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Neospora caninum in wildlife

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Neosporosis, which is caused by the coccidian parasite Neospora caninum, is recognized as a major disease of domestic animals that causes high abortion rates in cattle and fatal neurological disease in dogs. A life cycle of N. caninum in wild animals (i.e. sylvatic) has long been suspected because neosporosis has been detected in several wildlife species. Recently, the transmission of N. caninum has been confirmed in coyotes and whitetailed deer. The newly confirmed wild hosts and other wild animals are probably involved in the sylvatic cycle of the parasite. Control measures for neosporosis could now become more complicated, given the participation of wildlife in the life cycle of N. caninum.

Classification of Neospora caninum

Neospora caninum, the causative agent of neosporosis, is a cyst-forming coccidian protozoan parasite that belongs to the family Sarcocystidae. It causes neuromuscular disease in dogs and high rates of abortion in cattle [1]. The parasite was named in 1988 after a retrospective study of formalin-fixed paraffin-embedded tissues of dogs in which toxoplasmosis had been diagnosed or suspected [2]; in this study, the new parasite was identified in tissues of ten of the 23 examined dogs. This unknown parasite had previously been described but not classified in several earlier case reports involving dogs and calves [3-6].

After isolation of the parasite in cell culture [7], N. caninum tachyzoites were used in several studies, including the development of diagnostic tests and experimental reproduction of the disease. Since then, evidence of N. caninum infection has been detected in many canid and ruminant animals, as well as in horses (reviewed in Ref. [8]). A redescription of the parasite was recently published [9]. A second species of Neospora was proposed for the organism isolated from a horse in 1996 [10]. The new organism, Neospora hughesi, was classified on the basis of unique molecular and antigenic characteristics [11], which were also confirmed in other studies [12–16]. To date, *N. hughesi* has been identified only in horses.

Identifying Neospora caninum-infected animals

Detection of antibodies to N. caninum is a good indicator of exposure of animals to the parasite. However, when identifying exotic animal hosts of the parasite, in addition to the current serological techniques (indirect fluorescent antibody testing (IFAT), enzyme-linked immunosorbent assays (ELISAs) and agglutination tests) it is important to perform other tests to confirm infection. When only blood

is available for the tests, immunoblotting should be used as an additional test. PCR-based diagnosis has become an excellent method for confirmation of N. caninum in infected tissues and isolated parasite stages [9].

A potential confounding factor when performing serology for N. caninum in wild animals is infection with Hammondia heydorni, the closest phylogenetically related protozoan parasite to N. caninum [17,18]. Serological tests for *H. heydorni* are not yet available. Hammondia heydorni also has a canid-ruminant life cycle [19-21], and its oocysts appear morphologically similar to those of N. caninum. It is possible that serological cross-reactions can take place between N. caninum and H. heydorni, so it is necessary to be cautious when identifying new hosts of N. caninum in wildlife on the basis of only antibody detection. Molecular techniques are available to differentiate N. caninum and H. heydorni infections [18,20].

Transmission between dogs and cattle

The sexual reproduction of Sarcocystidae parasites, which include N. caninum, occurs in the intestine of a definitive host. Intermediate hosts are those animals that are infected only by the asexual stages of the parasites. When infected tissues from an intermediate host are ingested by a definitive host, environmentally resistant forms of the parasites are shed in the feces. Because of its worldwide distribution, N. caninum was suspected to have a definitive host that was a cosmopolitan carnivore. In 1998, domestic dogs were confirmed to be definitive hosts: they shed oocysts in their feces after consuming tissues of mice that have been infected with N. caninum [22].

Neospora caninum is transmitted transplacentally and horizontally. Endogenous transplacental infection is common in cattle [23], but it has been suggested that additional horizontal transmission might be needed to maintain the parasite in a population [24]. Horizontal transmission from dogs to cattle is believed to be necessary to spread the disease and to keep the observed levels of infection in cattle. It has been demonstrated that the oocysts shed by a single dog (usually up to 500 000 oocysts) after consuming infected tissues from a single calf are potentially capable of infecting hundreds or thousands of cattle [25].

Neospora caninum in wild herbivores

The first diagnosis of neosporosis in wildlife occurred in a California black-tailed deer Odocoileus hemionus columbianus found dead in the wild [26]. Other reports showed N. caninum in zoo animals. The parasite was observed in

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the brain of a full-term stillborn deer Cervus eldi siamensis from a zoo in France [27] and in two full-term twin antelope calves Tragelaphus imberbis from a zoo in Germany [28]. Neosporosis was diagnosed by immunohistochemistry in a 16-day-old white rhinoceros Ceratotherium simum calf kept free-ranging at a game-breeding centre in South Africa [29]. The evidence presented in the latter study [29], although highly suggestive of neosporosis, leaves open the possibility that the infection was caused by a closely related cross-reacting organism (similar to N. hughesi). It is perhaps pertinent to note that rhinoceros are more closely related to horses than to ruminants [30]. Further investigation of neosporosis in rhinoceros is of interest.

Seroepidemiological studies carried out in white-tailed deer *Odocoileus virginianus*, the most abundant deer species in North America [31], showed that 40–50% of the tested samples were positive for *N. caninum* antibodies, and some of these animals had high antibody titers, suggesting that deer might have a role in the sylvatic cycle (i.e. the cycle in wild animals) of the parasite in North America [32,33].

The role of deer as a natural intermediate host of *N. caninum* was recently confirmed and reported [34,35]. Dogs were induced to shed *N. caninum* oocysts after consuming tissues from naturally infected white-tailed deer; oocysts from one dog were confirmed to be *N. caninum* by a species-specific PCR and by sequencing the internal transcribed spacer 1 (ITS1) using DNA extracted from oocysts [34]. In another study, *N. caninum* was isolated from three naturally infected white-tailed deer, and tachyzoites from one isolate were successfully maintained in cell culture [35]. In these two studies [34,35], the ITS1 of the deer isolates were shown to be identical to ITS1 reported for domestic animals, suggesting that *N. caninum* is being transmitted between domestic animals and wildlife.

The spectrum of wild herbivores that could serve as intermediate hosts of *N. caninum* has been gradually increasing. Apart from white-tailed deer, antibodies to the parasite have been detected in zebra *Equus burchelli*, eland *Taurotragus oryx*, African buffalo *Syncerus caffer*,

Thompson gazelle Gazella thompsoni, impala Aepyceros melampus, warthog Phacochoerus aethiopicus, chamois Rupicapra rupicapra, roe deer Capreolus capreolus, red deer Cervus elaphus, moose Alces alces, Bison Bison bison, Caribou Rangifer tarandus, and musk ox Ovibos moschatus [34,36–38] (Table 1).

Wild carnivores as intermediate or definitive hosts

Antibodies to *N. caninum* have been detected in several species of wild canids. Five of 52 (10%) coyotes *Canis latrans* from Texas [39], 1 of 54 (2%) British foxes *Vulpes vulpes* and 15 of 169 (9%) Australian dingoes *Canis familiaris dingo* were seropositive to *N. caninum* [40]. These initial studies suggested that wild canids might be either intermediate or definitive hosts of *N. caninum*. Domestic dogs represent definitive hosts, so the chances are reasonable that other canid species could also be definitive hosts. A spatial study developed in Texas showed that the risk of exposure to *N. caninum* in beef cattle increased in association with higher concentrations of wild canids (coyotes and gray foxes) and greater densities of beef cattle [41].

Other attempts have been made to identify new definitive hosts for *N. caninum*. Three coyote pups were fed brains of mice experimentally infected with *N. caninum*, but none of the pups shed oocysts in their feces [39]. Serological and epidemiological evidence that foxes might be intermediate or definitive hosts of the parasite were found in several experiments [40–43]. Red foxes *Vulpes vulpes* were later confirmed to be natural intermediate hosts of *N. caninum* after detection of the parasite DNA in 13 of 122 (10.7%) red foxes [44].

Mustelids, which are carnivores with a global distribution, were tested to determine whether they could serve as definitive hosts of *N. caninum* [45]. Four captured wild ermine *Mustela erminea*, five captured wild long-tailed weasels *Mustela frenata* and four commercially acquired ferrets *Mustela putorius* were fed tissues of mice containing cysts of *N. caninum*. None of the tested mustelids shed *N. caninum* oocysts in their feces [45].

Schares *et al.* [21] tested the potential of European red foxes as definitive hosts of *N. caninum* by feeding foxes

Table 1. Antibodies to Neospora caninum reported in wild herbivores

Species	No. tested	Positive (%)	Test	Country	Refs
. White-tailed deer <i>Odocoileus virginianus</i>	400	162 (40.5%)	DATa	USA	[32]
	305	145 (48%)	DAT	USA	[33]
	193	50 (26%)	IFAT	USA	[34]
Chamois Rupicapra rupicapra	119	7 (5.9%)	DAT	Italy	[36]
Roe deer Capreolus capreolus	43	1 (2.3%)	DAT	Italy	[36]
Red deer Cervus elaphus	102	2 (1.9%)	DAT	Italy	[36]
Zebra <i>Equus burchelli</i>	41	29 (70.7%)	DAT	Kenya	[37]
Eland <i>Taurotragus oryx</i>	13	12 (92.3%)	DAT	Kenya	[37]
African buffalo Syncerus caffer	4	2 (50%)	DAT	Kenya	[37]
Thompson gazelle Gazella thompsoni	26	7 (26.9%)	DAT	Kenya	[37]
Impala Aepyceros melampus	14	2 (14.3%)	DAT	Kenya	[37]
Warthog Phacochoerus aethiopicus	6	4 (66.7%)	DAT	Kenya	[37]
Bison Bison bison	249	5 (2%)	DAT	USA	[38]
Caribou Rangifer tarandus	160	5 (3.1%)	DAT	USA	[38]
Moose Alces alces	61	8 (13%)	IFAT	USA	[34]
	162	4 (2.5%)	DAT	USA	[38]
Musk ox Ovibos moschatus	224	1 (0.5%)	DAT	USA	[38]

DAT, Neospora caninum direct agglutination test.

tissues from *N. caninum*-infected goats and sheep; although two of five control dogs shed *N. caninum* oocysts in their feces after consuming the infected tissues, none of six foxes excreted the parasite. These authors concluded that either red foxes are inefficient definitive hosts of *N. caninum* or they are not definitive hosts of the parasite. Recently, coyotes were identified as definitive hosts of *N. caninum*. Two of four coyotes shed the parasite oocysts in their feces after consuming tissues of experimentally infected calves [46], and oocysts from one coyote were confirmed to be *N. caninum*.

Other studies reported antibodies against the parasite in wild canids, such as gray wolves Canis lupus, coyotes, maned wolves Chrysocyon brachyurus, gray fox Lycalopex gymnocercus, red foxes, culpeo foxes Dusicyon culpaeus, South American gray foxes (Dusicyon griseus), North American gray foxes (Urocyon cinereoargenteus), crabeating foxes Cerdocyon thous and Chiloe foxes Pseudolapex fulvipes [34,47-51] (Table 2). Gray wolves are more closely related to dogs than are coyotes, so it is probable that wolves are also definitive hosts of the parasite [46]. Antibodies to N. caninum were also reported in raccoons Procyon lotor and raccoon dogs Nyctereutes procyonoides koreensis [52,53] (Table 2). Recently, N. caninum was confirmed by histology, immunohistochemistry and PCR in a free-ranging raccoon *Procyon lotor* with concurrent canine distemper virus infection [54].

So far, Neospora caninum infection has not been confirmed in felids. Domestic cats failed to shed oocysts after consuming N. caninum-infected tissues from mice [55]. Low titers of antibodies (1:50–1:200) to the parasite were found by IFAT in four of 68 wild felids from Africa, including three lions Panthera leo and one cheetah Acinonyx jubatus [56] (Table 2). However, the same four cats had high titers (1:200–1:25 600) for T. gondii. Thus, there is some possibility of crossreactivity between N. caninum and T. gondii. Neosporosis has never been diagnosed in domestic cats, but in one single study antibodies were found in low titers in cats from Brazil [57]. These findings associated with the fact that wild and domestic felids seem to be commonly exposed to

N. caninum-infected tissues from ruminants, are suggestive that felids are not important hosts for *N. caninum*.

Wild canids: diet versus seroprevalence

The feeding habits of wild canids seem to be crucial for their exposure to *N. caninum*. A high prevalence (39%) and high titers of antibodies against the parasite were found in free-ranging North American gray wolves, which hunt mostly wild ruminants, especially deer species [58]; in North America, white-tailed deer are a commonly infected and abundant natural intermediate host of *N. caninum*, which are common prey of gray wolves. Therefore, gray wolves are probably highly exposed to the parasite from consuming white-tailed-deer [34].

In two North American studies, the seroprevalence in coyotes was between 10% and 11% [34,39]. These values are lower than in gray wolves but higher than the seroprevalence in domestic dogs in North America, which was found to be 7% [59]. Note that, in most regions of North America, there is a deer-hunting season each fall, when ~6 million white-tailed-deer are killed by hunters [31]. When deer are hunted, the carcasses are eviscerated in the field and the offal is left behind, available for consumption by wild canids and also domestic dogs. Foxes and coyotes are less able to kill deer than are gray wolves, but each fall hunting season, North American foxes and coyotes have a greater opportunity to consume N. caninum-infected deer tissues than they would under natural predation. Their seropositivity could in part be a reflection of their exposure to infected offal left in the field after each hunting season. Foxes around Europe showed lower prevalences (0-20%) of antibodies than North American wolves [40,42,50,60–62], which could be due to their more diversified diets, including small mammals, birds and fruits; therefore, foxes are probably less often exposed to N. caninum than are gray wolves.

Wild rodents as intermediate hosts

Neospora caninum was recently identified in wild brown rats Rattus norvegicus captured in cattle farms in Taiwan. Nine of 55 rats were positive for antibodies against

Table 2. Antibodies to Neospora caninum reported in wild carnivores

Species	No. tested	Positive (%)	Test	Location	Refs
Coyote Canis latrans	52	5 (10%)	IFAT	USA	[39]
	113	12 (11%)	IFAT	USA	[34]
Australian dingo Canis familiaris dingo	169	15 (8.9%)	IFAT	Australia	[40]
Raccoon Procyon lotor	99	10 (10%)	DAT	USA	[53]
Raccoon dog Nyctereutes procyonoides koreensis	26	6 (23%)	IFAT	Korea	[52]
Gray wolf Canis lupus	164	64 (39%)	IFAT	USA	[34]
	122	4 (3.3%)	DAT	USA	[38]
Crab-eating fox Cerdocyon thous	15	4 (26.7%)	IFAT	Brazil	[48]
Gray fox Lycalopex gymnocercus	12	5 (41.7%)	IFAT	Brazil	[48]
Maned wolf Chrysocyon brachyurus	59	5 (8.5%)	IFAT	Brazil	[49]
Red fox Vulpes vulpes	54	1 (2%)	IFAT	UK	[40]
	123	21 (17%)	IFAT	Belgium	[42]
	549	111 (20%)	IFAT	UK	[61]
	70	1 (1.4%)	IFAT	Ireland	[50]
Culpeo fox Dusicyon culpaeus	28	17 (60.7%)	IFAT	Argentina	[69]
South American gray fox Dusicyon griseus	56	20 (35.7%)	IFAT	Argentina	[69]
North American gray fox Urocyon cinereoargenteus	26	4 (15.4%)	DAT	USA	[47]
Chiloe fox Pseudolapex fulvipes	2	2 (100%)	DAT	Chile	[51]
Cheetah Acinonyx jubatus	16	1 (6.3%)	IFAT	Southern Africa	[56]
Lion Panthera leo	18	3 (16.6%)	IFAT	Southern Africa	[56]

N. caninum, and DNA of the parasite was detected in two seropositive rats [63]. These authors speculated that the rats were probably infected through ingestion of oocysts shed by dogs, or after consuming infected placenta or infected tissues from aborted bovine fetuses. This finding has considerable epidemiological importance, because rats are cosmopolitan rodents that can reside in urban, rural and wild regions. Infected tissues from rats can potentially be consumed by wild and domestic animals, so it is crucial to investigate the possible importance of rats in transmitting this organism to definitive hosts. It is necessary to investigate whether other wild rodents might also be natural intermediate hosts of the parasite.

Neospora caninum in marine mammals

Recently, antibodies to N. caninum were detected in seven marine mammal species. Serological assay was performed using a Neospora agglutination test (NAT) and showed titers≥1:40 in three of 53 (6%) walruses Obobenus rosmarus, 28 of 145 (19%) sea otters Enhydra lutris, 11 of 311 (3.5%) harbor seals *Phoca vitulina*, one of 27 (3.7%) sea lions Zalophus californianus, four of 32 (12.5%) ringed seals Phoca hispida, one of eight (12.5%) bearded seals Erignathus barbatus and 43 of 47 (91%) bottlenose dolphins Tursiops truncatus [64]. These findings suggest that marine mammals might serve as intermediate hosts of N. caninum. However, more studies are needed to confirm the findings and to rule out the possibility of serological cross-reactivity with unidentified organisms. If these marine mammals are confirmed to be intermediate hosts of the parasite, then many fundamental questions will arise regarding its transmission through the oceans.

Are birds natural hosts of N. caninum?

Before the discovery that dogs are definitive hosts of *N. caninum*, some widely distributed birds were tested for their potential role as definitive hosts of the parasite. Nine carnivorous birds of four species, including two red-tailed hawks *Buteo jamaicensis*, two turkey vultures *Cathartes aura*, two barn owls *Tyto alba*, and three American crows *Corvus brachyrhynchus* were orally inoculated with *N. caninum*-infected tissues from rats or mice. No *N. caninum* oocysts were detected in the feces of any tested bird [65].

Some authors suspected that birds might be intermediate hosts of N. caninum because foxes, which were found to be seropositive for the parasite, do not usually prey on cattle, and birds are usually preyed on by foxes [66]. Three domestic pigeons Columbia livia and three zebra finches Poephila guttata, which are members of the widely distributed orders Columbiformes and Passeriformes, respectively, were each inoculated with 104-106 N. caninum tachyzoites; infection was induced in all three pigeons, but all three zebra finches resisted infection [66]. These results do not prove that pigeons are natural intermediate hosts of N. caninum, but their susceptibility to induced infection provides an artificial rationale for investigating wild birds to determine whether they can serve as intermediate hosts. Neospora caninum has not been detected in birds so far, but two studies have found a statistical association between the presence of poultry on

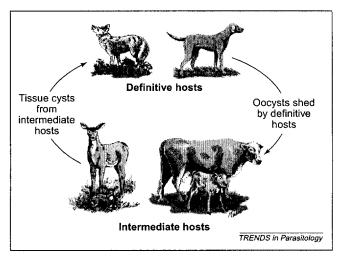


Figure 1. Dogs and coyotes Canis latrans, definitive hosts of Neospora caninum, become infected after consuming infected tissues from intermediate hosts. Cattle and white-tailed deer Odoicoleus virginianus, intermediate hosts of the parasite, can be infected by ingesting food or water contaminated with oocysts shed by definitive hosts. The organism is also transmitted transplacentally from infected mothers to their offspring. There are probably additional animal species that also participate in the transmission cycle of N. caninum.

dairy farms and neosporosis abortion problems, suggesting that infected birds might increase the odds of transmission to farm dogs [67,68].

Concluding remarks

Neospora caninum, a recognized cause of bovine abortion and fatal neuromuscular disease in dogs, has recently become recognized as a common parasite of wild animals. White-tailed-deer and coyotes are confirmed intermediate hosts and definitive hosts of N. caninum, respectively, proving the existence of a sylvatic cycle of the parasite, and these animals might occasionally transmit N. caninum to domestic animals (Figure 1). Because of the extremely close phylogenetic relationship of gray wolves to dogs, their common hunting of wild ruminants, and high seroprevalence rates found in wild wolves and deer, it is expected that gray wolves will be discovered to be another definitive host of N. caninum. Wild canids in different countries need to be studied for their potential role as definitive hosts. Other wild carnivores (raccoons and red foxes) and herbivores (many ruminant species and possibly rhinoceros) have also been confirmed as intermediate hosts of N. caninum, and they are probably involved in the sylvatic cycle of the parasite.

Control measures to consider for neosporosis in domestic animals, which have previously focused mainly on dogs and cattle, could become more complicated now that we must consider the participation of wildlife in the life cycle of *N. caninum*. The role of birds, rodents, marine mammals and other wildlife in the life cycle and transmission of *N. caninum* need to be confirmed. The research possibilities involving wildlife are numerous and should explain many of the current questions on *N. caninum* in wild animals.

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