. General biology

2.1. Host range

Past (Dubey et al., 2007a) and recent surveys (Tables 1–9) indicate that a wide range of domestic and wild animals have been exposed to *N. caninum*. However, viable *Neospora* has been isolated from only a few hosts (cattle, sheep, water buffalo, dog, horse, bison, white-tailed deer); recent reports on isolations are summarized in Table 1.

Abbreviations: BIOVET, BIOVET-Neospora caninum, indirect ELISA, sonicate lysate of tachyzoites, BIOVET Laboratories, Canada; BioX, NcSRS2 sandwhich ELISA, BioX, Belgium; CHEKIT, CHEKIT Neospora, indirect ELISA, detergent lysate of tachyzoites, IDEXX Laboratories, The Netherlands; CIVTEST, CIVTEST BOVIS NEOSPORA, indirect ELISA, soniate lysate of tachyzoites, Laboratorios Hipra S.A., Spain; ELISA, enzyme linked immunosorbent assay; H, histology; IB, immunoblotting; IDEXX, IDEXX HerdChek *Neospora caninum* antibody, indirect ELISA, sonicate lysate of tachyzoites, IDEXX Laboratories, USA; ID-VET, ID SCREEN *Neospora caninum* indirect, indirect ELISA, ID-VET, France; IFAT, indirect fluorescent antibody test; IH, in house; IHC, immunohistochemistry; IH-ISCOM, detergent extracted tachyzoite antigen incorporated in immune stimulating complex particles; IH-Ncp43P, recombinant NcSRS2; IH-p38, native immune-affinity purified surface antigen NcSRS2; IH-NcSAG1, recombinant NcSAG1; IH-tNcSAG1, truncated recombinant NcSAG1; IH-NcSRS2, recombinant NcSRS2; IH-tNcSRS2, truncated recombinant NcSRS2; MASTAZYME, MASTAZYME NEOSPORA, indirect ELISA, formaldehyde-fixed whole tachyzoites, MAST GROUP UK; NS, not stated; NAT, *Neospora* agglutionation test; NhSAG1, recombinant NhSAG1; PCR, polymerase chain reaction; Pourquier, Institut Pourquier, Montelellier, France; SVANOVA, commercialized ISCOM ELISA, SVANOVA Biotech AB, Sweden; VMRD, *Neospora caninum* cELISA Competitive ELISA GP65 surface antigen of tachyzoites VMRD, USA; WH, whole tachyzoite extract; WT-IHCA, kinetic ELISA-California, USA.

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Table 1
Recent viable isolates of *N. caninum*.

Hosts	Country	Tissue/origin	No. of isolates (designation)	Reference
Cattle (*Bos taurus*)	Brazil	Brain of an asymptomatic 4-month old calf	1(Nc-Goiás 1)	García-Melo et al. (2009)
	Israel	Fetal brain	2 (NcIs491,NcIs580)	Fish et al. (2007)
	Poland	Asymptomatic calf brain	NC-PolB1	Goździk and Cabaj (2007)
	Slovakia	Adult cow	Nc-SKB1	Reiterová et al. (2011)
	Spain	Brain of asymptomatic calves	9 (Nc-Spain 6,7,8,9,10, Nc-Spain 2H,3H, 4H, 5H)	Regidor-Cerrillo et al. (2008)
		Brain of asymptomatic calf	1 (Nc-Spain 1H)	Rojo-Montejo et al. (2009b)
European bison (*Bison bonasus bonasus*)	Poland	Blood	2 (NC-PolBb1 and 2)	Bień et al. (2010)
Dog (*Canis familiaris*)	Germany	Feces,bioassay in KO mice and cell culture	3 (NC-GER7, 8, 9)	Basso et al. (2009b)
	Portugal	Feces,bioassay in KO mice and cell culture	1 (NC-P1)	Basso et al. (2009a)

Table 2
Small mammals and birds as natural hosts for *N. caninum*.

Host	Country or region	Remarks	Reference
Avians			
Chicken (*Gallus domesticus*)	Americas[a]	Antibodies (IFAT, 1:25 or higher) detected in 39.5% of 1324 free range chickens	Martins et al. (in press)
	Brazil	DNA detected in 6 of 10 seropositive chickens Antibodies (IFAT, 1:50) detected in 23.5% of 200 free-range, and 1.5% of 200 indoors chickens	Costa et al. (2008)
Sparrow (*Passer domesticus*)	Brazil	DNA detected in 3 (7.5%) of 40 sparrows	Gondim et al. (2010)
Rodents			
Field mouse (*Apodemus sylvaticus*)	Italy	DNA detected in brain of 1, and muscle of 1 of 55 field mice from North West	Ferroglio et al. (2007a)
Rat (*Rattus norvegicus*)	Italy	DNA detected in brains of 2, kidneys of 4, and muscles of 10 of 103 rats from North West	
House mouse (*Mus musculus*)	Australia	DNA detected in 26.9% of 104 mice from Sydney and in 8 mice in extra neural tissues	Barratt et al. (2008)
	Italy	DNA detected in brain of 2, kidney of 1, and muscle of 8 of 75 mice from North West	Ferroglio et al. (2007a)
Capybara (*Hydrochaeris hydrochaeris*)	Brazil	DNA detected in 3 (11.5%) of 26; in lymph node of 2 and liver of 1capybara	Truppel et al. (2010)
		Antibodies (IFAT, 1:50) detected in 9.4% of 213 feral capybaras	Yai et al. (2008)
		Antibodies (IFAT, 1:50) detected in 39% of 63 feral capybaras	Valadas et al. (2010b)
Vole (*Microtus arvalis*)	Austria	DNA detected in brain of 4 (1.5%) of 264 voles	Fuehrer et al. (2010)
Water vole (*Arvicola terrestris*)	Austria	DNA detected in brain of 2 (2.3%) of 86 water voles	Fuehrer et al. (2010)
Lagomorphs			
Rabbit (*Oryctolagus cuniculus*)	UK	DNA detected in brain of 6 (10.5%) of 57 wild rabbits from Yorkshire	Hughes et al. (2008)
	Egypt	Antibodies (IH-tNcSAG1) found in 1.8% of 54 farm rabbits	Ibrahim et al. (2009)
Hare (*Lepus europaeus*)	Austria	Antibodies (VMRD) found in 37% of 383 hares	Bártová et al. (2010b)
	Czech Republic	Antibodies (VMRD) found in 39.7% of 333 hares	

[a] Antibodies to *N. caninum* were detected in 18.5% of 97 chickens from Mexico, 7.2% of 97 chickens from USA, 39.5% of 144 chickens from Costa Rica, 71.5% of 102 chickens from Grenada, 44% of 50 chickens from Guatemala, 83.6% of chickens from Nicaragua, 58.1% of 55 chickens from Argentina, 34.3% of 358 chickens from Brazil, 62.3% of 85 chickens from Chile, 11.2% of 62 chickens from Colombia, 38.7% of 80 chickens from Guyana, 18% of 50 chickens from Peru, and 21.7% of 46 chickens from Venezuela (Martins et al., in press).

Unlike *T. gondii*, it is difficult to isolate viable *N. caninum*. Additionally, some isolates were obtained as oocysts by feeding naturally infected tissues to dogs and these isolates were not cryopreserved for future studies. For example, to our knowledge none of the isolates from water buffalo from Brazil were grown in cell culture. Additionally, not all isolates of *N. caninum* could be cultivated in cell culture (Vianna et al., 2005). We emphasize that finding DNA is not comparable with finding viable *N. caninum*. It is notable that *N. caninum* DNA was demonstrated frequently in tissues of asymptomatic rodents but viable parasite has not been isolated (Table 2).

Humans are not regarded as intermediate host of *N. caninum* (McCann et al., 2008).

Table 3
Prevalence of *N. caninum*-like oocysts in feces of dogs.

Country	No. of dogs	Type	No. positive	Microscopic	NC-PCR	Bioassay	Reference
Costa Rica	34	Dairy farms	3	0	3	0	Palavicini et al. (2007)
Iran	174	89 farm, 85 house-hold	4	4	2	Not done	Razmi (2009)
Italy	230	Farms	0	0	Not done	Not done	Paradies et al. (2007)
Spain	285	Farms	1	1	Not done	Not done	Regidor-Cerrillo et al. (2010a)

Table 4
Prevalence of *N. caninum* antibodies in dogs.

Country	Type	No. tested	% positive	Test	Titer/Supplier	Reference
Algeria		100	21.0	ELISA	BioX	Ghalmi et al. (2009b)
	Pound	261	22.5	IFAT	NS	Ghalmi et al. (2009a)
	Police	85	6.6			
	Breeder	184	12			
	Farm	80	44.4			
Brazil						
Bahia, Salvador	Urban	49	32.7	Wb, ELISA	VMRD	Jesus et al. (2007)
Goiás	Urban	197	32.9	IFAT	1:50	Boaventura et al. (2008)
Mato Grosso	Clinics	60	45.0	IFAT	1:50	Benetti et al. (2008)
	Dairy farms	37	67.6	IFAT	1:200	Benetti et al. (2009)
Minas Gerais	Clinics	228	3.1	IFAT	1:50	Guimarães et al. (2009)
Pará	Rural	72	11.1	IFAT	1:50	Valadas et al. (2010a)
	Urban-stray	57	14			
Paraná state	Urban	181	12.7	IFAT		Fridlund-Plugge et al. (2008)
	Periurban	178	15.7		1:50	
	Rural	197	25.3			
Pernambuco						
Paulista	Domiciled	289	26.0	IFAT	1:50	Figueredo et al. (2008)
Amaraji	Domiciled	168	26.2			
Garanhuns	Domiciled	168	34.5			
Piauị	Urban	530	30.2	IFAT	1:50	Lopes et al. (2011)
Rio Grande do Sul	Rural	230	20.4	IFAT	1:50	Cunha Filho et al. (2008)
	Urban	109	5.5	IFAT	1:50	
São Paulo	Urban	108	15.7	IFAT	1:50	Bresciani et al. (2007)[a]
	Beef farms	963	25.4	IFAT	1:50	de Moraes et al. (2008)
Canada						
Northwest Territories	Clinics	108	3.7	IFAT	1:25	Salb et al. (2008)
Costa Rica	Farm	31	48.4	cELISA	VMRD	Palavicini et al. (2007)
Grenada, West Indies		107	2	IFAT	1:100	Dubey et al. (2008b)
India	Rural	126	21.4	ELISA	VMRD	Sharma et al. (2008)
	urban	58	6.9			
Iran	Farm	50	28	IFAT	1:50	Haddadzadeh et al. (2007)
	Urban	50	11.3	IFAT	1:50	
	Clinics	233	10.3	ELISA	P38	Hosseininejad et al. (2010)
				IFAT	1:50	
Urmia	Stray	135	27	IFAT	1:50	Yakhchali et al. (2010)
Italy	Urban	188	20.2 36.4	NAT	1:40	Ferroglio et al. (2007b)
	Rural	302				
	Kennel	144	14.6	ELISA	MASTAZYME	Paradies et al. (2007)[a]
	Farm	162	26.5	ELISA	MASTAZYME	Paradies et al. (2007)
Japan	Clinics	1206	10.4	ELISA	IH-tNcSAG1	Kubota et al. (2008)
Mexico						
Aguascalientes	Urban	116	20	ELISA	IDEXX	Cruz-Vázquez et al. (2008)
	Dairy farms	152	40.7			
Durango City	Pound	101	2	IFAT	1:25	Dubey et al. (2007b)
Peru	Farm	122	14.8	IFAT	1:50	Vega et al. (2010)
Poland	Clinics	257	21.7	ELISA		Goździk et al. (2011)
	Clinics	110	16.3	IFAT	1:50	Płoneczka and Mazurkiewicz (2008)
Senegal, West Africa		196	17.9	ELISA	VMRD	Kamga-Waladjo et al. (2010)
Spain						
Andalusia	Feral	28	17	ELISA	VMRD	Millán et al. (2009a)
Galicia	Farm	141	47.5	IFAT	1:50	Regidor-Cerrillo et al. (2010a,b)[a]
	Stray	134	39.5	IFAT	1:50	Regidor-Cerrillo et al. (2010a,b)
Majorca island	Kennel	44	0	ELISA	VMRD	Cabezón et al. (2010)
Several areas	House hold	102	2.9	IFAT	1:50	Collantes-Fernández et al. (2008)[a]
	Stray	94	24.5			
	Hunting	100	23			
	Farm	100	51			
Turkey						
Kirikkale	Stray	121	28.9	IFAT	1:16	Yildiz et al. (2009)[a]

NS, not stated.
[a] Risk factors.

2.2. Definitive hosts and transmission by oocysts

Experimental studies showed that the domestic dog and the Australian dingo (both *Canis domesticus*), and the coyote (*Canis latrans*) are definitive hosts for *N. caninum* (McAllister et al., 1998; Gondim et al., 2004; King et al., 2010). Of these, viable oocysts have been demonstrated only in feces of naturally-infected dogs (Basso

Table 5
Serologic prevalence of *N. caninum* antibodies in cattle.

Country	Region	No. of animal (relevant details)	% Positive	Assay	Cut-off titer or test	Reference
Algeria		102	3.9	ELISA	BioX	Ghalmi et al. (2009b)
Argentina		4190 no abortion	14.2	IFAT	1:200	Moore et al. (2009)
		1042 abortion	25.7	IFAT	1:200	Moore et al. (2008)
		173 dairy	80.9	IFAT	1:25	Moré et al. (2009)
		90 beef	73.0	IFAT	1:25	Moré et al. (2008a)
Brazil	Mato Grosso do Sul	1098 beef	62.5	IFAT	1:50	Andreotti et al. (2010)[a]
		2448	14.9	IFAT	1:50	Oshiro et al. (2007)[a]
		932 dairy	53.5	IFAT	1:200	Benetti et al. (2009)
	Minas Gerais	559 dairy	91.2	IFAT	1:200	Guedes et al. (2008)
		575 cows slaughter	97.2	IFAT	1:200	
		503 fetuses	12.7	IFAT	1:25	
	Pará	120 beef	19.2	IFAT	1:100	Minervino et al. (2008)
		40 dairy	17.5	IFAT	1:100	Minervino et al. (2008)
	Paraná	159 beef (*Bos indicus*)	15.1	ELISA	IDEXX	Marques et al. (2011)
	Pernambuco	469	31.7	IFAT	1:200	Silva et al. (2008)[a]
	Rio de Janeiro	563dairy	23.3	ELISA	IDEXX	Munhoz et al. (2009)[a]
Egypt		93	20.4	ELISA	IH-tNcSAG1	Ibrahim et al. (2009)
Estonia		320 bulk milk	16.0	ELISA	SVANOVA	Lassen et al. (2008)
Germany		1950 bulk milk	1.0	ELISA	IH-p38	Schares et al. (2009)
Greece		1573 milk	15.2	ELISA	IH-p38	Sotiraki et al. (2008)
Iran		285	12.6	ELISA	SVANOVA	Fard et al. (2008)
		237	32.0	ELISA	IDEXX	Youssefi et al. (2009)
Mexico	Nuevo Leon	813	11.6	ELISA	NS	Segura-Correa et al. (2010)
	Veracruz state	863	26.0	ELISA		Romero-Salas et al. (2010)
	4 provinces	596	11.6	ELISA	IDEXX	Garcia-Vazquez et al. (2009)
Norway		1657 herds bulk milk	0.7	ELISA	SVANOVA	Klevar et al. (2010)
Pakistan	Punjab province	240	43.8	cELISA	VMRD	Shabbir et al. (in press)
Peru	Department Junín	347	12.4	IFAT		Puray et al. (2006)
People's Republic of China		300	20.3	ELISA	IH-NcSRS2	Liu et al. (2007)
		540 dairy	13.3	ELISA	IDEXX	Wang et al. (2010)
	Beijing	212	43.4	ELISA	IH-tNcSRS2	Yao et al. (2009)
	Tianjin	601	5.7	ELISA	IH-tNcSRS2	Yao et al. (2009)
	South	370 dairy	18.9	ELISA	IDEXX	Xia et al. (2011)
Philippines		96	16.7	ELISA	IH	Konnai et al. (2008)
Romania	Cluj, Satu-Mare, Mureş, Sibiu, Alba	193	55.9	ELISA	IDEXX	Gavrea and Cozma (2010)
Spain	Galicia	37,090 dairy	22.5	ELISA	IDEXX	Eiras et al. (2011)[a]
		20,206 beef	25.6			
		2292 mixed	25.4			
		5196	15.7	IFAT	1:50	González-Warleta et al. (2008)
		178	7.3	c-ELISA	VMRD	Panadero et al. (2010)
Slovakia		716	20.1	ELISA	Pourquier	Reiterová et al. (2009)
Sweden		2754	2.8	ELISA	IH-ISCOM	Loobuyck et al. (2009)
Thailand	Khon Kean	424	8.0	ELISA	IH-ISCOM	Chanlun et al. (2007)
Turkey		25 aborted	60.0	ELISA	VMRD	Kul et al. (2009)
		40 heifers	40.0			
		6 calves	33.3			
		89 repeat breeder	13.4	ELISA	VMRD	Simsek et al. (2008)
		94 healthy	3.1			
		234 aborted	6.8	ELISA	VMRD	Yildiz et al. (2009)
		323 no abortion	10.7			
United Kingdom		15736	12.9	ELISA	IDEXX	Woodbine et al. (2008)
		460 dairy heifers	7.2	ELISA	MASTAZYME	Brickell et al. (2010)
USA		900 beef	16.7	Kinetic ELISA	WT-IHCA	Hoar et al. (2007)
Vietnam		254 (milk)	30.0	ELISA	SVANOVA	Geurden et al. (2008)
		215 dairy	41.0	ELISA	IH-ISCOM	Duong et al. (2008)

NS, not stated.
[a] Risk factors.

et al., 2009a,b), and recently in naturally-infected gray wolf (*Cains lupus*) (Dubey et al., in press). In foxes no viable oocysts have been observed yet, and in a survey in Germany no *N. caninum* oocyst were detected in fox feces (Constantin et al., 2011).

Oocysts are the key in the epidemiology of neosporosis. They are environmentally resistant like the oocysts of other coccidians (Uzeda et al., 2007; Neto et al., 2011).

N. caninum oocysts have been identified in only a few dogs worldwide. The number of oocysts shed by dogs is usually low. No or only a few oocysts were seen in recent surveys of canine feces (Table 3). Because *N. caninum* oocysts structurally resemble another coccidian in dog feces, *Hammondia heydorni*, it is epidemiologically important to properly identify *N. caninum* oocysts (Soares et al., 2011). Recently additional molecular tools for the differ-

Table 6
Diagnosis of *N. caninum*-associated abortion in dairy cattle from selected studies based on fetal examination.

Country	No. of fetuses examined	% Infected	Reference
Argentina	666	9.9[a]	Moore et al. (2008)
Brazil	258	34.0[b]	Pescador et al. (2007)
Germany	232	10.0[c]	Sörgel et al. (2009)
Iran	100	13.0[d]	Razmi et al. (2007)
	151	14.5[e]	Razmi et al. (2010)
	12	100[i]	Salehi et al. (2009)
Japan	15	27.0[h]	Ghanem et al. (2009)
People's Republic	16	4.0[h]	Zhang et al. (2007)
of China	26	57.7[j]	Yao et al. (2009)
Romania	9	33.0[j]	Suteu et al. (2010)
Switzerland	223	16.1[f]	Reitt et al. (2007)
	58	40.0[g]	Tschuor et al. (2010)

[a] 66 Positive by at least 1 method. Lesions in 70; 49 of these positive by IHC; 31 of 55 fetal serology positive. DNA detected in frozen tissues in 17 of 17 fetuses, and in 17 of 53 in fetuses from paraffin-embedded tissues. The positive PCR tissues were: liver 54.4%, CNS 24.2%, placenta 33.3%, and heart 10.5%.
[b] Lesions in 89 fetuses, IHC positive in 55 fetuses, lungs and brain most useful for histology.
[c] IHC (in 16), PCR (in 16-19), ELISA (in 14).
[d] 13 Fetuses PCR positive, lesions 12 fetuses, 3 IHC positive.
[e] 18 (11.9%) PCR positive, 6 of 52 IHC positive.
[f] Histologic lesions 71.4%, IHC 8.6%, nested PCR 6.7%, nested PCR-PLUS 20.9%.
[g] Maternal antibodies, histological examination of brain and heart of the fetus, PCR of fetal brains.
[h] PCR, in one case tissue cyst observed.
[i] 12 of 12 nested PCR positive; 3 of 12 histologically positive in brain.
[j] PCR.

entiation of *N. caninum* and *H. heydorni* were reported and applied to rodent tissues (Barratt et al., 2008).

How dogs become infected with *N. caninum* in nature is not fully understood. Historically, vertical transmission of neosporosis was first recognized in dogs. *N. caninum* is considered to be transmitted from the dam to the neonates during terminal stages of gestation or post-natally via milk. Unlike cattle, vertical transmission of *N. caninum* in dogs is considered highly variable and not likely to persist in the absence of horizontal infection.

Fecal transmission of *N. caninum* in dogs appears to be less important than carnivorism. Bandini et al. (2011) fed 4 dogs with 1000, 5000 or 10,000 *N. caninum* oocysts; none of the 4 dogs shed *N. caninum* – like oocysts in their feces during the observation period of 30 days. However, the 2 dogs fed with 10,000 oocysts seroconverted but the 2 dogs fed with 1000 or 5000 oocysts did not. Neither parasite DNA nor the parasite stages were demonstrable in tissues of the seropositive dogs euthanized 6 months after feeding oocysts. These findings suggest fecal transmission may not be an important mode of transmission of the parasite for the definitive host but results need confirmation.

Age-related prevalence data indicate that most dogs become infected after birth; higher prevalences have been documented in older versus younger dogs. The ingestion of infected tissues is the most likely source of infection for carnivores. Theoretically, tissues of any animal containing tissue cysts can be a source of infection for dogs. Tissues of infected prey of dogs may represent a logical source of infection; but viable parasite has not been isolated from potential dog prey as e.g. birds, rodents or lagomorphs (Table 2). Experimentally, chickens older than one week inoculated with tachyzoites intraperitoneally developed transient infection. Parasites or antibodies were not demonstrable 60 days p.i. However, inoculation of chicken embryonated eggs produced patent infection and the infected chorioallantoic membranes of theses eggs induced oocyst shedding when fed to a dog (Furuta et al., 2007). The susceptibility of chicken eggs for *N. caninum* infection was recently confirmed by Mansourian et al. (2009) using broiler chicken embryonated eggs. Pigeons (*Columba livia*) were also successfully infected with *N. caninum* tachyzoites and are also putative natural reservoirs for *N. caninum* (Mineo et al., 2009). Concerning natural infections in wild birds, in a recent work, *N. caninum* DNA has been observed in brain from magpies (*Pica pica*) and common buzzard (*Buteo buteo*), including these species as natural intermediate host for *N. caninum* (Darwich et al., submitted for publication).

Higher seroprevalences of *N. caninum* antibodies in rural dogs versus city dogs (Table 4) is probably related to availability of prey or infected animals for carnivorism. Improper disposal of dead infected cattle on the farm or wild life can be a source of infection. Both neural and extra-neural tissues can be a source of infection for dogs. Dogs fed masseter muscle, heart, liver, and brains of naturally-infected cattle or buffaloes shed oocysts (Bandini et al., 2011; Cavalcante et al., 2011). Until now *N. caninum* tissue cysts have been demonstrated only in neural and muscular tissues. Whether tissues containing only tachyzoites (acutely infected animals) can be orally infectious to animals is not known. Dogs fed tissues from infected bovine neonates did not shed oocyst (Cedillo et al., 2008), maybe because *N. caninum* often dies together with the host tissue.

2.3. Strain variation and virulence

It is now well established that *N. caninum* can cause serious illness in cattle and dogs, and occasionally in other animals. Infections in many hosts are common but clinical disease is rare. Clinical disease maybe associated with the strain of *N. caninum*. Isolates of *N. caninum* from various hosts are genetically similar although many strains have their own molecular signature as determined by multilocus microsatellite analysis (Regidor-Cerrillo et al., 2006; Al-Qassab et al., 2009a, 2010; Basso et al., 2009b, 2010). The molecular characteristics of a strain could be useful for epidemiological studies. Exogenous point source outbreaks of bovine neosporosis in Germany were associated with a common source of infection (Basso et al., 2010). In another investigation, there was clustering of *N. caninum* isolates according to geographical origin of aborted bovine fetuses in Spain (Pedraza-Díaz et al., 2009). Little is known of the strain variation with respect to their virulence. In limited studies some *N. caninum* strains were more virulent to mice than others and showed also differences during *in vitro* cultivation (García-Melo et al., 2009, 2010; Rojo-Montejo et al., 2009a,b; Regidor-Cerrillo et al., 2010b, 2011). It is not yet known, whether virulence in mice could reflect the effect an *N. caninum* infection in other host.

Table 7
Prevalence of antibodies to *N. caninum* in sheep and goats.

Host	Country	No. examined	% Positive	Assay	Cut-off titer or test	Reference
Sheep (*Ovis ovis*)	Australia	232	2.2	ELISA	VMRD	Bishop et al. (2010)
	Brazil					
	Alagoas	343	9.6	IFAT	1:50	Faria et al. (2010)[a]
	Campo Grande	441	30.8	IFAT	1:50	Andreotti et al. (2009)
			32.0	ELISA	IH-NcSRS2	
	Federal District	1028	8.8	IFAT	1:50	Ueno et al. (2009)
	Minas Gerais State	155	47.1	IFAT	1:64	Rossi et al. (2011)
		334	8.1	IFAT	1:50	Salaberry et al. (2010)
	Rio Grande do Norte	409	1.8	IFAT	1:50	Soares et al. (2009)
	Roraina	141	29.0	IFAT	1:50	Aguiar et al. (2004)
	São Paulo	382	12.8	IFAT	1:25	Langoni et al. (2011)
	Czech Republic	547	12.0	ELISA	VMRD	Bártová et al. (2009)
	Jordan[a]					
	North	339	63.0	ELISA	BioX	Abo-Shehada and Abu-Halaweh (2010)[a]
	South	320	4.3	ELISA	CHEKIT	Al-Majali et al. (2008)[a]
	New Zealand	137 (aborted)	37.0	IFAT	1:100	Howe et al. (2008)
		640	0.6	ELISA, IFAT	1:50	Reichel et al. (2008)
	Philippines	38	26.3	IB,ELISA	IH	Konnai et al. (2008)
	Slovakia	382	3.7	ELISA	ID-VET	Špilovská et al. (2009), Špilovská and Reiterová (2008)
	Spain					
	Galicia	177	57.0	ELISA	VMRD	Panadero et al. (2010)
Goat (*Capra hircus*)	Argentina	1594	6.6	IFAT	1:50	Moore et al. (2007)
	Brazil					
	Paraíba state	306	3.3	IFAT	1:50	Faria et al. (2007)
	Rio Grande do Norte	381	1.0	IFAT	1:50	Lima et al. (2008)
	São Paulo	923	19.7	NAT	1:25	Modolo et al. (2008)
	Jordan[a]					
	North	302	2.0	ELISA	BioX	Abo-Shehada and Abu-Halaweh (2010)[a]
	South	300	5.7	ELISA	CHEKIT	Al-Majali et al. (2008)[a]
	People's Republic of China	207 cashmere	7.7	ELISA	IH-NcSAG1	Lu et al. (2007)
	Philippines	89	23.6	ELISA	IH	Konnai et al. (2008)
	Poland	1060	0.4	ELISA	VMRD	Czopowicz et al. (2011)
	Slovakia	18	16.6	ELISA	ID-VET	Špilovská and Reiterová (2008)

Abortion or fetal infections have been induced in cattle using a variety of isolates in different laboratories but a meaningful comparison in pregnant cattle will be economically prohibitive to do (Dubey et al., 2007a). In a recent study, cows inoculated with a Spanish bovine isolate did not damage the fetus even though cows were inoculated at an early (70 days) stage of gestation age (Rojo-Montejo et al., 2009a). On the other hand, in beef cattle experimentally infected at 110 days of gestation with a beef strain, fetal death occurred in one fetus (Almería et al., 2010).

Studies aiming to examine virulence of *N. caninum* in cattle are difficult to interpret. Because experimentally infected dogs usually shed only few oocysts, this stage is often not available. Therefore, often tachyzoites are used for experimental infection of cattle although oocysts are the most likely source of postnatal infection in cattle and the outcome of disease might differ depending of the parasite stage by which an animal becomes infected. Studies using cell culture derived tachyzoites may further be complicated because *N. caninum* isolates maintained *in vitro* for long time may be altered regarding their virulence and other biological characteristics. Experimental induction of abortion may vary with the strain, the passage number of *N. caninum* or the route of inoculation; e.g. none of the 19 heifers inoculated intraconjunctively with 10^8 NC-1 tachyzoites delivered an infected calf (de Yaniz et al., 2007).

3. Neosporosis in cattle

3.1. Serologic prevalence

Serologic prevalences of *N. caninum* summarized in Table 5 indicate that there are considerable differences among countries, within countries, between regions, and between beef and dairy cattle. However, caution should be used in evaluating these results because of differences in serologic techniques, study design, and sample size used (Dubey et al., 2007a). Most of these surveys were made using individual cattle sera. Bulk milk serology is an economical way of estimating *N. caninum* prevalence on a herd basis (Wapenaar et al., 2007b; Frössling et al., 2008; Schares et al., 2009), but this method is not as accurate as the detection of antibodies in the serum.

There are indications that the *N. caninum* seroprevalence differs according to the cattle breed (Armengol et al., 2007; Duong et al., 2008; Munhoz et al., 2009). However, some of these results might have been caused by differences in the production system used for the different breeds and not by differences in the breed-related susceptibility to infection. In a study with large sample size, seroprevalences in beef cattle (25.6% of 20,206) and dairy cattle (22.5% of 37,090) were similar (Eiras et al., 2011). Whether improved breeds of dairy cattle are more susceptible to *N. caninum* infection than the zebu cattle or cross breeds needs further investigation (Munhoz et al., 2009).

Table 8
Prevalence of antibodies to *N. caninum* in miscellaneous domestic animals.

Host	Country	No. examined	% Positive	Assay	Cut-off titer or test	Reference
Domestic cat (*Felis catus*)	Spain	20	15.0	ELISA	VMRD	Millán et al. (2009a)
	Hungary	330	0.6	IFAT	1:40	Hornok et al. (2008)
Camel (*Camelus dromedarius*)	United Arab Emirates	1119	13.7	ELISA	VMRD	Wernery et al. (2008)
South american camelids	Argentina	308	4.6	IFAT	1:25	Moré et al. (2008b)
Llama (*Lama glama*)	Peru	175	2.9	IFAT	1:100	Casas et al. (2006)
Pig (*Sus scrofa*)	Senegal, West Africa	60 wild	58.3	ELISA	VMRD	Kamga-Waladjo et al. (2009)
	Brazil	130	3.1	IFAT	1:50	Azevedo et al. (2010)
Yak (*Bos grunniens*)	People's Republic of China	946	2.2	ELISA	IDEXX(Herd Check)	Liu et al. (2008)
Bali cattle (*Bos javanicus*)	Indonesia	438	5.5	ELISA	IH-p38	Damriyasa et al. (2010)
Gaur (*Bos gaurus f. frontalis*)	India	159	10.0	ELISA	VMRD	Rajkhowa et al. (2008)
Water buffalo (*Bubalus bubalis*)	Argentina	449	64.0	IFAT	1:100	Campero et al. (2007)
	Iran	181	37	ELISA	IDEXX	Hajikolaei et al. (2007)
	Pakistan	300	54.7	ELISA	VMRD	Nasir et al. (2011)
	Philippines	105	3.8	ELISA	IH	Konnai et al. (2008)

In this respect there are very few reports of *N. caninum* infection in indigenous breeds of cattle from Asia. In a survey from Pakistan, *N. caninum* seropositivity was lower in European dairy breeds than in cross bred and non descript cattle (Shabbir et al., in press). Rate of abortion and immune responses after *N. caninum* infection might also be affected by the breed of cattle (Armengol et al., 2007; Almería et al., 2009b; Romero-Salas et al., 2010; Santolaria et al., 2011).

Little information is available on the association of genetic traits and *N. caninum* infection. In a retrospective study of Holstein cattle in Canada, Schwab et al. (2009) found no association between *N. caninum* seropositivity and allele frequency distribution of DRB3 or DQA genes. However, independent of the serological status the alleles DRB3*1001 and DRB3*2703 were associated with resistance and susceptibility of pregnancy loss.

One of the short coming of serological surveys is the validity of the techniques used. As of yet, neither intact *N. caninum* nor parasite DNA were demonstrable in asymptomatic adult cows (Dubey et al., 2007a; Wapenaar et al., 2007a; Moré et al., 2008a; Santos et al., 2010). However, *N. caninum* could be isolated from the brains of asymptomatic naturally infected calves (Fish et al., 2007; Goździk and Cabaj, 2007; Regidor-Cerrillo et al., 2008; García-Melo et al., 2009; Rojo-Montejo et al., 2009b).

3.2. Transmission and epidemiology

Vertical transmission from the dam to the fetus, and post natal ingestion of oocysts are the only demonstrated modes of transmission in cattle. *N. caninum* is one of the most efficiently transplacentally transmitted parasites among all known microbes in cattle. Transplacental transmission can occur in postnatally acquired infections by ingestion of oocysts (exogenous) or reactivation of infection in a chronically infected cow (endogenous) and the rate of transmission may differ in these two scenarios (Williams et al., 2009).

The rate of vertical transmission may vary among herds. In selected Dutch dairy herds vertical transmission rates were estimated to be 61.8% (Bartels et al., 2007) in one study, and 58% in another one (Dijkstra et al., 2008). Vertical transmission rate was 37.1% in a dairy herd in Argentina; cows with high titers had more infected calves than cows with low titers (Moré et al., 2009). Serological examination of precolostral serum is a convenient way of measuring congenital infection. In the absence of active infection, transcolostrally-acquired antibodies decay with time depending on the titer in the colostrums and the detection of colostral antibodies in calves is also influenced by the sensitivity of serological test. In one study, passively acquired *N. caninum* antibodies persisted for five weeks (Cardoso et al., 2008).

The ingestion of sporulated *N. caninum* oocysts from the environment is the only demonstrated natural mode of infection in cattle after birth (McCann et al., 2007). To date cow to cow transmission of *N. caninum* has not been observed. In a very large sample size involving 37,090 dairy and 20,206 beef cattle in Spain, seroprevalence increased with age (Eiras et al., 2011). Seroprevalences in dairy cattle were: 10.4% in 12–24 months old, 14.1% in 25–36 months old, and 24.6% in >36 months old; similar increase was seen in beef cattle (12.9%, 15.3%, and 31.8% in the 3 age groups, respectively). These data indicate significant postnatal transmission in the area under examination.

Other modes of transmission suggested are via milk, and semen. Venereal transmission is possible, but unlikely since under experimental conditions large numbers of tachyzoites were necessary for infection (Serrano-Martínez et al., 2007b; Ferre et al., 2008). Dams naturally bred with experimentally infected bulls failed to seroconvert (Osoro et al., 2009).

3.3. Clinical neosporosis

N. caninum is a major cause of abortion in both dairy and beef cattle, and worldwide prevalences were summarized (Dubey, 2003a; Dubey et al., 2007a). Cows of any age may abort from three months gestation to term with most abortions occurring at five to six month gestation. Fetuses may die in utero, be resorbed, mummified, autolyzed, stillborn, born alive with clinical signs, or born clinically normal but persistently infected. Recently, *N. caninum* was demonstrated in tissues of 4 of 15 mummified fetuses (Ghanem et al., 2009); these fetuses tested negative for SLC35A3 gene that causes complex vertebral malformation in cattle, suggesting *N. caninum* caused mummification.

Table 9
Seroprevalence of *N. caninum* antibodies in free range wildlife.

Host	Country	No. examined	Assay	Cut-off titer or test	% Positive	Reference
Canids						
Coyote (*Canis latrans*)	USA	12	IFAT	1:100	16.7	Stieve et al. (2010)
Gray wolf (*Canis lupus*)	Scandinavia	109	IB, ELISA	ISCOM	3.7	Björkman et al. (2010)
	Spain	28	NAT, ELISA	VMRD	21.4	Sobrino et al. (2008)
	USA Alaska	324	IFAT	1:100	9.0	Stieve et al. (2010)
	Yellow Stone Park	220	IFAT	1:50	50.0	Almberg et al. (2009)
Red fox (*Vulpes vulpes*)	Ireland	220	IFAT	1:50	3.0	Murphy et al. (2007)
	Spain	95	NAT, ELISA, IFAT	VMRD	3.2	Sobrino et al. (2008)
		53	NAT	1:40	69.8	Marco et al. (2008)
Mustelids						
Stone martin (*Martes foina*)	Spain	14	NAT, ELISA, IFAT	VMRD	21.4	Sobrino et al. (2008)
Pine martin (*Martes martis*)	Spain	3	NAT, ELISA	VMRD	66.7	Sobrino et al. (2008)
Eurasian badger (*Meles meles*)	Spain	31	NAT, ELISA	VMRD	6.4	Sobrino et al. (2008)
Pole cat (*Mustella putorius*)	Spain	2	NAT, ELISA	VMRD	50	Sobrino et al. (2008)
Felids						
Feral cat (*Felis silvestris*)	Spain	59	IFAT, ELISA	VMRD	6.8	Millán et al. (2009b)
Eurasian lynx (*Lynx lynx*)	Spain	26	ELISA	VMRD	19	Millán et al. (2009a)
Iberian lynx (*Lynx pardinus*)	Spain	25	ELISA, IFAT	VMRD	12.0	Sobrino et al. (2008)
European wild cat (*Felis silvestris*)	Spain	6	NAT, ELISA	VMRD	16.7	Sobrino et al. (2008)
Egyptian mongoose (*Herpestes ichneumon*)	Spain	21	ELISA	VMRD	13	Millán et al. (2009a)
Cervids and ruminants						
Spanish ibex (*Capra pyrenaica hispanica*)	Spain	531	ELISA, IFAT	VMRD, 1:50	5.6	García-Bocanegra et al. (in press)
Mouflon (*Ovis ammon*)[a]	Czech Republic	105	IFAT	1:50	3	Bártová et al. (2007)
Mule deer (*Odocoileus hemionus hemionus*)	USA	42	NAT	1:25	16.6	Dubey et al. (2008a)
Black-tailed deer (*Odocoileus hemionus columbianus*)	USA	43	NAT	1:25	18.6	Dubey et al. (2008a)
White-tailed deer (*Odocoileus virginianus*)	USA-Iowa	170	NAT, IFAT	1:25	88.2	Dubey et al. (2009)
	USA-Minnesota	62	NAT, IFAT	1:25	70.0	Dubey et al. (2009)
Vietnam sika deer (*Cervus nippon pseudaxis*)	Czech Republic	14	IFAT, ELISA	1:50	14.0	Bártová et al. (2007)
Roe deer (*Capreolus capreolus*)	Belgium	73	ELISA	ID-VET	2.7	de Craeye et al. (2011)
	Czech Republic[a]	79	IFAT	1:50	14.0	Bártová et al. (2007)
	Spain Galicia	160	ELISA	VMRD	13.7	Panadero et al. (2010)
	Sweden	199	ELISA,IB	SVANOVA	1	Malmsten et al. (2011)
Fallow deer (*Dama dama*)	Belgium	4	ELISA	ID-VET	0	de Craeye et al. (2011)
	Czech Republic[a]	143	IFAT	1:50	1.4	Bártová et al. (2007)
	Poland	47 feral	ELISA,IB	IH-ISCOM	13	Goździk et al. (2010)
		106 farmed		IH-ISCOM	11	Goździk et al. (2010)
		335	ELISA	IDEXX	2.9	Bień et al. (in press)
Red deer (*Cervus elaphus*)	Belgium	7	ELISA	ID-VET	0	de Craeye et al. (2011)
Caribou (*Rangifer tarandus*)	USA-Alaska	453	IFAT	1:100	11.5	Stieve et al. (2010)
Moose (*Alces alces*)	Sweden	417	IH-ISCOMELISA,	IH-ISCOM	1.0	Malmsten et al. (2011)
	USA-Alaska	201	IFAT	1:100	0.5	Stieve et al. (2010)
Marine mammals						
Kuril harbor seal (*Phoca vitulina stejnegeri*)	Japan	234	ELISA, IH-tNcSAG1	In house	5.9	Fujii et al. (2007)
Spotted seal (*Phoca largha*)	Japan	13	ELISA, IH-tNcSAG1	In house	15.3	Fujii et al. (2007)
North American opossum (*Didelphis virginiana*)	USA	30	IFAT	1:100	0	Houk et al. (2010)
Sea otter (*Enhydra lutris neresis*)	USA	16	IFAT	1:40	68.7	Miller et al. (2010)
Avians						
Common raven (*Corvus corax*)	Spain	67	IFAT	1:50	35.8	Molina-López et al. (in press)

[a] Some of the animals were from hunting farms.

Neosporosis-induced abortions occur year-round. In some epidemic herd outbreaks as many as 57% of dairy cows have been reported to abort over just a few weeks up to months. Abortion outbreaks have been defined as epidemic if more than 10% or 12.5% of cows at risk abort within six to eight weeks. A small proportion (<5%) of cows may have repeated abortion due to neosporosis (Dubey et al., 2007a; Pabón et al., 2007). A previous *N. caninum* abortion is not considered a cause of sterility (Santolaria et al., 2009).

Clinical signs, other than abortion, which have only been reported in calves <two months of age, include neurologic signs, an inability to rise and below average birth

weight. The hind limbs and/or the forelimbs may be flexed or hyperextended and neurologic examination may reveal ataxia, decreased patellar reflexes, and loss of conscious proprioception. Exophthalmia or an asymmetrical appearance in the eyes may be achieved and occasionally birth defects including hydrocephalus and a narrowing of the spinal cord may occur.

3.4. Diagnosis

Diagnosis of neosporosis abortion is difficult, and often expensive. Serologic examination of the dam and the fetus, and the detection of lesions and *N. caninum* in a fetus by immunohistology and PCR can all aid diagnosis and we have reviewed these procedures in detail (Dubey and Schares, 2006). Establishing a cause-effect relationship between abortion and *N. caninum* is even more complex because asymptomatic congenital *N. caninum* infections are common and finding the presence of the parasite or parasite DNA does not mean that *N. caninum* caused the abortion. In comprehensive studies based on exclusion of all other causes of abortion and the observation of *N. caninum*-associated lesions and parasites in aborted fetuses in cattle from California and The Netherlands, about 20% of all abortions were associated with *N. caninum*. Recent reports of *N. caninum*-associated abortion are summarized in Table 6. In some of these only PCR was used for diagnosis of abortion; diagnostic rate varies with the method used (Sadrebazzaz et al., 2007; Sánchez et al., 2009).

Diagnosis of acute versus chronic *N. caninum* infection in adult cows is epidemiologically important. Avidity tests have been used to distinguish acute versus chronic phase of infection. Low avidity values are associated with acute infection (Basso et al., 2010) but the window for a diagnosis of an acute infection is short, i.e. lasts only several week post infection. Recently, Aguado-Martínez et al. (2008) described ELISAs based on the recombinant proteins NcGRA7 and NcSAG4 for the detection of antibodies during acute infection (tachyzoite replication), and chronic infection (bradyzoites), respectively. Detection of antibodies to both recombinant proteins may indicate reactivated infection.

Many serological tests are available for the diagnosis of bovine *N. caninum* infection (Dubey and Schares, 2006; Wapenaar et al., 2007a). It is worth noting that antibodies and white blood cell counts may fluctuate during pregnancy, even in non aborting cows (Lopez-Gatius et al., 2007a; Nogareda et al., 2007; Serrano et al., 2011), and some animals may become serologically negative (Nogareda et al., 2007; Dijkstra et al., 2008). The sub-class of antibodies detected may vary with clinical status; IgG2 antibodies dominated in almost all of the aborting cattle under examination while non-aborting cattle showed either a dominating IgG1 or a dominating IgG2 response (Almería et al., 2009a).

An ELISA based on the use of NcGRA7 protein was useful in the detection of antibodies in aborting cows versus those calving normally (Huang et al., 2007).

Further serological methods to diagnose *N. caninum* infection based on recombinant antigens are under development (Borsuk et al., 2011). Previous studies had indicated that the detection of pregnancy-associated substances could aid diagnosis of neosporosis abortion. In one report, the detection of pregnancy-associated glycoprotein-1(PAG-1) in plasma was not influenced by a chronic *N. caninum* infection. However, PAG-1 measurements in aborting animals could provide a useful parameter to assess the feto-placental status independent of the *N. caninum* infection (Lopez-Gatius et al., 2007a).

3.5. Pathogenesis of abortion

Bovine neosporosis is mainly a disease of the placenta and fetus, initiated following a maternal parasitemia, triggered either as the result of a primary (exogenous) maternal infection or following recrudescence of a persistent (endogenous) infection during pregnancy (Dubey et al., 2007a). Following a parasitemia *N. caninum* is able to establish itself in the maternal caruncular septum before crossing to the fetal placental villus. For abortion to occur the fetus, or its placenta, has to be so damaged that it is no longer viable and several factors may interact, to a greater or lesser extent, to influence this (Gibney et al., 2008). Primary parasite-induced placental damage may jeopardize fetal survival directly or cause release of maternal prostaglandins that in turn cause luteolysis and abortion. Fetal damage may occur due to primary tissue damage caused by the multiplication of *N. caninum* in the fetus or due to insufficient oxygen/nutrition, secondary to placental damage. In addition, it has been suggested that maternal immune expulsion of the fetus may occur, associated with the release of maternal pro-inflammatory cytokines in the placenta or hormonal deregulation. While clearly all these proposed mechanisms are related in one way or another, one or more of them may be more important in a given instance and all may be influenced by the stage of gestation (Dubey et al., 2006; Innes, 2007; Lopez-Gatius et al., 2007b; Gibney et al., 2008; Almería et al., 2010). Extensive lesions in vital organs can directly kill the fetus (Gibney et al., 2008). The production of regulatory cytokines (such as IL-10) and inflammatory (such as gamma interferon) cytokines, and a direct injury of the fetus by tachyzoites multiplication may determine the survival or death of the fetus (Innes, 2007; Rosbottom et al., 2007, 2008, 2011; Almería et al., 2010; Almeria et al., in press). High levels of prolactin in *Neospora* infected cows may have a protective effect on gestation (Garcia-Ispierto et al., 2009). Previous studies indicated that progesterone may have a positive effect on pregnancy in cattle by modulating the Th1/Th2 driven immune responses. In this effect, an interaction of *N. caninum* and *Coxiella burnetii* has been recently described. Non-aborting cows seropositive to both, *N. caninum* and *C. burnetii* showed higher plasma progesterone levels than the remaining animals examined (Garcia-Ispierto et al., 2010). However, an artificial progesterone supplementation of cows during pregnancy did not reduce neosporosis abortion but increased the risk of abortion in cows with high *N. caninum* antibody titres (Bech-Sàbat et al., 2007).

The risk of transmission and fetal disease maybe in part related to the stage of gestation at the time of infection. The transmission rate increases with gestational age perhaps related to placental vascularization because the placenta seems to be more permeable in the last trimester (Dubey et al., 2006, 2007a).

3.6. Risk factors

The knowledge on risk factors for herds to acquire *N. caninum* infection and *N. caninum*-associated abortion is important for the development and the implementation of measures to control bovine neosporosis. Potential risk factors have been extensively described (Dubey et al., 2007a). It is now generally accepted that the presence of farm dogs increases the chance of *N. caninum* infection in cattle (Dubey et al., 2007a; VanLeeuwen et al., 2010a). Dogs as definitive hosts increase the chance of a postnatal infection via oocyst contamination of the cattle food or environment. Specific feeding habits of farm dogs, like feeding on aborted fetuses and placenta may increase the chance of seropositivity in cattle (VanLeeuwen et al., 2010a). Differences in the farm management (e.g. feeding, pasture management, cattle density and housing) may have an influence on infection risk. In a survey of 5594 dairy and beef cows in Argentina, seropositive animals were 85% more likely to abort than seronegative and the results suggested a higher risk of seropositivity in dairy than in beef herds possibly due to not further specified differences between dairy and beef herds regarding herd management practices (Moore et al., 2009).

In chronic, congenitally infected cattle additional influences could increase the risk of neosporosis abortion. In two Holstein-Friesian dairy herds it was shown recently that in heifers and parous cows an increase in the cumulative number of days with a mean relative humidity lower than 60% during the second trimester of pregnancy was associated with a higher risk of abortion (Yániz et al., 2010). In parous cows an increased rainfall during the second trimester of gestation had the same effect (Yániz et al., 2010). The abortion risk was higher in parous cows with high *N. caninum* antibody titres and in cows which had been inseminated with Friesian semen compared to those inseminated with Limousin or Belgian Blue semen (Yániz et al., 2010).

N. caninum is considered a primary pathogen. However, concurrent infections may aggravate neosporosis. Bovine herpes virus1 co-infection was found in 27% of 948 cattle and considered a potential risk factor for bovine neosporosis in Italy (Rinaldi et al., 2007). In a small survey in Vietnam, there was a strong association between bovine virus diarrhea (BVD) and *Neospora* seropositivity (Duong et al., 2008). In a Canadian study, *N. caninum* seropositivity had a negative effect on reproduction parameters like first-service conception and calving intervals. Interestingly there seemed to be an interaction between BVD and neosporosis since *N. caninum* seropositivity had the negative effects on the parameter “first-service conception” mainly in BVD seronegative dams (VanLeeuwen et al., 2010b). Similar interactions were not observed regarding *Mycobacterium avium paratuberculosis* or Bovine leukemia virus seropositivity (VanLeeuwen et al., 2010b).

Another Canadian study examined the effects of climate (aridity), soil pH and agroecological region on seropositivity for *Mycobacterium avium paratuberculosis*, *N. caninum*, Bovine leukemia virus, and Bovine viral diarrhea virus. No significant effects were observed regarding *N. caninum* (Scott et al., 2007).

3.7. Prevention and control

The major economic loss due to neosporosis is reproductive failure in cattle in many countries. In addition to the direct costs involved in fetal loss, indirect costs include professional help and expenses associated with establishing a diagnosis, rebreeding, possible loss of milk yield, and replacement costs if aborted cows are culled. The diagnosis of neosporosis-associated abortion is difficult and expensive. Postnatal losses due to neosporosis are difficult to document because there are no obvious ill effects in adult cattle, other than fetal loss. Culling perhaps accounts for the major loss associated with neosporosis. In general, less is known of the causes of abortion in beef cattle than in dairy cattle because of the difficulty of monitoring when small fetuses are expelled in the first trimester, and so there are no accurate assessments of *N. caninum*-induced losses in beef cattle.

The economic production losses, other than reproduction are difficult to assess because there are no clinical signs in adult cattle. Although neosporosis has been reported to decrease milk production and weight gain, in a recent study, no differences in weight gain was found in seropositive versus negative beef cattle (Hoar et al., 2007; Moré et al., 2010). Effects of *N. caninum* infection on milk production are not clear, yet. In a Canadian study *N. caninum* seropositivity was associated with lower production of milk, fat and protein in primiparous cows versus *N. caninum*-seronegative primiparous cows (Tiwari et al., 2007).

Many controls measures have been discussed to reduce *N. caninum* infection in cattle (Dubey et al., 2007a), including embryo transfer, artificial insemination of seropositive dams with semen from beef bulls, culling, replacement heifers, chemotherapy, and vaccination. Studies from Spain indicated that the likely hood of abortion was significantly lower for heifers and parous cows inseminated with beef bull semen compared with those inseminated with Holstein-Friesian bull semen (Almería et al., 2009b; Yániz et al., 2010); this effect might be due to a favorable effect of cross-breed pregnancies on placental function.

Transfer of embryos from infected dams into uninfected recipients can prevent endogenous transplacental transmission of *N. caninum*. Embryo transfer should only be accomplished to seronegative recipient cows. This technique may be used to recover uninfected calves from genetically valuable but *N. caninum*-infected dams. As a consequence, pre-transfer testing of recipients for infection with *N. caninum* is highly recommended (Paz et al., 2007; de Oliveira et al., 2010). Congenital infection and abortion can occur if recipient cows are seropositive (de Oliveira et al., 2010). The earliest stage of pregnancy, the fetus acquires *N. caninum* infection is unknown; embryos from seropositive cows were found to be not infected with *N. caninum* (Moskwa et al., 2008).

Annual serological screening could be useful in a control strategy because a long term-study showed that *N. caninum* seropositivity was very stable during the observation period and *N. caninum* seropositive cows showed a high rate of repeat abortions (Pabón et al., 2007). A 'test and cull' strategy may include the following options: (i) test and cull seropositive dams or seropositive aborting dams; (ii) test and inseminate the progeny of seropositive dams with beef bull semen only; and (iii) test and exclude the progeny of seropositive dams from breeding.

Mathematical models can be applied to estimate costs of bovine neosporosis and to determine the benefit and the efficiency of various control measures (Häsler et al., 2008; Reichel and Ellis, 2009). By a mathematical approach losses were estimated to be 81-1875 Euros per small farm in Switzerland (Häsler et al., 2008). A modeling of the costs and benefits of different measures to control *N. caninum* "culling of animals that had experienced *N. caninum*-associated abortion" or "not breeding replacements from *N. caninum*-associated abortion" were not cost effective. However, the measure "not breeding replacements from *N. caninum* seropositive cows" on farms with a high prevalence (50%) was financially attractive (Häsler et al., 2008).

Treatment of cattle appears to be uneconomical in cattle due to the fact that it can only be used as a preventive measure and hence it must be long-term and likely produce unacceptable milk or meat residues or withdrawal periods. Currently, there is no chemotherapy for bovine neosporosis that has been shown to be safe and effective and any effort to treat cattle with existing drugs must therefore be discouraged at this stage. However, interesting experimental studies that may result in an option for chemotherapeutic control at a later stage have been conducted. An effect of toltrazuril and its derivative ponazuril on tachyzoites on *N. caninum* has been shown *in vitro* and *in vivo* in calves (Strohbusch et al., 2009). In calves treated with ponazuril, the parasite was no longer detectable in the brain and other organs. Attempts were made to alter the course of *N. caninum* infection by prophylactic medication with a slow-release Monensin bolus in cows but results were inconclusive (VanLeeuwen et al., 2011). In an epidemiological survey, feeding monensin in dry cows in Canada had a reduced risk for *N. caninum* seropositivity (VanLeeuwen et al., 2010b).

At present there is no commercial vaccine for neosporosis. Mouse models are being used to test efficacy of killed and recombinant *N. caninum* vaccines (e.g. Aguado-Martínez et al., 2009; Rojo-Montejo et al., 2011).

Studies indicate that cattle develop cellular and humoral immunity after inoculation with killed vaccine formulations (Innes et al., 2007; Baszler et al., 2008; Moore et al., 2011). Experimentally, fetal death can be prevented in cows vaccinated with live tachyzoites in exogenously challenged cows but such protection has not been demonstrated in endogenously infected cows. As a first step towards developing a non-infectious vaccine, Baszler et al. (2008) showed that cows injected with NcSRS2 immunogens developed cellular and humoral immunity.

4. Neosporosis in dogs

Serological surveys indicate widespread exposure to the parasite worldwide (Table 3). Most canine isolates of *N. caninum* were obtained from sick dogs. Recently, *N. caninum* DNA was detected in 28 (32%) of 87 asymptomatic pound dogs in Algeria; 19 of these dogs were seronegative and 8 seropositive dogs were PCR negative (Ghalmi et al., 2008), but results needs confirmation.

N. caninum is a primary pathogen in dogs and can cause clinical disease in dogs of all ages. Most cases of clinical canine neosporosis have been in congenitally infected dogs involving littermates and previous reports were summarized earlier (Lindsay and Dubey, 2000; Dubey and Lappin, 2006). In most instances dogs are born asymptomatic and begin to develop clinical signs three or more weeks after birth. Not all pups in the litter are affected (Dubey et al., 2004, 2005, 2007c). Heckeroth and Tenter (2007) tested progeny of a Doberman bitch in Germany; three of nine pups from litter 1, one of five pups from litter 2, and one of eight pups from litter 3 were seropositive, but only one pup from litter 3 developed clinical neosporosis. The clinically affected pup had the highest IFAT titer (1:5129) and showed an unique pattern in Western blot examination.

Paralysis of rear limbs, often with contracture, is the most consistent sign of neonatal neosporosis. A wide array of clinical signs have been reported in older dogs, often on immunosuppressive therapy (Holmberg et al., 2006; Crookshanks et al., 2007; Fry et al., 2009; Galgut et al., 2010; Garosi et al., 2010). Treatment of clinical neosprosis with currently available drugs, including clindamycin, is only partially effective. None of the drugs kill *N. caninum* tissue cysts (Dubey et al., 2004, 2007c). Co-infection of *T. gondii* could occur with *N. caninum* infection, and should be considered in differential diagnosis. A bitch that had high *N. caninum* IFAT titer during pregnancy delivered pups coinfected with *T. gondii* and *N. caninum*; the bitch was seronegative to *T. gondii* but viable *T. gondii* was isolated from the pups and *N. caninum* DNA was found in the brains of two of the six pups (Al-Qassab et al., 2009b).

5. Neosporosis in sheep and goats

The economic, clinical, and epidemiologic importance of *N. caninum* infection in sheep remains uncertain. Recent serological surveys in Table 7 indicate a very low (0.6% in New Zealand) to high (30.8% in Brazil) prevalence in asymptomatic sheep. Occasionally, neosporosis can cause abortion, neonatal mortality, and perhaps clinical signs in adult sheep. *N. caninum* DNA was detected in brains of 3 of 18 aborted fetuses from seven farms in New Zealand (Howe et al., 2008), 2% of 31 aborted fetuses in Italy (Masala et al., 2007), and in the brain of 1 of 7 sheep in Jordan (Abo-Shehada and Abu-Halaweh, 2010). West et al. (2006) found antibodies in fetuses of 4 of 5 aborted fetuses from 2 flocks in New Zealand. These studies indicate transplacental transmission of *N. caninum* in sheep but frequency and the etiology of abortion need definitive evidence. Finding of *N. caninum* DNA in the brain of an adult encephalitic Merino ewe in Australia (Bishop et al., 2010) suggests the parasite might cause clinical neosporosis in adult sheep.

Sheep are an excellent ruminant model for testing efficacies of vaccines against neosporosis abortion. Recently, Weston et al. (2009) performed an excellent dose titration of *N. caninum* tachyzoites in 90 day gestational ewes and concluded the clinical outcome was dose-dependent, ranging from 100% abortion in ewes infected with 10^6 parasites vesus 50% abortion in those infected with 10^5 tachyzoites, and no abortion in those given 50 tachyzoites.

Serologic surveys indicate 2–23% prevalence in goats (Table 7). *N. caninum* DNA was found in 8.6% of 31 aborted goat fetuses in Italy (Masala et al., 2007).

6. Neosporosis in miscellaneous domestic animals

Llamas and alpacas are important to the economy of some South American countries. *N. caninum* DNA was detected in the brain or heart of 2 of 7 llama aborted fetuses, and 7 of 12 alpaca aborted fetuses from Peru (Serrano-Martínez et al., 2007a).

Although *N. caninum* has been isolated from water buffaloes from Brazil by feeding tissues of naturally-infected animals to dogs, and examining dog feces for excretion of oocysts (Neto et al., 2011), there is no report of clinical neosporosis in buffalo. However, *N. caninum* was recently found in one of nine fetuses obtained from slaughtered buffaloes in Brazil (Chryssafidis et al., 2011).

Antibodies to *N. caninum* have been found in several other domestic animals (Table 8), but clinical neosprosis has not been reported in these hosts.

7. Neosporosis in horses

Another species of *Neospora*, *N. hughesi* is considered to parasitize equids. At present it is uncertain whether *N. caninum* also infects horses because these species cross-react serologically (Gondim et al., 2009). All three viable isolates of *Neospora* from horses were identified as *N. hughesi.* Antibodies (IFAT, 1:50) to *Neospora* were reported in 11.9% of 800 horses from Israel with higher seropositivity in horses with clinical signs and in aborted mare (Kligler et al., 2007), in 24% (c-ELISA-VMRD) of 552 horses from Czech Republic (Bártová et al., 2010a), 9.3% of 57 horses from Turkey (Kilbaş et al., 2008), and in 1 of 315 horses from Costa Rica (Dangoudoubiyam et al., 2011). High level antibodies to *N. hughesi* were detected in presuckling colostral sera of naturally exposed foals from three of 32 mares in California, USA (Pusterla et al., 2011). It is of interest that clinical neosporosis in adult horses has been reported only from the USA, including recent cases from California (Finno et al., 2007, 2010). One of these cases was in a 23 year old mule that had myeloencephalitis (Finno et al., 2010).

8. Neosporosis in wild animals

Antibodies to *N. caninum* have been found in a variety of free range wildlife (Table 9).

In addition, *N. caninum* antibodies have been found in wildlife in captivity. André et al. (2010) reported seroprevalence in following captive wildlife in zoos in Brazil: ocelot (*Leopardus pardalis*, 30 of 42), little spotted cat (*Leopardus tigrinus*, 11 of 35), Jaguar (*Panthera onca*, 8 of 13) Puma (*Pumo concolor*, 5 of 18), Jaguarandi (*Puma yagouaroundi*, 5 of 25), tiger (*Panthera tigris*, 4 of 6), Pampas cat (*Oncifelis colocolo*, 3 of 3), carcal (*Caracal caracal*, 1 of 1), serval (*Leptailurus serval*, 1 of 1), lion (*Panthera leo* 1 of 9), Fishing cat (*Prionailurus viverrinus*, 1 of 1), Bush dog (*Speothos venaticus*, 16 of 27), Crab-eating fox (*Cerdocyon thous*, 13 of 39), Maned wolf (*Cerdocyon brachyurus* 5 of 21), Hoary fox (*Pseudalopex vetulus* 4 of 7), and European wolf (*Canis lupus*, 2 of 3) tested by IFAT titer of 1:25 or higher.

Qin et al. (2007) found antibodies (IFAT, 1:40) in 3 of 73 Red pandas from zoos in People's Republic of China (PRC). Yu et al. (2009) reported 27.2% seropositivity (c-ELISA, VMRD) in 103 farm-bred blue foxes (*Alopex lagopus*) also from PRC.

Recently, *N. caninum* DNA was reported in brains of 6.6% of 304 red foxes, and 10% of 20 roe deer from Belgium (de Craeye et al., 2011). On the contrary, brain samples from 528 foxes, 224 wild mice, 16 deer and roe deer as well as from a wild boar were examined negative for the presence of *N. caninum* DNA by real time PCR (Constantin et al., 2011).

Clinical neosporosis in wildlife is rare (Dubey, 2003b). Fatal neosporosis has been diagnosed previously in a 16 day old rhinoceros, and in wild cervids (reviewed in Dubey, 2003a; Dubey et al., 2007a). Recently, fatal neosporosis was diagnosed in an aborted fetus from a white rhinoceros (*Ceratotherium simum*) in Taronga zoo Australia (Sangster et al., 2010). Hepatitis was the main lesion and the parasite was demonstrated histologically and by PCR. Both of these rhinos were originally from South Africa. A third case of acute fatal neosporosis was diagnosed in a 16-year old rhinoceros that died suddenly in captivity in a zoo in Thailand (Sommanustweechai et al., 2010). This animal also had massive hepatitis, with histologically demonstrable tachyzoites. Unlike the previous two cases, this animal was originally wild caught in Thailand.

Conflict of interest

The authors have no conflict of interest.

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